CHECKLIST



# Annotated checklist of family- and genus-group names associated with Scoliidae (Hymenoptera, Aculeata)

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Academic editor: Michael Ohl | Received 7 August 2024 | Accepted 25 September 2024 | Published 28 October 2024 https://zoobank.org/14E6E98C-7C98-4DBD-9599-D1E0F1DFD58D

**Citation:** Taylor CK (2024) Annotated checklist of family- and genus-group names associated with Scoliidae (Hymenoptera, Aculeata). Journal of Hymenoptera Research 97: 945–1006. https://doi.org/10.3897/jhr.97.134123

#### Abstract

Thirty-two family-group names and 161 genus-group names are listed for Scoliidae, including two fossil subfamilies and eight fossil genera, together with identification of type species and critiques of publication history. Campsomerinae was first made available in 1912. Contrary to previous usage, Argaman must be recognised as author of *Bellimeris, Catharinimeris* (not *Cathimeris*), *Colpacampsomeris, Fasciomeris* (not *Fascimeris*), *Garantimeris, Lindenimeris, Phaleromeris* (not *Phalerimeris*), *Tetrasciton* and *Tristomeris. Tristomeris* takes precedence as correct spelling over *Tristimeris*. A summary classification to genus level is provided for Scoliidae. Trielidina **stat. nov.** is recognised as a subtribe of Campsomerini.

#### Keywords

Nomenclature, Scolioidea, taxonomy

# Introduction

The Scoliidae, commonly known as hairy flower wasps, are a cosmopolitan family of relatively large, hairy aculeate wasps that develop as external parasitoids of larval scarabaeid beetles (Naumann 1991). Recent phylogenetic analyses support an isolated position for Scoliidae within the stinging wasps (Aculeata), forming a superfamily Scolioidea with the small family Bradynobaenidae (Zhang et al. 2024). Though their dramatic appearance and role as predators of pest species has long made them a subject of interest (Clausen et al. 1927; Inoue and Endo 2006; Abbate et al. 2018), scoliids

have also been notorious for their complicated taxonomy. Day et al. (1981) regarded the family as 'over-burdened nomenclatorially' whereas Argaman (1996) stated that its nomenclature was 'at the least, disastrous'. Most of this ire has been directed towards the arrangement of species and genera but confusion has also arisen in the application of higher taxa, particularly regarding the priority of Campsomerinae and Trielidini (Liu et al. 2021a).

The family Scoliidae was first recognised by Latreille (1802, as 'Scolietae'), including the genera *Scolia* Fabricius, 1775 and *Sapyga* Latreille, 1796. During the 1800s and early 1900s, Scoliidae was commonly recognised as including wasps now assigned to separate families such as Tiphiidae, Thynnidae, Mutillidae and Sapygidae (e.g. Westwood 1840; Dalla Torre 1897; Sharp 1899). Scoliids in the modern sense were assigned to a single genus *Scolia* or divided between a small number of genera. Saussure and Sichel's (1864) monograph recognised three genera, *Liacos* Guérin-Méneville, 1838, *Scolia* and *Elis* Fabricius, 1804, with each divided into two subgenera. Scoliidae was restricted to its modern sense by Ashmead (1903) who divided it between two subfamilies, the Scoliinae and the Elidinae. However, the name 'Elidinae' may no longer be used for Scoliidae as its type genus belongs to a different family (see comments below). The correct application of *Elis* and Elididae was recognised by Schrottky (1910) and appears to have been followed by all subsequent authors. *Elis* in the sense of Saussure and Sichel (1864) was then typically recognised as *Campsomeris* Guérin-Méneville, 1838.

For much of the 20<sup>th</sup> Century, scoliid taxonomy was dominated by the work of two authors, Johan George Betrem & J. Chester Bradley. In his revision of the Indo-Australian scoliids, Betrem (1928) assigned most species to just two genera, *Scolia* and *Campsomeris*. Each of these genera was divided into a complex system of sub- and infra-generic groups. Many of these subgroups would later be elevated to the status of distinct genera (e.g. Betrem 1941; Bradley 1964a; Bradley and Betrem 1967).

Unfortunately, Betrem and Bradley's numerous important publications on scoliid taxonomy are marred by a sometimes careless approach to the requirements of priority (Elliott 2011). Successive publications could be inconsistent in matters such as type-species designations and spellings of names (Elliott 2011; Taylor and Barthélémy 2021). During the 1960s and 1970s, Bradley produced a series of publications discussing the type material of historical taxa (Bradley 1964a, c, 1972, 1973, 1974b; Bradley and Betrem 1966, 1967, 1968). Revised taxonomic positions were regularly indicated for species covered by these publications. However, many species were assigned to new genus-group names without descriptions being provided for the latter. The International Code of Zoological Nomenclature (ICZN 1999, henceforth referred to as 'ICZN' or 'the Code') requires that all names published after 1930 must be accompanied by a description or definition of distinguishing characteristics and, for genus-group names, must have a fixed type species (ICZN Art. 13). Merely presenting a genus name in conjunction with a species does not suffice (though it did for names published before 1931). Multiple genus-group names employed by Betrem and Bradley do not meet these requirements, rendering them nomina nuda. Confusion has then arisen from uncritical citation of such names from their first appearance.

Betrem and Bradley (1972) divided the scoliids between the subfamilies Scoliinae and Campsomerinae, the latter corresponding to Ashmead's (1903) 'Elidinae'. This system has been followed by most subsequent authors (Osten 2005a), albeit with Rasnitsyn's (1977) description of the basal Proscoliinae leading to the reduction of Betrem and Bradley's (1972) subfamilies to tribes Scoliini and Campsomerini within a single subfamily Scoliinae. Rasnitsyn (1993) also established the extinct subfamily Archaeoscoliinae. A second fossil subfamily, Palaeoscoliinae, was established by Antropov et al. (2014).

Argaman (1996), in attempting to correct the 'disastrous' state of scoliid taxonomy, managed only to further confuse matters. He introduced numerous new taxa in a key to scoliid genera, dividing the family between no less than four subfamilies, 28 tribes and 143 genera. Many of these taxa were poorly defined and largely indistinguishable (Osten 2005a). For the most part, Argaman did not discuss the position of species not treated as generic types, meaning that the greater number of scoliid species were effectively unplaced in his system. Argaman also took recognition of nomina nuda to the point of absurdity, treating every name as defined by its first appearance and even regarding evident spelling variations as independently available taxa. Subsequent workers have either ignored Argaman's system (e.g. Gupta and Jonathan 2003) or explicitly rejected it (Osten 2005a). Nevertheless, Argaman (1996) is important in validating many of the taxa incorrectly introduced by Betrem and Bradley, as the first author to provide a description along with a type species fixation. Argaman's taxa were reviewed by Kimsey and Brothers (2016), though they omitted most of those taxa that Argaman incorrectly attributed to earlier authors. It is worth noting that the 4th edition of the ICZN (ICZN 1999) introduced the requirement that names published after 1999 must be explicitly introduced as new, making such accidental validation no longer possible.

The following catalogue of family- and genus-group names is presented in an attempt to resolve these confusions. A list of scoliid genera and species was provided by Osten (2005a) but the type species of genera were not indicated and many of the authorities for genera were inaccurate. At the end of the catalogue, a summary classification is provided for the Scoliidae.

# Format

Separate listings are provided below for family- and genus-group names (including names proposed for sections within subgenera, as per ICZN Art. 10.4); family-group names are organised by stem. Names historically included within Scoliidae but not relevant to the family in its modern sense are mostly not included. References to International Code of Zoological Nomenclature (ICZN) articles are to the current edition (ICZN 1999 and emendations), available online at https://www.iczn.org. Names and titles originally in Cyrillic are transliterated using International Standard ISO 9:1995 (Anonymous 2007), with the addition of ě and í for the archaic letters Ѣ and i, respectively. For authors and journal titles with more familiar traditional transliterations, citations are given for the latter with the ISO transliteration appended in square brackets.

# Family-group names

# AGOMBARD- Argaman, 1996

Agombardini Argaman, 1996: 193.

Type genus. Agombarda Argaman, 1996.

### ARCHAEOSCOLI- Rasnitsyn, 1993

Archaeoscoliinae Rasnitsyn, 1993: 85.

Type genus. Archaeoscolia Rasnitsyn, 1993. Comments. Fossil taxon.

#### Ascoli- Argaman, 1996

Ascoliini Argaman, 1996: 187.

Type genus. Ascolia Argaman, 1996.

### AUSTROSCOLI- Argaman, 1996

Austroscoliini Argaman, 1996: 191.

Type genus. Austroscolia Betrem, 1927b.

#### BETREMI- Argaman, 1996

Betremiini Argaman, 1996: 197.

Type genus. Betremia Bradley, 1950.

# CAMPSOMER- Bartlett, 1912

Campsomerinae Bartlett, 1912: 295, 308. Campsomerini—Bradley and Betrem 1967: 294. Campsomeridinae—Arnett 1985: 444. Campsomeridini-Arnett 1985: 444.

#### Type genus. Campsomeris Guérin-Méneville, 1838.

**Comments.** The name 'Campsomerinae' is commonly attributed to Betrem and Bradley (1972), in which it is described as new. However, it had previously been used by Bartlett (1912), who refers to it on p. 295 ('[Ashmead] also made two subfamilies the Scoliinae and Elidinae (now Campsomerinae)') and p. 308 ('The fact that there is but one recurrent nervure is of subfamily value separating the Scoliinae from the Campsomerinae'). As rudimentary as these statements are, the fact that Campsomerinae can obviously be derived from the available genus name *Campsomeris* may be taken as establishing this name by indication, a possibility for family-group names published before 1930 (ICZN Art. 12.2.4).

Liu et al. (2021a) suggested that Campsomerini may not have priority over the competing name Trielidini. However, even if Bartlett's use of Campsomerinae is not taken as establishing priority, Campsomerinae remains the senior name due to its use at a higher taxonomic level than Trielidini in Betrem and Bradley (1972; see comments under TRIELID- below).

Arnett (1985) used the forms 'Campsomeridinae' and 'Campsomeridini', evidently believing the correct root for *Campsomeris* to be Campsomerid-. However, I have not found any other usages of this form and the root 'Campsomer-' should be maintained by prevailing usage (ICZN Art. 29.3.1.1).

#### CARINOSCOLI- Argaman, 1996

Carinoscoliini Argaman, 1996: 191.

Type genus. Carinoscolia Betrem, 1927b.

#### COLP-Argaman, 1996

Colpinae Argaman, 1996: 180. Colpini—Argaman 1996: 184.

**Type genus.** *Colpa* Dufour, 1841. **Comments.** See comments under TRIELID- below.

#### COLPACAMPSOMER- Argaman, 1996

Colpacampsomerini Argaman, 1996: 209.

Type genus. Colpacampsomeris Betrem, 1941.

### CURTAURG- Argaman, 1996

Curtaurgini Argaman, 1996: 182.

Type genus. Curtaurga Argaman, 1996.

#### DASYSCOLI- Argaman, 1996

Dasyscoliini Argaman, 1996: 181.

Type genus. Dasyscolia Bradley, 1951.

### DIELID- Argaman, 1996

Dielidini Argaman, 1996: 212.

Type genus. Dielis Saussure & Sichel, 1864.

#### DISCOLI- Argaman, 1996

Discoliini Argaman, 1996: 197.

Type genus. Discolia Saussure, 1863.

#### DOBROBET- Argaman, 1996

Dobrobetini Argaman, 1996: 205.

Type genus. Dobrobeta Argaman, 1996: 206.

#### ELID- Ashmead, 1903

Elidinae Ashmead, 1903: 7, 8.

#### Type genus. *Elis* Fabricius, 1804.

**Current status.** Not applicable to Scoliidae.

**Comments.** Ashmead (1903) used this name for a collection of genera now mostly assigned to Campsomerini based on a misapplication of the type genus (see comments under *Elis* below).

### HANGASORN- Argaman, 1996

Hangasornini Argaman, 1996: 197.

Type genus. Hangasorna Argaman, 1996.

#### HETEREL- Argaman, 1996

Heterelini Argaman, 1996: 183.

Type genus. Heterelis Costa, 1887.

#### HETEROGYNA Latreille, 1817

Heterogyna Latreille, 1817: 481. Heterogynidae—Mocsáry 1881: 5–6.

#### Type genus. None.

Current status. Not available.

**Comments.** Latreille (1817) applied the name 'Heterogyna' to a family of Hymenoptera including representatives of modern Formicidae and Mutillidae. Mocsáry (1881) later emended the name to 'Heterogynidae' and used it to cover modern Mutillidae, Scoliidae, Sapygidae and Bethylidae. This name is unavailable as it was not based on an available genus-group name (ICZN Art. 11.7.1.1). The wasp genus *Heterogyna* Nagy, 1969 post-dates both Latreille (1817) and Mocsáry (1881), and does not retroactively validate the family name as Nagy (1969) intended.

#### LACOSI- Argaman, 1996

Lacosiini Argaman, 1996: 197–198.

#### Type genus. Lacosia Argaman, 1996.

**Comments.** Argaman (1996) attributed the tribe Lacosiini to 'Schrottky, 1910' but no such prior usage exists; it must therefore be attributed to Argaman himself.

# LIACOS- Schrottky, 1910

Liacosinae Schrottky, 1910: 196. Liacosini—Argaman 1996: 188.

Type genus. Liacos Guérin-Méneville, 1838.

### LISOC- Argaman, 1996

Lisocini Argaman, 1996: 199.

Type genus. Lisoca Costa, 1858.

Current status. Junior objective synonym of Scoliini.

**Comments.** As *Lisoca* is an objective synonym of *Scolia*, Lisocini is likewise an objective synonym of Scoliini. Argaman (1996) maintained *Lisoca* and *Scolia* as separate genera based on the incorrect designation of *S. citreozonata* as type species of the former. However, as *Lisoca* in this sense is likewise currently regarded as a junior synonym of *Scolia*, no action need be taken to preserve Argaman's concept.

#### MEGACAMPSOMER- Argaman, 1996

Megacampsomerini Argaman, 1996: 211.

Type genus. Megacampsomeris Betrem, 1928.

#### MEGASCOLI- Argaman, 1996

Megascoliini Argaman, 1996: 199.

Type genus. Megascolia Betrem, 1928.

#### PALAEOSCOLI- Antropov in Antropov et al., 2014

Palaeoscoliinae Antropov in Antropov et al., 2014: 399, 401.

**Type genus.** *Palaeoscolia* Antropov in Antropov et al., 2014. **Comments.** Fossil taxon.

# PROSCOLI- Rasnitsyn, 1977

Proscoliinae Rasnitsyn, 1977: 523-524.

Type genus. Proscolia Rasnitsyn, 1977.

# PSEUDOTRIELID- Argaman, 1996

Pseudotrielidini Argaman, 1996: 205.

Type genus. Pseudotrielis Betrem, 1928.

# SCOLI- Latreille, 1802

Scolietae Latreille, 1802: 345. Scolides—Leach 1815: 737. Scolida—Leach 1815: 737. Scoliadae—Samouelle 1819: 273. Scolioidea—Burmeister 1834: 433. Scholiites Newman, 1835: 399 (unjustified emendation). Scoliidae—Newport 1839: 858. Scoliides—Westwood 1840: 82. Scoliides—Westwood 1840: 82. Scoliides—Blanchard 1840: 370. Scoliites—Blanchard 1840: 370. Scoliidea—Perty 1841: 907. Scoliidea—Costa 1858: 1. Scoliini—Costa 1858: 5. Scoliinae—Mocsáry 1881: 51.

Type genus. Scolia Fabricius, 1775.

# **TETRASCITON- Argaman, 1996**

Tetrascitonini Argaman, 1996: 201.

Type genus. Tetrasciton Argaman, 1996.

#### TRIELID- Betrem, 1972

Trielini Betrem, 1965: 120 (*nomen nudum*). Trielidini Betrem in Betrem & Bradley, 1972: 26.

# Type genus. Trielis Saussure, 1863.

**Comments.** Liu et al. (2021a) suggested that this name may have priority over Campsomerini, hitherto regarded as its senior synonym by most authors. However, Liu et al.'s (2021a) attribution of Trielidini to 'Betrem, 1962' is in error. Betrem (1962a) is a brief note on the type status of *Trielis* Saussure, 1863 that makes no reference to its higher classification. Subsequent usages of 'Trielini' by Betrem (1965) and Bradley and Betrem (1967) represent *nomina nuda* due to their lack of an associated description, an absolute requirement for family-group names published after 1960 (ICZN Art. 13.2). The earliest available usage of Trielidini is that in Betrem and Bradley (1972), in which it is placed as a tribe of Campsomerinae.

*Trielis* Saussure, 1863 is currently placed as a junior synonym of *Colpa* Dufour, 1841. A recent molecular phylogenetic analysis of Scoliidae (Khouri et al. 2022) suggested that *Colpa* is more closely related to Scoliini than to other genera currently included in Campsomerini. If *Colpa* is raised to the status of its own tribe, the name Trielidini takes priority over Colpinae Argaman, 1996.

#### TRISCILO- Argaman, 1996

Trisciloini Argaman, 1996: 201.

Type genus. Trisciloa Gribodo, 1893.

#### TRISCOLI- Argaman, 1996

Triscoliini Argaman, 1996: 193.

Type genus. Triscolia Saussure, 1863.

#### YCASBRA- Argaman, 1996

Ycasbraini Argaman, 1996: 191.

Type genus. Ycasbraia Argaman, 1996.

# **Genus-group names**

Unless otherwise indicated, all scoliid genus-group names are feminine in gender.

# Aelocampsomeris Bradley, 1957b

Campsomeris subgenus Aelocampsomeris Bradley, 1957b: 74. Campsomeris subgenus Aeolocampsomeris—Bradley 1957b: 68 (incorrect original spelling).

**Type species.** *Campsomeris costalis* Lepeletier de Saint-Fargeau, 1845, by original designation.

**Comments.** This name appears as both 'Aelocampsomeris' and 'Aeolocampsomeris' in Bradley (1957b). Bradley's (1964b) subsequent usage of 'Aelocampsomeris' sets that as the correct spelling (ICZN Art. 24.2.4). Bradley (1957b) listed Scolia variegata Fabricius, 1793 as a synonym of Campsomeris costalis; S. variegata obviously takes priority and this species is currently known as Aelocampsomeris variegata.

# Agombarda Argaman, 1996

Agombarda Argaman, 1996: 194.

Type species. Scolia atra Illiger, 1802, by original designation.

# Annulimeris Betrem, 1967

Campsomeriella subgenus Annulimeris Betrem, 1967: 26, 28-29.

Type species. Tiphia annulata Fabricius, 1793, by original designation.

# Araripescolia Nel, Escuillie & Garrouste, 2013

Araripescolia Nel, Escuillie & Garrouste, 2013: 396.

Type species. Araripescolia magnifica Nel, Escuillie & Garrouste, 2013, by original designation.

**Comments.** Fossil taxon (Early Cretaceous).

#### Archaeoscolia Rasnitsyn, 1993

Archaeoscolia Rasnitsyn, 1993: 86.

Type species. *Archaeoscolia senilis* Rasnitsyn, 1993, by original designation. Comments. Fossil taxon (Early Cretaceous).

#### Ascoli Saussure, 1855

*Scolia* subgenus *Ascoli* Guérin-Méneville, 1838: 247 (not available). *Ascoli* Saussure, 1855: 33, 35, 36.

**Type species.** Either *Scolia flavifrons* Fabricius, 1775, by subsequent monotypy (Bartlett 1912), or *Scolia haemorrhoidalis* Fabricius, 1787, by subsequent designation (Betrem and Bradley 1964) (see below).

**Comments.** Unused senior synonym of *Megascolia* Betrem, 1928 and *Regiscolia* Betrem & Bradley, 1964, proposed for suppression. Gender masculine (ICZN Art. 30.2.4; D. Yanega, pers. comm.).

The name Ascoli has lurked in the corners of scoliid nomenclature for almost two hundred years as a vexatious boojum that has never been effectively exorcised. Guérin-Méneville (1838) published Ascoli as a hypothetical taxon (stating, "Nous n'en connaisson pas encore" ['We don't know any yet']), excluded from availability under the Code (ICZN Art. 1.3.1). Nevertheless, Saussure (1855) formally synonymised Ascoli with Scolia, stating that the two genera were separated by characters potentially subject to individual variation, and implying the existence of specimens that might otherwise have been assigned to 'Ascoli'. Saussure and Sichel (1864) cited Ascoli as an apparent synonym of their subgenus Triscolia. Names published in synonymy are not thereby made available (ICZN Art. 11.6) unless they were subsequently treated as valid prior to 1961 (ICZN Art. 11.6.1). Schrottky (1910) fulfilled this requirement by including Ascoli in a key to scoliid genera, preceded by the comment "Anstelle der bisherigen Triscolia Sauss. und Discolia Sauss. müssen die älteren Namen Guérins Ascoli und Lacosi gebraucht werden" ['instead of the previous Triscolia Sauss. and Discolia Sauss., Guérin's older names Ascoli and Lacosi must be used']. Though Schrottky (1910) did not explicitly name any species in combination with Ascoli, it may safely be presumed that he intended it to cover all species included in Triscolia by Saussure and Sichel (1864).

For the most part, subsequent authors did not follow Schrottky's (1910) usage of *Ascoli*. Bartlett (1912) recognised Guérin-Méneville's (1838) original usage as hypothetical and maintained recognition of *Triscolia*, with *Scolia flavifrons* Fabricius, 1775 designated as its type species. Nevertheless, Bartlett also noted that, "*If [Ascoli] should ever be adopted the writer sees no reason why* Scolia flavifrons *Fab. could not still remain the type under this older name*". *Scolia flavifrons* might be considered the first species name associated with *Ascoli* as a generic name published in synonymy, and therefore its type species by monotypy (ICZN Art. 67.12), but see below.

Betrem (1926), in a brief discussion of the generic arrangement of scoliids, noted that previous authors had divided Scolia into the subgenera Scolia and "Ascoli Guér. (=Triscolia S. et S.)", and opined that, "De Indische vertegenwoordigers van het oude subgenus Ascoli Guér (=Triscolia S. et S.) blijken tot een 4-tal natuurlijke subgenera te behooren" ['The Indian representatives of the old subgenus Ascoli... appear to belong to four natural subgenera']. He cited four examples of such species: Scolia haemorrhoidalis Fabricius, 1787, S. procer Illiger, 1802, S. rubiginosa Fabricius, 1793 and S. kollari Saussure, 1859. It is ambiguous whether Betrem (1926) intended to use Ascoli as a valid taxon or not Krombein (1951) listed Ascoli "Saussure and Sichel, 1864" as a synonym of Triscolia and designated Scolia flavifrons Fabricius, 1775 as type species, following Bartlett (1912). Both Bartlett (1912) and Krombein (1951) intended to fix Ascoli as an objective synonym of Triscolia. Unfortunately, neither author was aware that Triscolia was first published by Saussure (1863), not Saussure and Sichel (1864), and its correct type species was S. badia Saussure, 1863 (see below). Also, though Krombein attributed Ascoli to Saussure and Sichel (1864), its initial publication in synonymy had been by Saussure (1855), so it would retain priority over *Triscolia* even if the two were synonymous.

Jacot-Guillarmod et al. (1963) petitioned the ICZN to reject both *Ascoli* Guérin-Méneville, 1838 and *Ascoli* Betrem, 1926 as unavailable, essentially arguing that Betrem had validated *Ascoli* throught the inclusion of named species but that this had been unintentional. Schrottky (1910) was thought to have continued to treat *Ascoli* as hypothetical, overlooking his synonymisation of *Ascoli* and *Triscolia*. Nevertheless, "*just in case the Commission should rule that* Ascoli *Betrem is available*", Betrem and Bradley (1964) designated *Scolia haemorrhoidalis* as type species of *Ascoli* from among those mentioned by Betrem (1926). Jacot-Guillarmod et al. (1965) then modified their proposal, arguing that Saussure and Sichel's (1864) publication of *Ascoli* as a synonym of *Triscolia* automatically made the two names objective synonyms, with *S. badia* the correct type species for both. Unfortunately, no official decision by the ICZN on this matter was ever published.

The proper status of *Ascoli* remains open to debate. Unfortunately, Schrottky's (1910) usage of this name as valid means that it cannot simply be dismissed as having never been made available. Instead, it may be considered as published in synonymy by Saussure (1855). However, Jacot-Guillarmod et al.'s (1965) opinion that *Ascoli* was automatically an objective synonym of *Triscolia* is incorrect. ICZN Art. 67.12 states that the type species of a genus-group name first published in synonymy is that species (or one of those species) first directly associated with it by name. This would suggest that the type species of *Ascoli* should be *Scolia flavifrons*, as cited by Bartlett (1912). However, this designation might be considered invalid according to ICZN Art. 67.2.5, which excludes doubtfully or conditionally included species from consideration as types. Similar questions affect Betrem (1926). If neither Bartlett (1912) nor Betrem (1926) is considered to have validly associated species with *Ascoli*, then its type species becomes *S. flavifrons* as designated by Krombein (1951). If Bartlett's (1912)

inclusion is not considered valid but Betrem's (1926) inclusion is, then the type species must be selected from those cited by the latter publication, making Betrem and Bradley's (1964) designation of *Scolia haemorrhoidalis* valid. The question seems all but impossible to decide.

As it happens, both *S. haemorrhoidalis* and *S. flavifrons* are currently regarded as conspecific with *Megascolia* (*Regiscolia*) *maculata* (Drury, 1773) (Hamon and Osten 1994). *Ascoli* is therefore a senior synonym of both *Megascolia* Betrem, 1928 and *Regiscolia* Betrem & Bradley, 1964, whichever its correct type species. Considering that *Ascoli* has almost universally been rejected since its original publication, it seems inappropriate to displace these established names in its favour. Until such a time as it is formally suppressed by the ICZN, *Ascoli* is provisionally maintained as invalid.

#### Ascolia Argaman, 1996

Ascolia Argaman, 1996: 188.

Type species. Scolia flavifrons Fabricius, 1775, by original designation.

**Comments.** Argaman (1996) introduced *Ascolia* as an intended emendation of *Ascoli* Guérin-Méneville, 1838, an unavailable name (see above). *Ascolia* should therefore be treated as newly introduced by Argaman (1996), as noted by Kimsey and Brothers (2016), and is an objective junior synonym of *Regiscolia* Betrem & Bradley, 1964.

#### Aureimeris Betrem in Betrem & Bradley, 1972

Aureimeris Betrem in Betrem & Bradley, 1972: 244.

Type species. Elis africana Saussure, 1859, by original designation.

#### Australelis Betrem, 1962a

*Trielis* subgenus *Australelis* Betrem, 1962a: 146. *Austromeris*—Betrem and Bradley 1972: 33 (misspelling).

Type species. Elis consanguinea Saussure, 1855, by original designation.

**Comments.** Elis consanguinea was reduced to a variety of Scolia anthracina Burmeister, 1854 (now Australelis anthracina) by Turner (1909). Argaman (1996) lists 'Campsomeria Bradley, 1966' as a synonym of Australelis; this name appears in Bradley and Betrem (1966) as a clear misprint for Campsomeris Guérin-Méneville, 1838 and nothing more.

#### Austroscolia Betrem, 1927b

Scolia subgenus Austroscolia Betrem, 1927b: xcviii.

Type species. Scolia ruficeps Smith, 1855, by original designation.

**Comments.** Betrem (1928) mistakenly stated the type species to be *Scolia nitida* Smith, 1858.

#### Bagonasuna Argaman, 1996

Bagonasuna Argaman, 1996: 186.

Type species. Trielis tartara Saussure, 1880, by original designation.

**Comments.** Type species misattributed by Argaman (1996) to Morawitz (1897) who merely redescribed Saussure's (1880) species.

#### Batalanga Argaman, 1996

Batalanga Argaman, 1996: 205.

Type species. *Elis phalerata* Saussure, 1858, by original designation.

**Comments.** Argaman (1996) proposed *Batalanga* as a replacement name for *Phalerimeris* Betrem in Bradley & Betrem, 1967, under the belief that the latter was preoccupied by Bradley and Betrem (1966). However, the usage of *Phalerimeris* in the 1966 paper was as a *nomen nudum* only, and thus unavailable. As such, *Batalanga* stands as a junior objective synonym of *Phalerimeris* Betrem in Bradley & Betrem, 1967.

#### Bellimeris Argaman, 1996

Megacampsomeris subgenus Bellimeris Bradley, 1972: 6 (nomen nudum). Bellimeris Argaman, 1996: 213.

Type species. *Elis bella* Bingham, 1897, by original designation.

**Comments.** *Bellimeris* appeared as a *nomen nudum* in Bradley (1972), in the combination '*Megacampsomeris* (*Bellimeris*) *bella*' attributed to Betrem. The first author to provide a description for *Bellimeris* was Argaman (1996) to whom it must be attributed despite his own citation of 'Betrem, 1972'.

*Bellimeris* has subsequently been accepted as a valid genus (Schulten et al. 2011; Kim 2021), synonymised with *Sericocampsomeris* (Gupta and Jonathan 2003), or effectively synonymised with *Megacampsomeris* (Osten 2005a; Liu et al. 2021a). Until its position is better established, it is provisionally listed herein as a distinct genus.

# Betremia Bradley, 1950

Betremia Bradley, 1950: 358.

Type species. Scolia apicipennis Turner, 1911, by original designation.

# Borongorba Argaman, 1996

Borongorba Argaman, 1996: 213.

Type species. Scolia habrocoma Smith, 1855, by original designation.

### Bradleyella Krombein, 1963

Scolia subgenus Bradleyella Krombein, 1963: 629.

Type species. Scolia vulsa Krombein, 1963, by original designation.

#### Burgamurga Argaman, 1996

Burgamurga Argaman, 1996: 194.

Type species. Scolia cyanipennis Fabricius, 1804, by original designation.

### Buzatlana Argaman, 1996

Buzatlana Argaman, 1996: 199–200.

Type species. Sphex fuciformis Scopoli, 1786, by original designation.

### Campsomeriella Betrem, 1941

Campsomeris subgenus Campsomeriella Betrem, 1941: 86-87.

Type species. Scolia thoracica Fabricius, 1787, by original designation.

Scolia subgenus Campsomeris Guérin-Méneville, 1838: 247. Compsomeris—Ashmead 1903: 8 (misspelling) Campsomeria—Uchida 1933: 233 (misspelling).

Type species. Scolia atrata Fabricius, 1775, by subsequent designation (Bequaert 1926).
Comments. Guérin-Méneville (1838) attributed this name to a manuscript by Lepeletier de Saint-Fargeau, who would not use it in print until 1845. Betrem (1927a) designated Campsomeris aureicollis Lepeletier de Saint-Fargeau, 1845 as type species, in the mistaken belief that the genus was first published by Lepeletier de Saint-Fargeau (1845). After recognising Guérin-Méneville's (1838) earlier publication, Betrem (1927b) replaced this designation with Scolia thoracica Fabricius, 1787. Both designations were preoccupied by Bequaert (1926).

#### Campsoscolia Betrem, 1933

Campsoscolia Betrem, 1933: 259–260.

Type species. Scolia sexmaculata Fabricius, 1782, by original designation.

**Comments.** Scolia sexmaculata Fabricius, 1782 is a distinct species from Vespa sexmaculata Müller in Allionius, 1766, itself now included in Scolia, but the two species are not currently considered congeneric. Costa (1858) synonymised S. sexmaculata Fabricius with the simultaneously published S. interrupta Fabricius, 1782, now Colpa interrupta, and awarded priority to the latter. Osten's (2005a) listing of S. sexmaculata as having priority over S. interrupta is in error.

#### Canimeris Betrem, 1972

Megameris subgenus Megameris section Canimeris Betrem in Betrem & Bradley, 1972: 174.

Type species. Megameris canens Betrem & Bradley, 1972, by original designation.

#### Carbonelis Betrem in Betrem & Bradley, 1972

*Trielis* subgenus *Carbonelis* Bradley & Betrem, 1968: 325 (*nomen nudum*). *Trielis* subgenus *Carbonelis* Betrem in Betrem & Bradley, 1972: 59.

Type species. Scolia carbonaria Klug, 1832, by original designation.

# Carinoscolia Betrem, 1927

Scolia subgenus Carinoscolia Betrem, 1927b: xcvii.

Type species. Scolia opalina Smith, 1857, by original designation.

#### Catharinimeris Argaman, 1996

*Campsomeris* subgenus *Catharinimeris* Bradley, 1964a: 18 (*nomen nudum*). *Catharinimeris* Argaman, 1996: 207.

Type species. Scolia deserta Tullgren, 1904, by original designation.

**Comments.** This name appears as a *nomen nudum* in Bradley (1964a) in the combination '*Campsomeris* (*Catharinimeris*) *lundi*'. It presumably represents a variant spelling of the genus later described as *Cathimeris* in Betrem and Bradley (1972), in which *C. lundi* is synonymised with *Cathimeris deserta* (Tullgren 1904). Nevertheless, Argaman (1996) treated *Catharinimeris* and *Cathimeris* as distinct taxa, though the former must be attributed to Argaman himself as the first author to provide a description. Argaman (1996) cited the type species of *Catharinimeris* as '*(Campsomeris lundi* Betrem, 1964) = *Scolia deserta* Tullgren, 1904'; this is here accepted as a designation of *Scolia deserta* as type species.

# Cathimeris Betrem in Betrem & Bradley, 1972

Cathimeris Betrem in Betrem & Bradley, 1972: 199-202.

Type species. Elis hymenaea Gerstaecker, 1871, by original designation.

### Charimeris Betrem in Betrem & Bradley, 1972

Charimeris Betrem in Betrem & Bradley, 1972: 192–193.

**Type species.** *Charimeris jacoti* Betrem in Betrem & Bradley, 1972, by original designation.

# Cillimeris Betrem in Betrem & Bradley, 1972

Megameris subgenus Cillimeris Betrem in Betrem & Bradley, 1972: 179–180.

Type species. Megameris penicillifera Betrem & Bradley, 1972, by original designation.

#### Citberaysa Argaman, 1996

Citberaysa Argaman, 1996: 192.

Type species. Scolia ebenina Saussure, 1858, by original designation.

#### Clypeiscolia Bradley, 1974a

Scolia subgenus Clypeiscolia Bradley 1974a: 186.

Type species. Scolia clypealis Bradley, 1974a, by original designation.

**Comments.** *Clypeiscolia* and its type species were omitted from Osten's (2005a) listing. It is retained as a subgenus of *Scolia* pending future revision.

#### Colpa Dufour, 1841

Colpa Dufour, 1841: 378, 413, 486.

Type species. Scolia interrupta Fabricius, 1782, by monotypy.

**Comments.** Dufour (1841) cited this name as used for a new unpublished genus by Lepeletier de Saint-Fargeau, who would not use it in print until 1845. Betrem (1928) designated *Colpa peregrina* Lepeletier de Saint-Fargeau, 1845 as type species, under the mistaken belief that this represented the genus' earliest publication.

#### Colpacampsomeris Argaman, 1996

*Campsomeris* subgenus *Colpacampsomeris* Betrem, 1941: 101–102 (*nomen nudum*). *Colpacampsomeris* Argaman, 1996: 209.

Type species. Scolia indica Saussure, 1855, by original designation.

**Comments.** Colpacampsomeris provides a prime example of the confusion arising from J. G. Betrem's often indirect manner of presenting taxonomic changes. The name was first used by Betrem (1941) with the statement on p. 96, "J'en ai déjà détaché [from Dielis] les sous-genres... Sericocampsomeris et Colpacampsomeris, qui comprennent mon groupe VI" ['I have already separated the subgenera Sericocampsomeris and Colpacampsomeris, which represents my group VI'], and later on pp. 101–102, "J'ai divisé le groupe VI de mon ancien sous-genre Dielis en deux groups que j'ai elevés à la valeur de sous-genre. Le premier de ces sous-genres est le nouveau sous-genre Colpacampsomeris. La forme typique est la C. indica" ['I have divided group VI of my old subgenus Dielis into two groups that I have elevated to the value of subgenus. The first of these subgenera is

the new subgenus *Colpacampsomeris*. The typical form is *C. indica*']. However, no direct description was provided for the new subgenus, making it potentially a *nomen nudum*. The Code does allow a bibliographic reference to a pre-existing description to stand in place of a direct description (ICZN Art. 13.1) but this allowance cannot be applied here. Even if one is charitable enough to accept the reference to '*mon groupe VT*' as an inferred reference to Betrem's (1928) description of such a group, it seems clear that Betrem intended *Colpacampsomeris* to encompass only part of *Dielis* Group VI, not its entirety, and the original description of the latter cannot be directly applied to the former.

Despite multiple subsequent usages of *Colpacampsomeris* to refer to the large southern Asian species *C. indica* (e.g. Bradley and Betrem 1967; Krombein 1978), no actual description of the genus with an associated type species designation appeared until Argaman (1996). Though still attributed therein to 'Betrem, 1941', *Colpacampsomeris* must be attributed to Argaman himself.

#### Cretaproscolia Rasnitsyn & Martínez-Delclòs, 1999

Cretaproscolia Rasnitsyn & Martínez-Delclòs, 1999: 771.

Type species. Cretaproscolia josai Rasnitsyn & Martínez-Delclòs, 1999, by original designation.

Comments. Fossil taxon (Lower Cretaceous).

### Cretoscolia Rasnitsyn, 1993

Cretoscolia Rasnitsyn, 1993: 88.

Type species. Cretoscolia promissiva Rasnitsyn, 1993, by original designation. Comments. Fossil taxon (Late Cretaceous).

#### Crioscolia Bradley, 1951

*Campsoscolia* subgenus *Crioscolia* Bradley, 1951: 431–432.

Type species. Campsomeris flammicoma Bradley, 1928, by original designation.

**Comments.** Betrem and Bradley (1972) raised *Crioscolia* to the status of a distinct genus. For unspecified reasons, this action was not followed by Osten (2005a), but it is maintained herein.

Curtaurga Argaman, 1996: 183.

Type species. Scolia aliena Klug, 1832, by original designation.

**Comments.** Unnecessarily proposed by Argaman (1996) as a replacement name for *Guigliana* Betrem in Bradley & Betrem, 1967, under the mistaken belief that the latter was preoccupied by the use of *Guigliana* as a *nomen nudum* in Bradley (1964c).

#### Dasyscolia Bradley, 1951

Campsoscolia subgenus Dasyscolia Bradley, 1951: 432, 437.

Type species. *Tiphia ciliata* Fabricius, 1787, by original designation.

#### Dielis Saussure & Sichel, 1864

Elis subgenus Dielis Saussure & Sichel, 1864: 161.

Type species. Scolia radula Fabricius, 1775, by subsequent designation (Betrem 1928). Comments. The type status of this genus was discussed by Betrem (1962b) who confirmed Scolia radula as type. Krombein (1951) miscited Tiphia radula Fabricius, 1775, which Betrem (1962b) made type of Radumeris Betrem, 1962b. Scolia radula was synonymised with Sphex plumipes Drury, 1770 (now Dielis plumipes) by Saussure and Sichel (1864).

#### Diliacos Saussure & Sichel, 1864

Diliacos Saussure & Sichel, 1864: 36.

**Type species.** *Campsomeris violacea* Lepeletier de Saint-Fargeau, 1845, by subsequent designation (Ashmead 1903).

**Comments.** Bradley (1957c) renamed the type species *Scolia* (*Diliacos*) *praslini* Bradley, 1957, due to its preoccupation in the genus *Scolia* by *S. violacea* Panzer, 1799. As this replacement occurred prior to 1961, it remains valid whether *S. praslini* is included in *Scolia* or not (ICZN Art. 59.3).

### Discolia Saussure, 1863

Scolia subgenus Discolia Saussure, 1863: 18.

**Type species.** *Scolia nobilitata* Fabricius, 1804, by subsequent designation (Betrem and Bradley 1964).

**Comments.** Ashmead (1903) designated *Scolia apicicornis* Guérin-Méneville, 1838 as type species, under the belief that *Discolia* was first published by Saussure and Sichel (1864). As the name had previously been used by Saussure (1863), *S. apicicornis* is not among the eligible originally included species.

### Dobrobeta Argaman, 1996

Dobrobeta Argaman, 1996: 206.

Type species. Campsomeris socotrana Kirby, 1900, by original designation.

#### Elis Fabricius, 1804

Elis Fabricius, 1804: 248.

Type species. Scolia sexcincta Fabricius, 1775, by subsequent designation (Bingham 1897). Comments. Elis was originally established for an assemblage of species now divided between the families Scoliidae and Thynnidae. The type species is now regarded as a synonym of Myzinum quinquecinctum (Fabricius, 1775), a species of Thynnidae (Krombein 1938; Bartalucci 2004). Ashmead's (1903) later type designation of Scolia septemcincta Fabricius, 1775, a synonym of the scoliid Radumeris radula (Fabricius, 1775) (Elliott 2011), is not valid.

#### Elpaholta Argaman, 1996

Elpaholta Argaman, 1996: 194.

Type species. Scolia fulvifrons Saussure, 1855, by original designation.

#### Enigmatimeris Betrem in Betrem & Bradley, 1972

Aureimeris subgenus Enigmatimeris Betrem in Betrem & Bradley, 1972: 256.

Type species. Scolia fasciatella Klug, 1832, by original designation.

# Extrameris Betrem in Betrem & Bradley, 1972

Extrameris Betrem in Betrem & Bradley, 1972: 158–159.

**Type species.** *Extrameris mansuefactoides* Betrem & Bradley, 1972, by original designation.

#### Fascimeris Betrem in Betrem & Bradley, 1972

Megameris subgenus Fascimeris Betrem in Betrem & Bradley, 1972: 175–176.

Type species. Megameris calcigera Betrem & Bradley, 1972, by original designation.

#### Fasciomeris Argaman, 1996

*Campsomeris* subgenus *Fasciomeris* Bradley, 1964a: 23 (*nomen nudum*). *Fasciomeris* Argaman, 1996: 211.

Type species. Scolia quinquefasciata Fabricius, 1782, by original designation.

**Comments.** This name was used as a *nomen nudum* by Bradley (1964a) in the combination '*Campsomeris* (*Fasciomeris*) *quinquefasciata*'. It presumably represents a variant spelling of the taxon later described as *Fascimeris* by Betrem in Betrem and Bradley (1972). Nevertheless, Argaman (1996) treated *Fascimeris* and *Fasciomeris* as distinct taxa. Because *Fascimeris* and *Fasciomeris* differ in spelling, they must both be accepted as available names (ICZN Art. 56.2), with the latter attributed to Argaman himself as the first author to provide a description.

#### Fiharbuxa Argaman, 1996

Fiharbuxa Argaman, 1996: 212.

Type species. Scolia prismatica Smith, 1855, by original designation.

# Floriscolia Rasnitsyn, 1993

Floriscolia Rasnitsyn, 1993: 93.

Type species. *Floriscolia relicta* Rasnitsyn, 1993, by original designation. Comments. Fossil taxon (Oligocene).

### Garantimeris Argaman, 1996

Cathimeris subgenus Garantimeris Betrem in Betrem & Bradley, 1972: 242 (nomen nudum).
 Garantimeris Argaman, 1996: 207.

Type species. *Elis auraria* Saussure, 1858, by original designation.

**Comments.** When this name was first used by Betrem and Bradley (1972), it was described in full but remained unavailable as no type species was fixed (ICZN Art. 13.3). The criteria for availability were not met until Argaman (1996) who must therefore be regarded as this taxon's author.

#### Gondiconda Argaman, 1996

Gondiconda Argaman, 1996: 210.

Type species. Elis vittata Sichel in Saussure & Sichel, 1864, by original designation.

#### Guigliana Betrem in Bradley & Betrem, 1967

*Guigliana* Betrem, 1965: 120 (*nomen nudum*). *Guigliana* Betrem in Bradley & Betrem, 1967: 293–294.

Type species. Scolia aliena Klug, 1832, by original designation. Comments. See below for comments on Guigliana Argaman, 1996.

#### Guigliana Argaman, 1996

Scolia subgenus Guigliana Bradley, 1964c: 192 (nomen nudum). Guigliana Argaman, 1996: 196.

Type species. Sphex azurea Christ, 1791, by original designation.

**Comments.** It is debatable whether this should be treated as a separately available name from *Guigliana* Betrem in Bradley & Betrem, 1967, or simply a variant application. However, the type species nominated in both cases are widely divergent, belonging to separate tribes of the Scoliinae, and it seems unlikely that Bradley and Betrem would have ever considered them congeneric. *Guigliana* was used by Bradley (1964c) as a *nomen nudum*, in the combination '*Scolia* (*Guigliana*) *azurea azurea*'. Argaman (1996) misinterpreted this usage as available, preoccupying Bradley and Betrem (1967), and unnecessarily coined *Curtaurga* Argaman, 1996 as a replacement name for the latter. Argaman would then be the correct author of *Guigliana* as typified by *Sphex azurea*, as the first

author to provide a description, despite attributing it to 'Bradley (1964)'. If accepted as a validly available name, *Guigliana* Argaman is a junior homonym of *Guigliana* Betrem.

# Hangasorna Argaman, 1996

Hangasorna Argaman, 1996: 197.

Type species. Scolia quadripustulata Fabricius, 1782, by original designation.

**Comments.** Scolia quadripustulata has a long history of confusion with S. binotata Fabricius, 1804 (Gupta and Jonathan 2003; Taylor and Barthélémy 2021). It is uncertain which of these species Argaman (1996) had before him when describing Hangasorna. Some of the features described are equally applicable to both but the description of the male flagellum as strongly clavate suggests S. binotata rather than S. quadripustulata (Gupta and Jonathan 2003). Nevertheless, as Hangasorna is likely to remain a synonym of Scolia subgenus Discolia whichever species is accepted as type, Argaman (1996) is here accepted as having correctly designated S. quadripustulata, in accordance with ICZN Art. 70.3.1.

### Haralambia Argaman, 1996

Haralambia Argaman, 1996: 215.

Type species. *Tiphia dorsata* Fabricius, 1787, by original designation.

# Hayderiba Argaman, 1996

Hayderiba Argaman, 1996: 209.

**Type species.** *Colpa peregrina* Lepeletier de Saint-Fargeau, 1845, by original designation. **Comments.** Proposed by Argaman (1996) to refer to *Colpa* in the sense of Lepeletier de Saint-Fargeau (1845), not Dufour (1841).

# Hesperoscolia Bradley, 1974b

Scolia subgenus Hesperoscolia Bradley, 1974b: 419.

**Type species.** *Scolia rufiventris* Fabricius, 1804, by original designation.

**Comments.** Osten (2005a) listed *Hesperoscolia* as a subgenus on p. 26 but treated it as a distinct genus in the following list of species names. It has been retained as a subgenus of *Scolia* by subsequent authors (Santos et al. 2015; Añino et al. 2020).

# Heterelis Costa, 1887

Heterelis Costa, 1887: 104. Hetrelis—Osten 2005b: 1454 (misspelling).

**Type species.** *Scolia quinquecincta* Fabricius, 1793, by subsequent designation (ICZN 1985).

**Comments.** *Heterelis* was established by Costa (1887) with only a single included species, *'Elis villosa* Fab.' However, as explained by Betrem et al. (1963), this was based on a misidentification of *Tiphia villosa* Fabricius, 1793 which is not a scoliid. Betrem et al. (1963) argued that the species actually described by Costa (1887) was *Scolia quinquecinc-ta* Fabricius, 1793, whose status as type species was confirmed by the ICZN (1985).

#### Hexelis Betrem in Betrem & Bradley, 1972

Guigliana subgenus Hexelis Betrem in Betrem & Bradley, 1972: 73.

**Type species.** *Guigliana hexensis* Betrem in Betrem & Bradley, 1972, by original designation.

#### Hirtimeris Betrem, 1967

Campsomeriella subgenus Campsomeriella section Hirtimeris Betrem, 1967: 27, 29.

Type species. Scolia hirticollis Fabricius, 1804, by original designation.

**Comments.** Originally published as an infrageneric section, *Hirtimeris* was later used as a full subgenus by Bradley (1973, 1974b). It was not listed by Osten (2005a) who included *S. hirticollis* in *Campsomeriella* without a subgenus placement.

#### Hitfoidra Argaman, 1996

Hitfoidra Argaman, 1996: 192.

Type species. Scolia carnifex Coquerel, 1855, by original designation.

#### Iforborha Argaman, 1996

Iforborha Argaman, 1996: 203.

**Type species.** *Tiphia collaris* Fabricius, 1775, by original designation.

# Iksalonca Argaman, 1996

Iksalonca Argaman, 1996: 198–199.

Type species. Scolia jurinei Saussure, 1855, by original designation. Comments. Scolia jurinei was synonymised with S. affinis Guérin-Méneville, 1838 by Bradley (1974b).

# Ilkamilka Argaman, 1996

Ilkamilka Argaman, 1996: 212.

**Type species.** *Scolia luzonensis* Rohwer, 1921, by original designation. **Comments.** *Ilkamilka* was synonymised with *Laevicampsomeris* by Castagnet (2021).

# Immanimeris Betrem in Betrem & Bradley, 1972

Megameris subgenus Immanimeris Betrem in Betrem & Bradley, 1972: 189.

Type species. Megameris immanis Betrem & Bradley, 1972, by original designation.

# Junodelis Betrem in Betrem & Bradley, 1972

Trielis subgenus Junodelis Betrem in Betrem & Bradley, 1972: 56-57.

Type species. Trielis junodi Betrem & Bradley, 1972, by original designation.

# Jupadora Argaman, 1996

Jupadora Argaman, 1996: 193.

**Type species.** *Scolia cereberia* Bradley, 1959, by original designation (misspelled as '*cerberia*').

# Katapolda Argaman, 1996

Katapolda Argaman, 1996: 198.

Type species. Scolia desidiosa Bingham, 1896, by original designation.

#### Kokarevta Argaman, 1996

Kokarevta Argaman, 1996: 200.

Type species. Tiphia histrionica Fabricius, 1787, by original designation.

#### Kukkiya Argaman, 1996

Kukkiya Argaman, 1996: 187.

Type species. Scolia moricei Saunders, 1901, by original designation.

### Lacosi Guérin-Méneville, 1838

Scolia subgenus Lacosi Guérin-Méneville, 1838: 247.

**Type species.** *Scolia quadripunctata* Fabricius, 1775, by subsequent designation by Bequaert (1926).

**Comments.** Junior objective synonym of *Scolia* Fabricius, 1775. Gender masculine (ICZN Art. 30.2.4; D. Yanega, pers. comm.). Betrem (1928) erroneously designated *S. quadripustulata* Fabricius, 1782 as type species; not only is this designation preoccupied by Bequaert (1926) but *S. quadripustulata* was not among the originally included species.

#### Lacosia Argaman, 1996

Lacosia Argaman, 1996: 199.

**Type species.** *Scolia quadripunctata* Fabricius, 1775, by objective synonymy with *Lacosi* Guérin-Méneville, 1838 (ICZN Art. 67.8).

**Comments.** *Lacosia* was ostensibly introduced as an emendation of *Lacosi* Guérin-Méneville, 1838, but Argaman's (1996) treatment of this name can only be described as baffling. Argaman emended the names *Ascoli* and *Lacosi* to *Ascolia* and *Lacosia* on the basis of their being "grammatically invalid arbitrary combination[s] of letters". Under the current version of the Code, such an emendation is not justified as arbitrary names are explicitly permitted (ICZN Art. 11.3), and *Lacosia* has not been validated by prevailing usage (see ICZN Art. 33.2.3.1). Argaman (1996) stated that *Scolia pygmaea* Saussure, 1858 was the type species of *Lacosia "through the inclusion by Saussure (1858)*. However, *S. pygmaea* was only one of numerous species included in *Lacosi* by Saussure (1858), and was certainly not one of the species originally included by Guérin-Méneville (1838). Earlier designations of a type species by Bequaert (1926) and Betrem (1928) were rejected on the basis that they were "selected as type of Lacosi, a generic group

*name without status in nomenclature*", but that supposed lack of status was apparently no barrier to Argaman continuing to attribute his own concept to Guérin-Méneville!

As noted by Kimsey and Brothers (2016), *Lacosia* must be attributed to Argaman himself (ICZN Art. 33.2.3). However, ICZN Arts 33.2.3 and 67.8 state that any genus name introduced as an unjustified emendation is an objective synonym of the original name emended. The type species of *Lacosia* is therefore *Scolia quadripunctata* Fabricius, 1775, despite Argaman's (1996) indication to the contrary, and *Lacosia* is also an objective synonym of *Scolia* Fabricius, 1775.

The status of *Scolia pygmaea* is uncertain. Petersen (1970) synonymised it with *Scolia hottentotta* Saussure, 1858, a species of subgenus *Scolia (contra* its listing in subgenus *Discolia* by Osten 2005a). This synonymy was disputed by Argaman (1996) who designated a neotype for *S. pygmaea*. Argaman's neotype designation does not meet the requirements of ICZN Art. 75.3; most notably, Argaman does not attribute the neotype to a recognised scientific collection (the description of Argaman's habits by Kimsey and Brothers 2016 suggests that it may have been in Argaman's personal collection and may no longer be identifiable). Final resolution of this question is beyond the scope of the current publication.

#### Laevicampsomeris Betrem, 1933

Campsomeris subgenus Laevicampsomeris Betrem, 1933: 238.

Type species. Scolia nigerrima Smith, 1861, by original designation.

#### Laeviscolia Betrem, 1928

Scolia subgenus Laeviscolia Betrem, 1928: 222.

Type species. Scolia frontalis Saussure, 1855, by original designation.

# Laskariska Argaman, 1996

Laskariska Argaman, 1996: 188.

Type species. Scolia haemorrhoidalis Fabricius, 1787, by original designation.

#### Leomeris Betrem in Betrem & Bradley, 1972

*Leomeris* Betrem in Betrem & Bradley, 1972: 110.

Type species. Scolia leonina Dalman, 1823, by original designation.

#### Liacos Guérin-Méneville, 1838

Scolia subgenus Liacos Guérin-Méneville, 1838: 246.

Type species. Scolia dimidiata Guérin-Méneville, 1838, by monotypy.

**Comments.** Despite being generally assumed to be feminine, the name *Liacos* is masculine in gender (ICZN Art 30.2.4; D. Yanega, pers. comm.) *Scolia dimidiata* was synonymised with *S. analis* Fabricius, 1804, now *Liacos analis*, by Saussure and Sichel (1864). Bingham's (1897) incorrect listing of *L. analis* as type species was presumably informed by this synonymy.

#### Lindenimeris Argaman, 1996

*Campsomeris* subgenus *Lindenimeris* Bradley, 1964c: 191 (*nomen nudum*). *Lindenimeris* Argaman, 1996: 212.

**Type species.** *Campsomeris lindenii* Lepeletier de Saint-Fargeau, 1845, by original designation.

**Comments.** *Lindenimeris* was first used by Bradley (1964c) as a *nomen nudum* only, in the combination '*Campsomeris* (*Lindenimeris*) *lindenii*', with the claim that "*Dr. Betrem plans soon to describe [it]*". No such description by Betrem appears to have ever been published and the name would not be validated until its description by Argaman (1996). Despite Argaman's continued attribution to 'Bradley, 1964', the name must be attributed to Argaman himself.

*Lindenimeris* was listed as a subgenus of *Megacampsomeris* including *M. lindenii* by Osten (2005a). However, other species of *Megacampsomeris* were not assigned to subgenus. Until relationships in this genus are better established, *Lindenimeris* is treated here as a junior synonym of *Megacampsomeris*.

#### Lisoca Costa, 1858

*Lisoca* Costa, 1858: 8–9.

**Type species.** *Scolia quadripunctata* Fabricius, 1775, by subsequent designation (Krombein 1951).

**Comments.** The publication dates of Costa's '*Fauna del Regno di Napoli*' have long been difficult to establish; those for the sections covering Hymenoptera are provided by Baker (1994). Betrem (1928) designated *Scolia citreozonata* Costa, 1861 as type species of *Lisoca* but that species did not appear in print until three years after the folio in which the genus name first appeared. Krombein's (1951) designation of *S. quadripunctata* was therefore the first to select from among the eligible originally included species. This designation makes *Lisoca* a junior objective synonym of *Scolia* Fabricius, 1775.

# Lissocampsomeris Bradley, 1957b

Campsomeris subgenus Lissocampsomeris Bradley, 1957b: 75.

Type species. Colpa wesmaeli Lepeletier de Saint-Fargeau, 1845, by original designation.

# Lobhargita Argaman, 1996

Lobhargita Argaman, 1996: 208.

Type species. Scolia aureola Klug, 1832, by original designation.

### Madonimeris Betrem, 1967

Campsomeriella subgenus Annulimeris section Madonimeris Betrem, 1967: 28-29.

Type species. *Dielis madonensis* Buysson, 1910, by original designation.

# Malagaselis Betrem in Betrem & Bradley, 1972

Guigliana subgenus Malagaselis Betrem in Betrem & Bradley, 1972: 74.

Type species. *Elis elliotiana* Saussure, 1891, by original designation.

# Mansuetimeris Betrem in Betrem & Bradley, 1972

Aureimeris subgenus Mansuetimeris Betrem in Betrem & Bradley, 1972: 250.

Type species. Scolia mansueta Gerstäcker in Peters, 1858, by original designation.

# Megacampsomeris Betrem, 1928

Campsomeris subgenus Megacampsomeris Betrem, 1928: 138.

**Type species.** *Tiphia grossa* Fabricius, 1804, by original designation.

### Megameris Betrem, 1967

*Campsomeris* subgenus *Megameris* Betrem in Bradley & Betrem, 1967: 294. *Magameris*—Osten 2005a: 18 (misspelling).

Type species. Elis soleata Gerstaecker, 1871, by original designation.

### Megascolia Betrem, 1928

Scolia subgenus Triscolia section Megascolia Betrem, 1928: 239.

Type species. Scolia procer Illiger, 1802, by original designation.

### Micromeriella Betrem in Betrem & Bradley, 1972

Micromeriella Betrem in Betrem & Bradley, 1972: 116–117.

**Type species.** *Scolia marginella* Klug, 1810, by original designation.

**Comments.** Replacement name for *Micromeris* Betrem in Bradley & Betrem, 1967 *non* Conrad, 1866.

# Micromeris Betrem in Bradley & Betrem, 1967

*Campsomeris* subgenus *Micromeris* Bradley, 1964c: 188, 189 (*nomen nudum*). *Campsomeris* subgenus *Micromeris* Betrem in Bradley & Betrem, 1967: 294.

Type species. Scolia marginella Klug, 1810, by original designation.

**Comments.** Preoccupied by *Micromeris* Conrad, 1866 (Bivalvia), subsequently replaced by *Micromeriella* Betrem in Betrem & Bradley, 1972.

#### Microscolia Betrem, 1927b

Scolia subgenus Microscolia Betrem, 1927b: xcvi-xcvii.

Type species. Scolia cephalotes Burmeister, 1854, by original designation.

# Molzinarda Argaman, 1996

Molzinarda Argaman, 1996: 192.

Type species. Scolia nitida Smith, 1858, by original designation.

# Mookitena Argaman, 1996

Mookitena Argaman, 1996: 214–215.

Type species. Campsomeris hesterae Rohwer, 1927, by original designation.

### Murahutka Argaman, 1996

Murahutka Argaman, 1996: 190.

Type species. Scolia quadriceps Smith, 1858, by original designation.

# Mutilloscolia Bradley, 1959

Scolia subgenus Mutilloscolia Bradley, 1959: 361.

Type species. Scolia campanulata Bradley, 1959, by original designation.

# Naysebwa Argaman, 1996

Naysebwa Argaman, 1996: 200.

Type species. Scolia fulvofimbriata Burmeister, 1854, by original designation.

# Niyaranta Argaman, 1996

Niyaranta Argaman, 1996: 213.

Type species. Scolia aurulenta Smith, 1855, by original designation.

# Nokbibula Argaman, 1996

Nokbibula Argaman, 1996: 191.

Type species. *Scolia vittifrons* Sichel in Saussure & Sichel, 1864, by original designation.

# Noybarilta Argaman, 1996

Noybarilta Argaman, 1996: 211.

Type species. Scolia hoffmannseggii Klug, 1805, by original designation.

# Nyaselis Betrem in Betrem & Bradley, 1972

Trielis subgenus Nyaselis Betrem in Betrem & Bradley, 1972: 61-62.

**Type species.** *Trielis nyasensis* Betrem in Betrem & Bradley, 1972, by original designation.

#### Onkoknoa Argaman, 1996

Onkoknoa Argaman, 1996: 195.

**Type species.** *Scolia bilunata* Saussure, 1858, by original designation (misspelled '*bi-lunulata*').

# Ordatirga Argaman, 1996

Ordatirga Argaman, 1996: 185.

Type species. Dielis mima Buysson, 1897, by original designation.

# Orlovinga Argaman, 1996

Orlovinga Argaman, 1996: 199.

Type species. Scolia gussakovskii Steinberg, 1953, by original designation.

# Oscalosca Argaman, 1996

Oscalosca Argaman, 1996: 214.

Type species. Elis pilipes Saussure, 1858, by original designation.

# Paconzitva Argaman, 1996

Paconzitva Argaman, 1996: 196.

Type species. Scolia alecto Smith, 1858, by original designation.

# Palaeoscolia Antropov in Antropov et al., 2014

Palaeoscolia Antropov in Antropov et al., 2014: 401.

**Type species.** *Palaeoscolia relicta* Antropov in Antropov et al., 2014, by original designation. **Comments.** Fossil taxon (Late Eocene).

# Pardesiya Argaman, 1996

Pardesiya Argaman, 1996: 200.

Type species. Scolia neglecta Cyrillo, 1787, by original designation. Comments. Scolia neglecta was synonymised with S. carbonaria (Linné, 1767) by Hamon (1994).

# Peltatimeris Betrem in Betrem & Bradley, 1972

Peltatimeris Betrem in Betrem & Bradley, 1972: 311.

Type species. Peltatimeris peltata Betrem & Bradley, 1972, by original designation.

# Penimeris Betrem in Betrem & Bradley, 1972

Megameris subgenus Penimeris Betrem in Betrem & Bradley, 1972: 181.

**Type species.** *Megameris pseudofasciatipennis* Betrem in Betrem & Bradley, 1972, by original designation.

#### Phalerimeris Betrem in Bradley & Betrem, 1967

Campsomeris subgenus Phalerimeris Betrem in Bradley & Betrem, 1967: 294-295.

Type species. Elis phalerata Saussure, 1858, by original designation.

#### Phaleromeris Argaman, 1996

*Phaleromeris* Bradley, 1964c: 193 (*nomen nudum*). *Phaleromeris* Argaman, 1996: 205.

Type species. *Tiphia annulata* Fabricius, 1793, by original designation.

**Comments.** *Phaleromeris* was first used by Bradley (1964c) as a *nomen nudum*, in the combination '*Campsomeris* (*Phaleromeris*) *annulata*'. This name presumably represents a variant spelling of what would eventually be established as *Phalerimeris* Betrem in Bradley & Betrem, 1967, though *Tiphia annulata* would not be included in the final concept. Nevertheless, Argaman (1996) adopted Bradley's (1964c) usage as valid. Because *Phalerimeris* and *Phaleromeris* differ in spelling, they must both be accepted as available names (ICZN Art. 56.2), with the latter attributed to Argaman (1996) as the first author to provide a description. *Phaleromeris* is a junior objective synonym of *Annulimeris* Betrem, 1967.

#### Proscolia Rasnitsyn, 1977

Proscolia Rasnitsyn, 1977: 524–525.

Type species. Proscolia archaica Rasnitsyn, 1977, by monotypy.

#### Protoscolia Zhang, Rasnitsyn & Zhang, 2002

Protoscolia Zhang, Rasnitsyn & Zhang, 2002: 80.

**Type species.** *Protoscolia sinensis* Zhang, Rasnitsyn & Zhang, 2002, by original designation. **Comments.** Fossil taxon (latest Jurassic or Early Cretaceous).

#### Pseudotrielis Betrem, 1928

Campsomeris subgenus Pseudotrielis Betrem, 1928: 83.

Type species. Scolia zonata Smith, 1855, by original designation.
#### Punctelis Betrem in Betrem & Bradley, 1972

Crioscolia subgenus Punctelis Betrem in Betrem & Bradley, 1972: 66.

Type species. *Elis punctum* Saussure, 1891, by original designation.

**Comments.** Listed by Osten (2005a) as a section of *Colpa* subgenus *Crioscolia*. Betrem and Bradley's (1972) original status as a subgenus of a distinct genus *Crioscolia* is maintained herein.

#### Pupunhuga Argaman, 1996

Pupunhuga Argaman, 1996: 203.

Type species. Campsomeris sauteri Betrem, 1928, by original designation.

# Pygodasis Bradley, 1957b

*Pygodasis* Bradley, 1957b: 72.

**Type species.** *Scolia quadrinotata* Fabricius, 1804, by original designation. **Comments.** *Scolia quadrinotata* was synonymised with *Scolia quadrimaculata* Fabricius, 1775, now *Pygodasis quadrimaculata*, by Bradley (1964b).

#### Pyrrhoscolia Bradley, 1959

Scolia subgenus Pyrrhoscolia Bradley, 1959: 347.

Type species. Scolia fax Bradley, 1959, by original designation.

#### Radumeris Betrem, 1962b

Campsomeris subgenus Radumeris Betrem, 1962b: 206–207.

Type species. *Tiphia radula* Fabricius, 1775, by original designation.

#### Rahosmula Argaman, 1996

Rahosmula Argaman, 1996: 190.

**Type species.** *Liacos sicheli* Saussure, 1859, by original designation of misidentified type species (see below).

**Comments.** Argaman (1996) originally designated the type species of this genus as *Scolia sicheli* Saussure, 1859. However, it is evident that the intended species was *Liacos sicheli* Saussure, 1859, described in the same paper and included in *Scolia* by Betrem (1928). The provided description matches *Liacos sicheli*, not *Scolia sicheli*, and *Rahosmula* is stated to be Oriental in distribution as for *Liacos sicheli*, whereas *Scolia sicheli* is southern African. Identification of the correct type species is significant in this case as *Liacos sicheli* is currently included in *Diliacos* whereas *Scolia sicheli* belongs to *Scolia* subgenus *Discolia* (Osten 2005a). Therefore, in accordance with ICZN Art. 70.3, *Liacos sicheli* Saussure, 1859 is officially designated herein as the type species of *Rahosmula* Argaman, 1996.

#### Regiscolia Betrem & Bradley, 1964

*Megascolia* subgenus *Regiscolia* Bradley, 1964a: 10, 11, 13, 14, 21, 23, 33 (*nomen nudum*).

Megascolia subgenus Regiscolia Betrem & Bradley, 1964: 441.

Type species. Scolia flavifrons Fabricius, 1775, by original designation.

**Comments.** Betrem and Bradley (1964) introduced *Regiscolia* for *Scolia* subgenus *Triscolia* section *Triscolia* as used in Betrem (1928), based on his mistaken identification of the type species for *Triscolia* Saussure, 1863 (see below). Their treatment satisfies the requirements of ICZN Art. 13.1.2, though they also included a comparison of the type species with *Triscolia* proper.

Argaman (1996) attributed *Regiscolia* to Bradley (1964a), in which it was used as a *nomen nudum* only, and incorrectly identified *Sphex bidens* Linné, 1767 as type species; he assigned the actual type species *Scolia flavifrons* to *Ascolia* Argaman, 1996.

#### Rhabdotomeris Bradley, 1957b

*Campsomeris* subgenus *Rhabdotomeris* Bradley, 1957b: 72. *Rhabdotimeris*—Osten 2005a: 3 (misspelling).

Type species. Scolia rokitanskyi Dalla Torre, 1897, by original designation.

**Comments.** Scolia rokitanskyi was introduced by Dalla Torre (1897) as a replacement name for *Elis mexicana* Cameron, 1893, preoccupied in *Scolia* by Saussure (1858). The type species of *Rhabdotomeris* was cited by Bradley (1957b) as '*[Elis Mexicana* Cameron, 1893] = *Campsomeris (Rhabdotomeris) rokitanskyi* (D.T.)', accepted herein as a valid designation of *S. rokitanskyi*.

#### Rihamlika Argaman, 1996

Rihamlika Argaman, 1996: 195.

Type species. Scolia venusta Smith, 1855, by original designation.

#### Rodriguimeris Betrem, 1967

Campsomeriella subgenus Rodriguimeris Betrem, 1967: 27, 29.

Type species. Campsomeris fax Bradley, 1936, by original designation.

#### Rostopasca Argaman, 1996

Rostopasca Argaman, 1996: 187.

Type species. Scolia erivanensis Radoszkovsky, 1879, by original designation.

**Comments.** The status of *Scolia erivanensis* remains uncertain. Osten (2005a) listed it in *Scolia* with a query, without assigning it to subgenus, but Argaman (1996) included it in his tribe Ascoliini with taxa here assigned to *Megascolia* subgenus *Regiscolia*. Until its position can be better determined, *Rostopasca* is provisionally accepted as a valid genus.

#### Rucarcana Argaman, 1996

Rucarcana Argaman, 1996: 205–206.

Type species. Campsomeris flavidula st. congener Turner, 1909, by original designation. Comments. Turner (1909) used the abbreviation 'st.' (possibly standing for 'strain') to denote variants within species. It is unclear whether such taxa were intended at subspecific or infra-subspecific rank. Infra-subspecific taxa published before 1961 are unavailable under the *Code* unless used for a valid species or subspecies prior to 1985 (ICZN. Art. 45.6.4.1). *Campsomeris congener* Turner, 1909 was recognised as a distinct species by Betrem (1928), thus confirming its availability whatever its prior status.

#### Scolia Fabricius, 1775

*Scolia* Fabricius, 1775: 355. *Scholia* Newman, 1835: 399 (unjustified emendation). *Scobia*—Agassiz 1846: 6 (misspelling). Solia—Dalla Torre 1897: 144 (misspelling).

**Type species.** *Scolia quadripunctata* Fabricius, 1775, by subsequent designation (Latreille 1810).

**Comments.** As indicated by Betrem (1928), subsequent designations of type species for *Scolia* (Bingham 1897: *S. flavifrons* Fabricius, 1775; Schrottky 1910: *S. atrata* Fabricius, 1775) are preoccupied by Latreille (1810). *Scolia quadripunctata* was synonymised with *S. sexmaculata* (Müller in Allionius, 1766) by Betrem (1936).

# Scolioides Guiglia & Capra, 1934

Scolia subgenus Scolia section Scolioides Guiglia & Capra, 1934: 115.

Type species. Apis hirta Schrank, 1781, by original designation.

## Sericocampsomeris Betrem, 1941

Campsomeris subgenus Sericocampsomeris Betrem, 1941: 91-92.

Type species. Scolia quadriguttulata Burmeister, 1854, by original designation. Comments. Scolia quadriguttulata was synonymised with Scolia stygia Illiger, 1802, now Sericocampsomeris stygia, by Betrem and Bradley (1972).

# Sinoproscolia Zhang, Zhang, Rasnitsyn & Jarzembowski, 2015

Sinoproscolia Zhang, Zhang, Rasnitsyn & Jarzembowski, 2015: 580–581.

**Type species.** *Sinoproscolia yangshuwanziensis* Zhang, Zhang, Rasnitsyn & Jarzembowski, 2015, by original designation.

**Comments.** Fossil taxon (Lower Cretaceous).

#### Sisakrosa Argaman, 1996

Sisakrosa Argaman, 1996: 204.

**Type species.** *Dielis angulata* Morawitz, 1888, by original designation.

**Comments.** *Dielis angulata* was treated as a subspecies of *Micromeriella hyalina* (Klug, 1832) by Betrem and Bradley (1972).

## Sobolpiha Argaman, 1996

Sobolpiha Argaman, 1996: 190.

Type species. Scolia ribbei Betrem, 1928, by original designation.

#### Sphenocampsomeris Bradley, 1957b

Campsomeris subgenus Sphenocampsomeris Bradley, 1957b: 76–77.

Type species. Dielis obesa Saussure, 1869, by original designation.

#### Stiboranna Argaman, 1996

Stiboranna Argaman, 1996: 198.

Type species. Scolia hova Saussure, 1891, by original designation.

#### Stigmatelis Betrem in Betrem & Bradley, 1972

Trielis subgenus Heterelis section Stigmatelis Betrem in Betrem & Bradley, 1972: 47.

Type species. Elis stigma Saussure, 1859, by original designation.

**Comments.** In order to simplify Betrem and Bradley's (1972) complex system of infra-generic divisions, *Stigmatelis* is here raised to a distinct subgenus of *Colpa* from *Heterelis*.

#### Stygocampsomeris Bradley, 1957b

Campsomeris subgenus Campsomeris section Stygocampsomeris Bradley, 1957b: 75.

Type species. Scolia servillei Guérin-Méneville, 1838, by original designation.

## Sugorpilfa Argaman, 1996

Sugorpilfa Argaman, 1996: 196.

Type species. Scolia philippinensis Rohwer, 1921, by original designation.

## Susaynata Argaman, 1996

Susaynata Argaman, 1996: 212.

Type species. Campsomeris cochinensis Betrem, 1928, by original designation.

## Tatusdayca Argaman, 1996

Tatusdayca Argaman, 1996: 208.

Type species. Scolia ephippium Say, 1837, by original designation.

## Tenebromeris Betrem, 1963

*Campsomeris* subgenus *Tenebromeris* Betrem, 1963: 71–72.

Type species. *Campsomeris tenebrica* Bradley, 1957a, by original designation.

## Tetrasciton Argaman, 1996

*Tetrasciton* Betrem, 1927a: 289 (*nomen nudum*). *Tetrasciton* Argaman, 1996: 204.

**Type species.** *Campsomeris aureicollis* Lepeletier de Saint-Fargeau, 1845, by original designation.

**Comments.** Argaman (1996) attributed *Tetrasciton* to Betrem (1927a), in which it appears as a *nomen nudum* only, possibly as an error for *Trisciloa*. As such, *Tetrasciton* as an available genus name must be attributed to Argaman himself. *Campsomeris aureicollis* was regarded as conspecific with *Campsomeriella collaris* (Fabricius, 1775) by Bradley (1964c).

# Tetrascolia Ashmead, 1903

Tetrascolia Ashmead, 1903: 8.

**Type species.** *Campsomeris urvillii* Lepeletier de Saint-Fargeau, 1845, by original designation.

**Comments.** *Campsomeris urvillii* was synonymised with *Scolia dimidiata* Guérin-Méneville, 1838, itself now a synonym of *Liacos analis* (Fabricius, 1804), by Betrem (1928).

## Titbisayda Argaman, 1996

Titbisayda Argaman, 1996: 213.

Type species. Campsomeris binghami Betrem, 1928, by original designation.

#### Tonsoygata Argaman, 1996

Tonsoygata Argaman, 1996: 192.

Type species. Scolia verticalis Fabricius, 1775, by original designation.

#### Torbesula Argaman, 1996

Torbesula Argaman, 1996: 211.

Type species. *Elis columba* Saussure, 1858, by original designation.

#### Trielis Saussure, 1863

*Triselis* Saussure, 1863: 18. *Triselis*—Schulz 1908: 464 (misspelling). *Triolis*—Micha 1927: 142 (misspelling).

## Type species. Elis xantiana Saussure, 1863, by monotypy.

**Comments.** Ashmead (1903) designated *Elis consanguinea* Saussure, 1855 as type species under the belief that *Trielis* had first been published by Saussure and Sichel (1864). The type status of *Trielis* was clarified by Betrem (1962a).

#### Triliacos Saussure & Sichel, 1864

Liacos subgenus Triliacos Saussure & Sichel, 1864: 33.

Type species. *Scolia dimidiata* Guérin-Méneville, 1838, by subsequent designation (Betrem 1928).

**Comments.** Scolia dimidiata was included in *Triliacos* by Saussure and Sichel (1864) as a synonym of *Liacos analis* (Fabricius, 1804), but is still eligible to be selected as type as an originally included nominal species, having been cited by an available name (ICZN Art. 67.2.1). *Triliacos* is therefore a junior objective synonym of

*Liacos* Guérin-Méneville, 1838. Argaman (1996), under the misapprehension that *S. dimidiata* was not eligible for selection, erroneously designated *Scolia erythrosoma* Burmeister, 1854 as type species.

## Trisciloa Gribodo, 1893

*Trisciloa* Gribodo, 1893: 146–147. *Tetrasciloa*—Betrem 1927b: xcv (misspelling).

Type species. Trisciloa saussurei Gribodo, 1893, by monotypy.

#### Triscolia Saussure, 1863

Scolia subgenus Triscolia Saussure, 1863: 17.

Type species. Scolia badia Saussure, 1863, by monotypy.

**Comments.** Bartlett (1912) nominated *Scolia flavifrons* Fabricius, 1775 as type species of *Triscolia*, believing the latter to have first been published by Saussure and Sichel (1864). However, *Triscolia* had earlier been used by Saussure (1863), in which *S. badia* is the only species included (Betrem and Bradley 1964).

#### Tristomeris Argaman, 1996

Campsomeris subgenus Tristomeris Bradley & Betrem, 1966: 81 (nomen nudum). Campsomeris subgenus Tristimeris Bradley & Betrem, 1967: 315 (nomen nudum). Tristimeris Betrem in Bradley, 1974b: 457 (nomen nudum). Tristomeris Argaman, 1996: 203.

**Type species.** *Campsomeris javana* Lepeletier de Saint-Fargeau, 1845, by original designation.

**Comments.** Bradley & Betrem used *Tristomeris* as a *nomen nudum* in 1966, in the combination '*Campsomeris* (*Tristomeris*) *javana*', and then with the spelling '*Tristimeris*' in 1967, in the combination '*Campsomeris* (*Tristimeris*) *bradleyi*'. Bradley (1974b) later used the *Tristimeris* spelling with the statement, "Tristimeris *is here introduced by Betrem as a new genus with the type-species* Campsomeris javana *Lepeletier*". Unfortunately, no description was provided for this new genus, meaning it remained a *nomen nudum*. The first author to provide a description and establish a type species was Argaman (1996) to whom the genus must be attributed. However, Argaman used '*Tristomeris*' in place of '*Tristimeris*', so the former must be the spelling used.

# Turbatimeris Betrem in Betrem & Bradley, 1972

Turbatimeris Betrem in Betrem & Bradley, 1972: 113–114.

**Type species.** *Turbatimeris turbata* Betrem in Betrem & Bradley, 1972, by original designation.

# Turturayca Argaman, 1996

Turturayca Argaman, 1996: 190.

Type species. *Scolia fulgidipennis* Smith, 1858, by original designation.

# Ululanca Argaman, 1996

Ululanca Argaman, 1996: 189.

Type species. Scolia nigrita Fabricius, 1782, by original designation.

# Uthakkara Argaman, 1996

Uthakkara Argaman, 1996: 202.

Type species. Campsomeris celebensis Betrem, 1928, by original designation.

# Vardombra Argaman, 1996

Vardombra Argaman, 1996: 198.

Type species. Scolia picteti Saussure, 1855, by original designation.

# Vobalayca Argaman, 1996

Vobalayca Argaman, 1996: 201.

Type species. Scolia hortorum Fabricius, 1787, by original designation.

# Wogungela Argaman, 1996

Wogungela Argaman, 1996: 198.

Type species. *Scolia micromelas* Sichel in Saussure & Sichel, 1864, by original designation.

# Xanthocampsomeris Bradley, 1957b

Campsomeris subgenus Xanthocampsomeris Bradley, 1957b: 70.

Type species. *Tiphia tricincta* Fabricius, 1775, by original designation.

# Xanthimeris Betrem in Betrem & Bradley, 1972

*Aureimeris* subgenus *Xanthimeris* Betrem in Betrem & Bradley, 1972: 262–263. *Xantimeris*—Osten 2005a: 3 (misspelling).

Type species. Elis xanthura Saussure, 1858, by original designation.

#### Xirgoniqua Argaman, 1996

Xirgoniqua Argaman, 1996: 196.

Type species. Scolia capitata Fabricius, 1804, by original designation.

## Ycasbraia Argaman, 1996

Ycasbraia Argaman, 1996: 192-193.

**Type species.** *Scolia rufiventris* Fabricius, 1804, by original designation. **Comments.** Junior objective synonym of *Hesperoscolia* Bradley, 1974b.

# Yohaida Argaman, 1996

Yohaida Argaman, 1996: 186.

Type species. Scolia klugii Linden, 1827, by original designation.

## Zazilayza Argaman, 1996

Zazilayza Argaman, 1996: 188.

**Type species.** *Triscolia haemorroidalis* [*sic*] var. *rubida* Gribodo, 1893, by original designation.

# Summary classification of Scoliidae

The current classification of Scoliidae is presented below as an aid to future research. For the most part, it corresponds to the classification used by Osten (2005a); where it differs, the reasons are discussed in the relevant catalogue entries above. Fossil taxa are marked with a dagger (†). Subgenera are indicated by the abbreviation 'subg.'

A recent molecular phylogenetic analysis of Scoliidae (Khouri et al. 2022) supported division of the family between Proscoliinae and Scoliinae, and mostly supported division of Scoliinae into Scoliini and Campsomerini. However, *Colpa* was placed sister to Scoliini rather than the remaining Campsomerini, raising the possibility of its reclassification. To reflect this possible distinction, Betrem and Bradley's (1972) 'Trielidini' (including *Colpa*) is recognised below as a subtribe Trielidina within Campsomerini. *Crioscolia* and *Guigliana* were not included in Khouri et al.'s (2022) analysis but are included in Trielidina following Betrem and Bradley (1972).

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†Archaeoscoliinae Rasnitsyn, 1993
    †Archaeoscolia Rasnitsyn, 1993
   †Cretoscolia Rasnitsyn, 1993
   †Floriscolia Rasnitsyn, 1993
   †Protoscolia Zhang, Rasnitsyn & Zhang, 2002
<sup>†</sup>Palaeoscoliinae Antropov in Antropov et al., 2014
   †Palaeoscolia Antropov in Antropov et al., 2014
Proscoliinae Rasnitsyn, 1977
   †Cretaproscolia Rasnitsyn & Martínez-Delclòs, 1999
   Proscolia Rasnitsyn, 1977
   †Sinoproscolia Zhang, Zhang, Rasnitsyn & Jarzembowski, 2015
Scoliinae Latreille, 1802
   Campsomerini Bartlett, 1912
       Campsomerina Bartlett, 1912
           (= Colpacampsomerini Argaman, 1996)
           (= Dasyscoliini Argaman, 1996)
           (= Dielidini Argaman, 1996)
           (= Dobrobetini Argaman, 1996)
           (= Megacampsomerini Argaman, 1996)
           (= Pseudotrielidini Argaman, 1996)
           (= Tetrascitonini Argaman, 1996)
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(= Trisciloini Argaman, 1996) Aelocampsomeris Bradley, 1957 Aureimeris Betrem in Betrem & Bradley, 1972 subg. Aureimeris Betrem in Betrem & Bradley, 1972 subg. Enigmatimeris Betrem in Betrem & Bradley, 1972 subg. Mansuetimeris Betrem in Betrem & Bradley, 1972 subg. Xanthimeris Betrem in Betrem & Bradley, 1972 Australelis Betrem, 1962a Bellimeris Argaman, 1996 Campsomeriella Betrem, 1941 subg. Annulimeris Betrem, 1967 (= *Phaleromeris* Argaman, 1996) subg. Campsomeriella Betrem, 1941 (= Iforborha Argaman, 1996) (= *Pupunhuga* Argaman, 1996) (= Tetrasciton Argaman, 1996) subg. Hirtimeris Betrem, 1967 subg. Madonimeris Betrem, 1967 subg. Rodriguimeris Betrem, 1967 Campsomeris Guérin-Méneville, 1838 (= *Hayderiba* Argaman, 1996) Cathimeris Betrem in Betrem & Bradley, 1972 subg. Cathimeris Betrem in Betrem & Bradley, 1972 (= *Catharinimeris* Argaman, 1996) (= *Dobrobeta* Argaman, 1996) subg. Garantimeris Betrem in Argaman, 1996 Charimeris Betrem in Betrem & Bradley, 1972 Colpacampsomeris Argaman, 1996 Dasyscolia Bradley, 1951 Dielis Saussure & Sichel, 1864 (= Haralambia Argaman, 1996) (= Oscalosca Argaman, 1996) Extrameris Betrem in Betrem & Bradley, 1972 Laevicampsomeris Betrem, 1933 (= Ilkamilka Argaman, 1996) Leomeris Betrem in Betrem & Bradley, 1972 Lissocampsomeris Bradley, 1957 (= Noybarilta Argaman, 1996) (= *Torbesula* Argaman, 1996) Megacampsomeris Betrem, 1928 (= *Borongorba* Argaman, 1996) (= *Fiharbuxa* Argaman, 1996) (= Lindenimeris Argaman, 1996) (= Susaynata Argaman, 1996)

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(= *Orlovinga* Argaman, 1996) (= *Pardesiya* Argaman, 1996) (= *Vobalayca* Argaman, 1996)

Subfamily incertae sedis

†Araripescolia Nel, Escuillie & Garrouste, 2013

# Conclusion

Thirty family-group names and 160 genus-group names are currently available for Scoliidae, including fossil taxa. Of these, 23 family-group names (77% of the total) and 73 genus-group names (46%) may be attributed to a single publication, Argaman (1996). A further 61 genus-group names (38%) were made available by Betrem and/or Bradley. Only 16% of available genus-group names in Scoliidae were not established by these three authors. Two genus-group names (*Micromeris* Betrem in Bradley and Betrem 1967, and *Guigliana* Argaman 1996) are invalid due to being preoccupied. One further name, *Ascoli* Saussure, 1855, is available but proposed for suppression due to its confused history and lack of general usage.

Subsequent authors have not accepted many of the taxa recognised by Argaman (1996). None of his family-group names are currently recognised as valid. Of those genera he proposed *de novo*, only one, *Rostopasca*, is provisionally accepted above, albeit only as a reflection of the uncertain classification of its type species. Nevertheless, twelve names attributed by Argaman (1996) to earlier authors must be regarded as published by Argaman himself due to the absence of earlier descriptions and/or their status as emendations. Three of these, *Bellimeris, Colpacampsomeris* and *Tristomeris*, have been accepted as valid by subsequent authors, though the correct spelling for the last name differs from that regularly used.

Recent years have seen an upswing of interest in scoliid systematics (Castagnet and Bitsch 2019; Castagnet 2021; Kim 2021; Liu et al. 2021b; Taylor and Barthélémy 2021; Ramírez-Guillén et al. 2022; Golfetti and Noll 2023). Khouri et al.'s (2022) phylogenetic analysis of the family, though preliminary, suggests that some genera as currently recognised may not be monophyletic. It is to be hoped that future revisions are able to avoid the nomenclatural pitfalls of the past.

# Acknowledgements

Thanks are due to Mark Harvey who provided nomenclatural advice, particularly regarding the challenging issue of *Ascoli*. Denis Brothers and Ivan Fernandes Golfetti provided invaluable criticism of the manuscript. Douglas Yanega also provided comments. I must also acknowledge the creators of the Biodiversity Heritage Library (https://www.biodiversitylibrary.org) who have made a study of this kind far more achievable than would have once been possible. This work has been funded by Australian Research Council (ARC) Laureate Fellowship (KG #FL210100103). The author has declared that no competing interests exist.

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CHECKLIST



# An annotated checklist of the bees of Washington state

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Academic editor: Jack Nef	f   Received 4 June 2024	Accepted 4 September 2024	Published 1 November 2024
	https://zoobank.org/95B34948	8-7979-418A-B325-215CCB7582	21F

Citation: Bartholomew CS, Murray EA, Bossert S, Gardner J, Looney C (2024) An annotated checklist of the bees of Washington state. Journal of Hymenoptera Research 97: 1007–1121. https://doi.org/10.3897/jhr.97.129013

#### Abstract

Bees (Hymenoptera: Apoidea) are vital components of global ecosystems, yet knowledge of their distribution is limited in many regions. Washington state is located in an ecologically diverse part of North America and encompasses habitat types and plant communities known for high bee species richness. To establish a baseline for future studies on bee communities in the state, we used published and unpublished datasets to develop a preliminary annotated checklist of bees occurring in Washington state. We document, with high confidence, 565 species of bees in Washington and identify an additional 102 species likely to occur in the state. We anticipate future research survey efforts, such as the newly initiated Washington Bee Atlas, will discover several species that have the potential to occur in Washington and provide new data for 84 species which have not been recorded in more than 50 years.

#### Keywords

Anthophila, Apoidea, faunal list, new state records, Pacific Northwest, pollinators

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# Introduction

Despite the global importance of bees and the risk of disrupting vital ecosystem services due to pollinator decline, our basic knowledge of many bee species is still limited (Brown and Paxton 2009; Winfree et al. 2011). Documenting regional bee faunas is essential for monitoring ecosystem health by providing a baseline for understanding changes in species composition at local and regional scales (Winfree et al. 2011; Mathiasson and Rehan 2019; Decker et al. 2020; Kilpatrick et al. 2020). Efforts to fill this gap have resulted in a push to document the bee fauna across the United States, with recent checklists and other biogeographic summaries published for Colorado (Scott et al. 2011), Indiana (Jean 2010), Illinois (Decker et al. 2020), Louisiana (Owens et al. 2018), Maine (Dibble et al. 2017), Massachusetts (Veit et al. 2021), Michigan (Gibbs et al. 2017), Minnesota (Portman et al. 2023), Oregon (Best et al. 2021, 2022), Pennsylvania (Kilpatrick et al. 2020), and Wisconsin (Wolf and Ascher 2009).

Washington state is located in the North American Pacific Northwest, an ecologically diverse region that encompasses wet, coastal forests, geologically active mountains, arid, interior forests, and extensive shrub-steppe plant communities (Franklin and Dyrness 1973). Increased population growth throughout the Puget Sound in the western part of state (Robinson et al. 2005; Zank et al. 2016) and widespread agriculture usage in the eastern part of the state has converted many native ecological communities to heavily modified anthropogenic landscapes (Daubenmire 1970). In fact, Daubenmire's (1970) efforts to characterize the pre-European vegetation of Washington's shrub-steppe communities found that most of eastern Washington had already been either heavily grazed by livestock or was already in cultivation after less than 100 years of colonization. The prominence of agriculture in eastern Washington is particularly of concern given that temperate grassland ecosystems are among the most threatened in the world (Lane et al. 2022) and xeric regions such as those east of the Cascade Mountain Range are associated with high bee diversity (Michener 1979; Cane 2011; Orr et al. 2021). For example, the Palouse Prairie in southeastern Washington state and adjacent Idaho is a critically endangered ecosystem, with native plant communities possibly occupying as little 1% of their historic range (Black et al. 1998; Looney and Eigenbrode 2012). Even so, Palouse prairie remnants have been shown to support many rare or endangered species such as ferruginous hawk, white-tailed jackrabbit, and sharp-tailed grouse despite high fragmentation and overall habitat loss (Black et al. 1998; Hanson et al. 2008; Looney and Eigenbrode 2012). Meanwhile, the central xeric regions are historically under-sampled and poorly known compared to the Puget Sound and the Palouse Prairie, despite expecting high bee diversity in such habitats.

It is therefore critical to establish a baseline of the species present to assess current regional species richness to inform future state-level conservation planning.

The objective of this checklist is to document the species currently encountered in Washington state, but it is interesting to note that the presence of bees in Washington has also been documented in the fossil record. A fossil of Bombus proavus was discovered during 1927–1928 in the Latah Formation (11.63 Ma to 5.333 Ma) near Spokane in Spokane County (Cockerell 1931), and plant fossils showing possible leaf cutter bee damage were discovered near Republic in Ferry County in the Klondike Mountain Formation (15.97 Ma to 11.63 Ma) (Lewis 1994). Several studies have been made of the bee fauna in parts of Washington, which collectively contribute to a baseline of species presence in the state, but there has yet been no synthesis of these records, or a checklist developed for the state. Contemporary lists perhaps begin with Viereck et al. (1904a; 1904b; 1904c; 1905; 1906) who summarized the known bee species of the Pacific Northwest in a series of five publications, including Washington, Oregon, and British Columbia. This established the first baseline of bee diversity in the region and reported 157 species at the time (although after accounting for synonymies this number drops to 116 species). The next comprehensive bee survey in Washington was not until Tepedino and Griswold (1995) published a technical report on the bees of the Columbia Basin, including parts of Washington, Oregon, and Idaho. They reported 647 species in the Columbia Basin, but emphasize that the area was under-sampled and estimate the actual number of species to be closer to 1000. Mayer et al. (2000) reported 72 species in a small area near the Snake River in southeastern Washington, although this did not include any *Lasioglossum* identified to species. Wilson et al. (2010) surveyed bees in the Tonasket Ranger District of Okanogan-Wenatchee National Forest (in north-central Washington), reporting 140 species. Hatten et al. (2013) published a list of the Bombus of the Palouse Prairie (including parts of Washington and Idaho) based on bycatch from pitfall traps and identifying ten species. Subsequent work by Rhoades et al. (2017) in the same areas resulted in a more comprehensive sample of the Palouse bee taxa, reporting 174 identified species and 36 undetermined morphospecies, 57 of which were new to the Palouse.

To obtain a baseline bee fauna of Washington state, data from these disparate studies and other literature records must first be compiled. Examination of museum specimens and collection of fresh material is also needed, especially in areas that are not previously well-studied. The objective of this checklist is to provide such a baseline for the state of Washington for use by the public, policymakers, and researchers to guide future research and conservation plans.

# Materials and methods

The checklist was compiled using online biodiversity database portals [Global Biodiversity Information Facility (GBIF; gbif.org) and Discover Life Global Mapper (discoverlife.org; Ascher and Pickering 2022)], specimens in private and institutional collections, and literature review. GBIF records were searched by selecting a coordinate polygon to include only Washington records (GBIF 2022a). Because not all Washington records have explicit geocoordinates associated with them, a second search was conducted using Washington as the state location (GBIF 2022b). Online records accessed by GBIF and Discover Life Global Mapper were obtained from various museum collections and the Barcode of Life Data System (BOLD; boldsystems.org; Ratnasingham and Hebert 2007) as well as citizen or community science records from citizen or community science portals iNaturalist, Bumble Bee Watch, and BugGuide. Table 1 presents a list of all private or institutional collections used to compile this checklist, accessed through GBIF, the Discover Life Global Mapper, or personal communications.

Data quality of records accessed through online biodiversity database portals such as GBIF and Discover Life Global Mapper can be inconsistent (Goodwin et al. 2015; Gibbs et al. 2017). Similarly, it is important to evaluate the accuracy of data collected from community science programs such as Bumble Bee Watch and BugGuide to determine their appropriate use (MacPhail et al. 2020). To ensure that this checklist is reasonably accurate, records were filtered to only include records from collections currently or previously managed by known bee experts, and community science submissions that were confirmed by known bee experts. Nonetheless, this contribution must be regarded as a preliminary checklist, as we were not able to verify every single record, and several entries warrant reassessment.

Literature sources were reviewed for any bees recorded from Washington. Not all such records include collection dates or locality data. Where possible, some of this information was inferred from the methods section. Records without county were georeferenced using the USGS Domestic Names Database (https://edits.nationalmap.gov/ apps/gaz-domestic/public/search/names). If the location could not be found by searching in the USGS domestic names database, we used other historical documents (e.g. antique maps) to identify the location in the state and then manually locate it on a map.

Species names are updated to match current taxonomy. Taxonomy generally follows the Integrated Taxonomic Information System (itis.gov) and Michener (2007), with the following exceptions: the higher-level classification of Apidae follows Bossert et al. (2019; 2020); the generic classification of Eucerini follows Freitas et al. (2023); the taxonomy for *Bombus* follows Williams (1998; and the regularly updated website *Bombus*: bumblebees of the world), Williams et al. (2014), Williams et al. (2015), Martinet et al. (2019), Ghisbain et al. (2020), and Lhomme et al. (2021); *Epeolus* follows Onuferko (2017); *Nomada* follows Droege et al. (2010), and *Brachymelecta* follows Onuferko et al. (2021). The *Andrena* subgenera classification follows Pisanty et al. (2022).

We based much of the structure and format of this list on the updated checklist of Pennsylvanian bees (Kilpatrick et al. 2020). The Washington checklist is organized alphabetically by family with each subsequent level (i.e., subfamily, tribe, genus, subgenus, and species) also organized alphabetically. Records for each species include, if available, the county where it was recorded, each month it was recorded as well as the most recent year it was recorded (in parentheses), the collection where specimens can be found, conservation status, and any floral and host associations noted in the literature and specific to Washington.

AMNH	American Museum of Natural History, New York, NY
BugGuide	BugGuide (bugguide.net)
OSUC	C. A. Triplehorn Insect Collection, Ohio State University, Columbus, OH
CAS	California Academy of Sciences, San Francisco, CA
CSCA	California State Collection of Arthropods, California Department of Food and Agriculture,
	Sacramento, CA
CMNH	Cleveland Museum of Natural History, Cleveland, OH
CNC	Canadian National Collection of Insects, Arachnids, and Nematodes, Agriculture Canada, Ottawa,
	Ontario, Canada
CUIC	Cornell University Insect Collection, Ithaca, NY
FMNH	Field Museum of Natural History, Chicago, IL
PSUC	Frost Entomological Museum, Penn State University, State College, PA
NMDG	Nate Green's Private Collection
INHS	Illinois Natural History Survey, University of Illinois, Champaign, IL
iNaturalist	iNaturalist (inaturalist.org)
JRYA	Jessica Rykken's Database
LACM	Los Angeles County Museum, Los Angeles, CA
Miliczky	Miliczky's Private Collection
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA
TTU	Museum of Texas Tech University, Lubbock, TX
UMNH	Natural History Museum of Utah, Salt Lake City, UT
NMNH	National Museum of Natural History, Smithsonian Institution, Washington, D.C. (formerly USNM,
	United States National Museum)
NMSU	New Mexico State Collection of Arthropods, Las Cruces, NM
NYSM	New York State Museum, Albany, NY
NCSU	North Carolina State University Insect Museum, Raleigh, NC
PCYU	Packer Collection, York University, Toronto, Ontario, Canada
PWRC	Patuxent Wildlife Research Center, US Geological Survey, Laurel, MD
ANSP	Philadelphia Academy of Natural Sciences, Philadelphia, PA
BBSL	Pollinating Insect – Biology, Management, Systematics Research Unit, Logan, UT
RSKM	Royal Saskatchewan Museum, Regina, Saskatchewan, Canada
RUAC	Rutgers University Entomological Museum, New Brunswick, NJ
TAMU	Texas A&M University Insect Collection, College Station, TX
Hanson	Thor Hanson's Private Collection
UCDC	University of California, Bohart Museum of Entomology, Davis, CA
EMEC	University of California, Essig Museum of Entomology, Berkeley, CA
UCRC	University of California, Riverside, CA
UCMC	University of Colorado Museum of Natural History, Boulder, CO
UCMS	University of Connecticut Insect Collection, Storrs, CT
SEMC	University of Kansas, Snow Entomological Museum Collection, Lawrence, KS
UNSM	University of Nebraska-Lincoln State Museum, Morrill Hall, Lincoln, NE
UNHC	University of New Hampshire Collection of Insects and Arthropods, Durham, NH
UNM	University of New Mexico, Museum of Southwestern Biology, Division of Arthropods, Albuquerque, NM
FWSE	U.S. Fish and Wildlife Service, Vancouver, WA
WFBM	University of Idaho, W. F. Barr Entomological Collection, Moscow, ID
WSDA	Washington State Department of Agriculture, Tumwater, WA
WSUC	Washington State University, M. T. James Entomological Collection, Pullman, WA
WWUC	Western Washington University Insect Collection, Bellingham, WA
BOMBUS	Xerces Society – Bumble Bee Watch

Table 1. List of collections and databases holding species records.

PMNH Yale University, Peabody Museum of Natural History, New Haven, CT

Records of subspecies are kept in the checklist as they were identified, but were only considered at the species level for purposes of calculating species richness. In some cases, the same records appear in multiple databases or literature sources (e.g. the same specimens may be referred to in a revision and again in a subsequent summary). Since this list is not quantitative at the species level, we did not attempt to address the "first" appearance per se or otherwise parse these duplicative instances, instead opting to report each dataset. Records that were not previously published in a peer-reviewed journal are treated as new state records and/or county records. A denotation of state record does not mean that we discovered the species through our own efforts, but rather that we highlight a digital record or database entry that we deem reliable, or that we present newly digitized information from the Washington State University M. T. James Entomological Collection (WSUC). Newly reported state records are denoted by a dagger symbol (†). Counties are listed in bold to denote new county records. We considered any species with a likely native range that does not include Washington state (e.g. species from Europe or known only from the eastern United States) to be introduced and denote them with an asterisk (\*).

When available conservation status was assessed using the International Union for Conservation of Nature (IUCN), NatureServe, and the Xerces Society Red List of Pollinating Insects of North America. Species categorized as critically endangered may have an extremely high risk of extinction, while species categorized as vulnerable may have a high risk of extinction. Species categorized as least concern do not meet the criteria for other categories and are generally not the target of conservation action. Species missing data critical for the determination of its conservation status are categorized as data deficient. A more detailed description of the criteria determining each category can be found in IUCN Red List Categories and Criteria: Version 3.1 (IUCN 2001). NatureServe assesses and assigns ranks for species and ecosystems at the global (G1 – G5) and state levels (S1 – S5) (NatureServe 2024). Ranks range from critically endangered (G1 and S1) to secure (G5 and S5). A more detailed description of how NatureServe assigns conservation status can be found at https://www.natureserve.org/ conservation-status-assessment (NatureServe 2024).

Some records were for species far outside of their known and expected range, with no known specimens or other information available to verify their accuracy. While these data contribute to an accurate account of species *recorded* in Washington, they could represent identification or labelling errors and seem less likely to occur in the state. Because this list may be used to inform conservation and research decisions, we placed such questionable records in a separate section to ensure that they are readily identifiable as unverified and caution readers to consider them in this context.

Expected species were determined from reviewing published species distribution maps that included Washington. Species with an expected distribution in Washington but no known records were highlighted as likely to occur in Washington. Additionally, species occurring near Washington in Oregon, Idaho, and/or British Columbia in habitats similar to those within Washington or with host plants occurring within Washington were also considered to likely occur in Washington. By these criteria, at least 120 additional species of bees are likely to occur in Washington. However, many specimens in museum collections await identification or formal description (Orr et al. 2021) and thus some of these species may already have been collected in the state. Currently undescribed species would add to this total expected species.

Additionally, an interactive map with county-level data and the option to map bee records by family is available online (https://phylosolving.shinyapps.io/WA\_bee\_catalog/) as a shiny app (Chang et al. 2024), which was created using leaflet (Cheng et al. 2024) in R (R Core Team 2023). The dataset is associated with this paper and is not intended to be updated; instead, these data and new records generated by the Washington Bee Atlas or other research will be migrated to a "living" interface that is currently being developed.

# **Results and discussion**

Using these data, we record 565 described species of bees in Washington State, representing 44 genera from all 6 families of bees known from North America (Table 2). The remaining bee family, Stenotritidae, is known only from Australia. We found records or data for 603 potential bee species in Washington state but removed 38 questionable records. *Andrena*, with 109 species, had the highest species richness of any genus in Washington state, comprising 20% of the total species. This is not surprising, as *Andrena* is known to be species rich in temperate bee communities of North America (e.g., Kilpatrick et al. 2020; Rhoades et al. 2018). As an example, 12% of the observed species in a survey of just montane areas of north-central Washington were *Andrena* (Wilson et al. 2010; Rhoades et al. 2018).

Ground nesting species frequently outnumber other bee groups in regional bee faunas (Cane 2008), and Washington's fauna is no exception (Fig. 1; see Suppl. material 1 for all the life history data for each species). Most Washington bees with known or presumed ecological data are ground nesting (254 species), followed by cavity nesting species (180 species). Some Megachile species are known to nest in cavities in the ground as well as excavate nests in the ground (Michener 2007). The literature is not always clear on this point, and some of these species may actually be cavity nesting instead of ground nesting and vice versa. Washington's bee fauna is primarily solitary (380 species) as are most species globally (Danforth et al. 2019), followed by cleptoparasites (90 species), social species (33 species), and social parasites (4 species). Floral preference is unknown for many of Washington's bees. However, for those with known floral preference data, Washington's bee fauna appears to be more polylectic (163 species) than oligolectic (110 species). Notable among the solitary ground nesting species found in Washington is the alkali bee, Nomia melanderi Cockerell, which is of considerable agricultural importance as an alfalfa pollinator (Cane 2008). Known for being the only managed solitary groundnesting species of bee in the world, large aggregations of N. melanderi can be found in Walla Walla County where nesting beds consisting of moist silty and periodically salted soils have been maintained and protected for decades (Cane 2008; Kapheim et al. 2021; Cane 2024), including reduced local speed limits to minimize mortality (Vinchesi 2014). Other notable native Washington solitary bees include the mason bees Osmia aglaia Sandhouse, O. atriventris Cresson, and O. lignaria Say, all of which are important raspberry pollinators (Drummond and Stubbs 1997; Andrikopoulos and Cane 2018).

Andrenidae	Andrena	109 (1)	Halictidae	Agapostemon	3
	Calliopsis	4		Dufourea	5
	Panurginus	3		Halictus	6
	Perdita	9		Lasioglossum	63 (4)
	Total	124 (1)		Nomia	1
				Sphecodes	8
				Total	84 (4)
Apidae	Anthophora	15	Megachilidae	Anthidiellum	2
-	Apis	1 (1)	-	Anthidium	11 (2)
	Bombus	25 (1)		Ashmeadiella	8
	Brachymelecta	1		Atoposmia	2
	Ceratina	5		Chelostoma	2
	Diadasia	6		Coelioxys	8
	Epeolus	6		Dianthidium	7
	Epimelissodes	1		Dioxys	4
	Eucera	10		Heriades	4
	Habropoda	4		Hoplitis	12
	Melecta	3		Megachile	31 (3)
	Melissodes	23		Osmia	70 (2)
	Nomada	35		Protosmia	1
	Oreopasites	1		Stelis	15
	Triepeolus	8		Total	177 (7)
	Xylocopa	1(1)			
	Zacosmia	1			
	Total	150 (3)			
Colletidae	Colletes	14	Melittidae	Macropis	1
	Hylaeus	16 (2)		Total	1
	Total	30 (2)			

**Table 2.** Bee species recorded from Washington state, not including questionable records. The number of introduced species is indicated in parentheses.



**Figure 1.** Total number of Washington bees with known ecological data by lifestyle, nesting preference, and floral preference.
The peak of bee activity in Washington statewide is between April and September with Megachilidae being the most species rich during this period (Fig. 2a). However, some species of Andrenidae, Apidae, and Megachilidae are active throughout the year. When comparing the seasonality geographically, Andrenidae has a higher peak in the spring on the west side of the Cascades indicating that the west side has more species of spring flying Andrenidae than the east side (Fig. 2b, c). Also, the Apidae peak earlier in the season on the west side than the east side. Different bee taxa vary in their seasonality (Oglivie and Forrest 2017). *Andrena*, except the subgenera *Callandrena* and *Cnemidandrena*, are mostly early spring species (LaBerge 1986b; Larkin et al. 2008; Oglivie and Forrest 2017). Most *Osmia* (Megachilidae) are also spring species; in contrast, *Megachile* spp. tend to be more active in the late summer (Oglivie and Forrest 2017).

Most of Washington is under sampled for bees (Figs 3, 4). The number of species by county almost certainly reflects which parts of the state have been more heavily sampled than others, rather than the actual species richness of that county (Fig. 5). Counties with more than 100 documented species (e.g., Benton, Chelan, King, Kittitas, Klickitat, Okanogan, Pierce, Spokane, Thurston, Walla Walla, Whitman, and Yakima Counties) are also home to Washington's largest cities and/or popular recreational areas and are more likely to have documented citizen or community scientist records. In addition, some of these same counties (e.g., Okanogan and Whitman Counties) were locations of research projects targeting bee biodiversity.

Washington is an ecologically diverse state, with the Cascade Mountains separating the western coastal forests from the arid interior forests and shrub-steppe to the east (Franklin and Dyrness 1973). According to EPA's Level III and IV Ecoregions of Washington map, the state has nine Level III ecoregions and 57 Level IV ecoregions (US Environmental Protection Agency 2012). The Columbia Plateau, located east of the Cascade Mountains, has the highest richness of bee species (Table 3; see Suppl. material 2 for species by ecoregion). Additionally, nine of the 44 genera in this dataset have been recorded from only east of the Cascade Mountains (Fig. 6), although some of these will likely be detected in western Washington in future surveys. Even so, we expect that some genera are indeed restricted to eastern Washington. For example, Zacosmia is a genus of cleptoparasites whose hosts (Anthophora (Micranthophora)) are associated with xeric or semi-xeric habitats (Michener 2007; Orr et al. 2018). No genus was recorded from only the west side of the state in the records we reviewed. Orr et al. (2021) found bee species richness was greatest in regions characterized by high solar insolation, high average potential evapotranspiration, low precipitation during the driest month, and decreased seasonal variation. Additionally, tree presence negatively impacted bee richness (Orr et al. 2021). As the Columbia Plateau meets these conditions, it is unsurprising that there is more species richness as well as more unique species in this ecoregion compared to the ecoregions west of the Cascade Mountains, where there are more trees and precipitation.



**Figure 2.** Seasonality of Washington bee species by family for **A** Washington state **B** east of the Cascade Mountains, and **C** west of the Cascade Mountains, based on collection or observation dates from records reviewed for this checklist.



**Figure 3.** Map of the records for all families, excluding *Apis mellifera* and *Bombus* spp. This map was built in QGIS using a Level IV Shapefile from EPA as a basemap.



**Figure 4.** Map of the records for *Apis mellifera* and *Bombus* spp. This map was built in QGIS using a Level IV Shapefile from EPA as a basemap.



**Figure 5.** Bee species richness for each of the 39 counties of Washington. Whitman county in eastern Washington has the most recorded species (288), while Wahkiakum in western Washington has the least (16). This interactive map with additional county-level data and the option to filter records by family is available at: https://phylosolving.shinyapps.io/WA\_bee\_catalog/. This map was built in Leaflet (http://agafonkin.com/en/) using tiles from USGS.

EPA Level III Ecoregion	Number of Species				
Blue Mountains	32				
Cascades	74				
Coast Range	66				
Columbia Plateau	399				
Eastern Cascades Slopes and Foothills	157				
North Cascades	160				
Northern Rockies	139				
Puget Lowlands	213				
Willamette Valley	35				

Table 3. The number of bee species recorded in each EPA Level III Ecoregion.

Eighty-four species (15%) on this list have not been documented in the state since before 1970, with more than 80% of these from eastern Washington. More than a quarter of these species are cleptoparasites. In fact, nearly half of the recorded species of the cleptoparasitic genus *Nomada* haven't been reported in decades. Of the 84 species not documented in over 50 years, 16 are only known from their type specimens, 10 of which are cleptoparasites. Notable among these 16 species is the *Lysimachia* (loosestrife) specialist *Macropis steironematis opaca*, the single representative of Melittidae in Washington state. This species has not been sighted since 1882 when it was collected from Morgan's Ferry along the Yakima River, despite focused survey efforts in



**Figure 6.** Map of the genera only recorded on the east side of the Cascade Mountains. This map was built in QGIS using a Level IV Shapefile from EPA as a basemap.

recent decades. *Macropis* are ecologically unusual in that they collect floral oils from *Lysimachia* spp. for nest provisioning as well as for lining nest cell walls (Cane et al. 1983; Michez and Patiny 2005; Packer 2023).

Of the 158 bee species with a federally and/or state determined conservation status, Washington has 42 bee species that have been determined to have a conservation status of vulnerable, imperiled or critically imperiled or endangered by organizations such as IUCN, the Xerces Society, and NatureServe (Table 4). Included are the following six species which have not been documented in the state in more than 50 years: *Andrena aculeata, Perdita similis pascoensis, Megachile legalis, Osmia lanei, O. nigrobarbata*, and *Macropis steironematis opaca*. Currently, the Washington Department of Fish and Wildlife State Wildlife Action Plan only identifies *Bombus morrisoni, B. occidentalis*, and *B. suckleyi* as species of greatest conservation need (SGCN) (Washington Department of Fish and Wildlife 2015). Future research should focus on determining the conservation needs of the remaining 39 species of possible conservation concern as well as the 407 species without conservation status determination. Nesting and floral resources are such vital components of bee survival, yet this data is lacking for so many species making it difficult to assess conservation statuses (Orr et al. 2022).

The bee fauna of Washington state is more species rich than its northern neighbor British Columbia, which has 483 documented species (Sheffield and Heron 2018). Future studies of Washington's more under-surveyed counties, such as Adams, Douglas, Franklin, Grant, and Lincoln in the Columbia Plateau as well as the 22 other counties with fewer than 100 documented species (Fig. 5), will add to this documented richness.

**Table 4.** Species with conservation statuses of possible conservation concern. CE = critically endangered and Vul = vulnerable (National Research Council); G2 = imperiled, G3 = vulnerable, S1 = critically imperiled, S2 = imperiled, S3 = vulnerable (NatureServe 2024).

Family	Species	CE	Vul	G2	G3	<b>S1</b>	<b>S2</b>	<b>S</b> 3
Andrenidae	Andrena aculeata		Х					
	Perdita similis pascoensis		Х					
	Perdita wyomingensis sculleni		Х					
Apidae	Anthophora crotchii				Х			
	Anthophora neglecta				Х			
	Anthophora occidentalis				Х			
	Bombus appositus				Х			
	Bombus caliginosus		Х	Х				Х
	Bombus fervidus complex		Х		Х			
	Bombus flavidus							Х
	Bombus frigidus						Х	
	Bombus insularis				Х			
	Bombus kirbiellus					Х		
	Bombus lapponicus sylvicola							Х
	Bombus morrisoni		Х		Х			
	Bombus occidentalis		Х		Х		Х	
	Bombus suckleyi	Х		Х		Х		
	Bombus vagans						Х	
	Bombus vandykei							Х
	Eucera douglasiana		Х					
	Eucera frater lata		Х					
	Habropoda miserabilis			Х				
Megachilidae	Anthidium banningense				Х			
Ū.	Anthidium edwardsii				Х			
	Hoplitis orthognatha		Х					
	Hoplitis producta subgracilis		Х					
	Megachile anograe				Х			
	Megachile dentitarsus				Х			
	Megachile legalis				Х			
	Megachile nevadensis				Х			
	Megachile snowi				Х			
	Megachile umatillensis				Х			
	Osmia austromaritima				Х			
	Osmia iridis				Х			
	Osmia lanei				X*			
	Osmia nigrobarbata				Х			
	Osmia obliqua				Х			
	Osmia odontogaster			Х				
	Osmia pulsatillae			Х				
	Osmia thysanisca				Х			
	Osmia trifoliama				X*			
Melittidae	Macropis steironematis opaca	Х						

\* possibly extirpated in Washington (NatureServe 2024).

Based on recent records of bees from adjacent states and British Columbia, we anticipate at least another 102 species are likely to be recorded in Washington state making the species richness more comparable to the nearly 700 species expected to occur in Oregon (Best et al. 2022). Future efforts should also target the 84 species that have not

been documented in over 50 years. It is likely many of these species have been undetected over time due to characteristics that make them inherently uncommon such as limited distributions, floral specialization, cleptoparasitic habits, or difficulty in identification (Colla et al. 2012). There are also many specimens in museum and private collections that, due to various reasons, are still waiting for identification or for formal species descriptions (Orr et al. 2021). As museums work towards digitizing their collections, some of these long-absent species may be rediscovered and new species may be detected or even described. Cleptoparasitic bee species have been found to be good indicator taxa for assessing bee communities (Sheffield et al. 2013a, 2013b), so determining the status of these missing cleptoparasitic species will help future assessments of the bee community health in Washington state.

# Checklist

Sources used to compile this checklist: <sup>1</sup>GBIF (polygon); <sup>2</sup>GBIF (without coordinates); <sup>3</sup>Ascher and Pickering 2022 (Discover Life); <sup>4</sup>Ratnasingham and Hebert 2007 (BOLD); <sup>5</sup>Hanson Collection; <sup>6</sup>WSDA; <sup>7</sup>WSUC; <sup>8</sup>Mayer et al. 2000; <sup>9</sup>Rozen 1992; <sup>10</sup>Fabian 2014; <sup>11</sup>LaBerge 1980; <sup>12</sup>LaBerge 1973; <sup>13</sup>LaBerge 1989; <sup>14</sup>LaBerge and Ribble 1975; <sup>15</sup>LaBerge 1986a; <sup>16</sup>LaBerge 1985; <sup>17</sup>LaBerge 1977; <sup>18</sup>Bouseman and LaBerge 1978; <sup>19</sup>LaBerge 1969; <sup>20</sup>LaBerge and Ribble 1972; <sup>21</sup>LaBerge and Bouseman 1970; <sup>22</sup>Hanson and Ascher 2018; <sup>23</sup>Miliczky 2008; <sup>24</sup>Mitchell 1935a; <sup>25</sup>Mitchell 1937a; <sup>26</sup>Mitchell 1937b; <sup>27</sup>Mitchell 1935b; <sup>28</sup>Mitchell 1937c; <sup>29</sup>Mitchell 1936a; <sup>30</sup>Mitchell 1936b; <sup>31</sup>Rightmyer et al. 2010; <sup>32</sup>Rhoades et al. 2017; <sup>33</sup>Looney et al. 2019; <sup>34</sup>Michener 1935; <sup>35</sup>Linsley 1939; <sup>36</sup>Adlakha 1969; <sup>37</sup>Stephen 1952; <sup>38</sup>Gibbs 2010; <sup>39</sup>Roberts 1973; <sup>40</sup>Sinha and Michener 1958; <sup>41</sup>Gonzalez and Griswold 2013; <sup>42</sup>Michener 1938a; <sup>43</sup>Michener 1938b; <sup>44</sup>Michener 1939; <sup>45</sup>Michener 1938c; <sup>46</sup>Clement et al. 2006; <sup>47</sup>Koch et al. 2017; <sup>48</sup>Timberlake 1971; <sup>49</sup>LaBerge 1961; <sup>50</sup>Cockerell 1906a; <sup>51</sup>Cockerell 1911; <sup>52</sup>Cockerell 1904; <sup>53</sup>Timberlake 1943; <sup>54</sup>Timberlake 1951; <sup>55</sup>Snelling 1970; <sup>56</sup>Gibbs 2011; <sup>57</sup>McGinley 2003; <sup>58</sup>Daly 1973; <sup>59</sup>Wilson et al. 2010; <sup>60</sup>Ribble 1974; <sup>61</sup>Thompson and Pellmyr 1992; <sup>62</sup>Thorp 1969; <sup>63</sup>Ribble 1968; <sup>64</sup>Onuferko and Sheffield 2022; <sup>65</sup>Droege et al. 2010; <sup>66</sup>Timberlake 1958; <sup>67</sup>Timberlake 1968; <sup>68</sup>Ghisbain et al. 2020; <sup>69</sup>Koch et al. 2016; <sup>70</sup>Strange and Tripodi 2019; <sup>71</sup>Shapiro et al. 2014; <sup>72</sup>LaBerge 1956a; <sup>73</sup>Onuferko 2017; <sup>74</sup>Onuferko 2018; <sup>75</sup>Rightmyer 2008; <sup>76</sup>Cockerell 1910; <sup>77</sup>Rodeck 1947; <sup>78</sup>Cane 2008; <sup>79</sup>Gardner and Gibbs 2020; <sup>80</sup>Gibbs et al. 2013; <sup>81</sup>McGinley 1986; <sup>82</sup>Bohart 1948; <sup>83</sup>Snelling 1966; <sup>84</sup>Stephen 1954; <sup>85</sup>Donovan 1977; <sup>86</sup>Thorp and LaBerge 2005; <sup>87</sup>Crawford 1926; <sup>88</sup>Timberlake 1956; <sup>89</sup>Timberlake 1964; <sup>90</sup>Baker 1975; <sup>91</sup>Grigarick and Stange 1968; <sup>92</sup>Mitchell 1944; <sup>93</sup>Raw 2002; <sup>94</sup>Mitchell 1942; <sup>95</sup>Mitchell 1927; <sup>96</sup>Hurd and Michener 1955; <sup>97</sup>Michener 1936a; <sup>98</sup>Swenk 1914; <sup>99</sup>Mitchell 1933; <sup>100</sup>Sandhouse 1939; <sup>101</sup>White 1952; <sup>102</sup>Griswold 1983; <sup>103</sup>Michener 1947; <sup>104</sup>Rowe 2017; <sup>105</sup>Thorp et al. 1983; <sup>106</sup>Brooks 1983; <sup>107</sup>Orr et al. 2018; <sup>108</sup>La-Berge 1956b; <sup>109</sup>Timberlake 1969; <sup>110</sup>Broemeling 1988; <sup>111</sup>Rodeck 1949; <sup>112</sup>Tepedino and Griswold 1995; <sup>113</sup>Viereck 1916; <sup>114</sup>Cockerell 1937; <sup>115</sup>Viereck et al. 1904a; <sup>116</sup>Viereck et al. 1904b; <sup>117</sup>Viereck et al. 1904c; <sup>118</sup>Viereck et al. 1905; <sup>119</sup>Viereck et al. 1906; <sup>120</sup>Cockerell 1903; <sup>121</sup>Cockerell 1906b; <sup>122</sup>Gardner and Gibbs 2023; <sup>123</sup>Rozen 1958; <sup>124</sup>National Park Service (personal communication); <sup>125</sup>Michener 1936b; <sup>126</sup>Swenk 1908; <sup>127</sup>Cockerell 1913; <sup>128</sup>Akre et al. 1982; <sup>129</sup>Cockerell 1912; <sup>130</sup>Taylor 2008; <sup>131</sup>Mitchell 1938; <sup>132</sup>Zack 1984; <sup>133</sup>Waters 2023; <sup>134</sup>Miliczky 2000; <sup>135</sup>Green Collection; <sup>136</sup>Combs 2019

- † State record
- \* Introduced
- **§** Species of possible conservation concern
- # Most recent record before 1970

### Andrenidae: Andreninae: Andrenini

### Genus Andrena Fabricius

- \$‡ Andrena (Andrena) aculeata LaBerge, 1980. County records: Whitman<sup>11</sup>. Seasonality: May<sup>11</sup> (1913<sup>11</sup>). Conservation status: Vulnerable (Shepherd 2005a, National Research Council 2007)
- **2.** ‡ *Andrena* (*Andrena*) *birtwelli* Cockerell, 1901. County records: Kittitas<sup>1,2,11</sup>. Seasonality: Jul<sup>1,2</sup> (1949<sup>1,2</sup>). Collections: SEMC
- **3.** *Andrena* (*Andrena*) *buckelli* Viereck, 1924. County records: Garfield<sup>1,2,3,46</sup>, Kittitas<sup>1,2,11</sup>, Whitman<sup>7,11</sup>. Seasonality: May<sup>1,2,3</sup>, Jun<sup>7,46</sup>, Jul<sup>1,2</sup> (1989<sup>1,2,3</sup>). Collections: BBSL, SEMC, WSUC. Floral records: FABACEAE: *Astragalus* sp.<sup>3</sup>
- **4.** Andrena (Andrena) ceanothifloris cretata LaBerge, 1980. County records: Okanogan<sup>1,2,3,59</sup>. Seasonality: Jul<sup>1,2,3</sup> (2004<sup>1,2,3,59</sup>). Collections: BBSL. Floral records: ERICACEAE: Ledum glandulosum<sup>3,59</sup>
- 5. Andrena (Andrena) frigida Smith, 1853. County records: King<sup>1,2,3,11,117</sup>, Kit-sap<sup>2,3,11</sup>, Pend Oreille<sup>3,11</sup>, Pierce<sup>3,11</sup>, Snohomish<sup>3,11</sup>, Walla Walla<sup>3</sup>, Whitman<sup>3,11,117</sup>, Yakima<sup>3,11</sup>. Seasonality: Feb<sup>117</sup>, Mar<sup>1,2,3,117</sup>, Apr<sup>2,3</sup>, Jul<sup>2</sup> (1996<sup>1,2</sup>). Collections: INHS, NYSM, UNHC, UCRC, WSUC. [= Cilissa albihirta Ashmead, 1890]
- 6. Andrena (Andrena) hemileuca Viereck, 1904. County records: Ferry<sup>3,11</sup>, Island<sup>7</sup>, King<sup>1,2,3,7,11,117</sup>, Kitsap<sup>3,11</sup>, Lewis<sup>7</sup>, Pierce<sup>3,11</sup>, Skagit<sup>10</sup>, Snohomish<sup>1,2,3</sup>, Thurston<sup>133</sup>, Whitman<sup>3,11,117</sup>. Seasonality: Apr<sup>7</sup>, May<sup>1,2,3,7,133</sup> (2017<sup>133</sup>). Collections: ANSP, INHS, NMNH, SEMC, WSUC, WWUC. Holotype. USA, Washington Territory; PANS 10286. [= Andrena (Andrena) asmi Viereck, 1904]. Holotype. USA, Washington, Whitman County, Pullman; C. V. Piper. Floral records: ASPARA-GACEAE: Camassia quamash<sup>133</sup>; ROSACEAE: Sorbus scopulina<sup>8</sup>.
- 7. ‡ Andrena (Andrena) jennei Viereck, 1916. County records: Yakima<sup>1,2,3,113</sup>. Seasonality: May<sup>1,2,113</sup> (1903<sup>1,2,113</sup>). Collections: ANSP. Holotype. USA, Washington, Yakima County, North Yakima; 20 May 1903; Eldred Jenne; No. 60, ANSP 4013
- 8. † *Andrena* (*Andrena*) *laminibucca* Viereck and Cockerell, 1914. County records: Jefferson<sup>1,2</sup>, Kittitas<sup>2,3</sup>. Seasonality: May<sup>2,3</sup>, Jun<sup>1,2</sup> (2014<sup>1,2</sup>). Collections: BBSL, INHS

- 9. † Andrena (Andrena) macoupinensis Robertson, 1900. County records: Benton<sup>2,3,7</sup>, Kittitas<sup>2,3</sup>, Yakima<sup>2,3</sup>, Whitman<sup>7</sup>. Seasonality: Apr<sup>2,3,7</sup> (1989<sup>2,3</sup>). Collections: INHS, WSUC
- 10. Andrena (Andrena) milwaukeensis Graenicher, 1903. County records: Chelan<sup>1,2</sup>, Kittitas<sup>7</sup>, Klickitat<sup>1,2</sup>, Lewis<sup>1,2,4</sup>, Spokane<sup>1,2,7</sup>, Thurston<sup>133</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,4</sup>, June<sup>133</sup> (2019<sup>133</sup>). Collections: BBSL, RSKM, WSUC. Floral records: FABACEAE: Lupinus albicaulis<sup>133</sup>
- 11. Andrena (Andrena) perarmata Cockerell, 1898. County records: King<sup>1,2,3,11</sup>, Kitsap<sup>2,3</sup>, Kittitas<sup>2,3</sup>, Pierce<sup>3,11</sup>, Thurston<sup>3,7,11</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>7,8</sup>, Yakima<sup>3,11</sup>. Seasonality: Feb<sup>1,2</sup>, Mar<sup>1,2,3,7,11</sup>, Apr<sup>1,2,3</sup> (1989<sup>2,3</sup>). Collections: BBSL, INHS, NMNH, WSUC. Holotype. USA, Washington, King County, Seattle; 15 March 1897; USNM 18982, USNM ENT 00533688. Floral records: API-ACEAE: Lomatium<sup>8</sup>
- **‡** Andrena (Andrena) prolixa LaBerge, 1980. County records: Pierce<sup>1,2,3,11</sup>. Seasonality: Apr<sup>1,2,11</sup> (1945<sup>1,2,11</sup>). Collections: INHS
- 13. Andrena (Andrena) rufosignata Cockerell, 1902. County records: Clallam<sup>1,2,3,11</sup>, King<sup>1,3,11</sup>, Okanogan<sup>1,2,3,59</sup>, Pierce<sup>3,11</sup>, Thurston<sup>133</sup>, Whatcom<sup>1,2</sup>. Seasonality: May<sup>1,2,133</sup>, Jun<sup>1,2,3,133</sup>, Jul<sup>1,2,3</sup> (2020<sup>133</sup>). Collections: BBSL, INHS, OSUC, SEMC. Floral records: APIACEAE: Lomatium pugetensis<sup>133</sup>; ASPARAGACEAE: Camassia quamash<sup>133</sup>; BORAGINACEAE: Myosotis laxa<sup>59</sup>; CAPRIFOLIACEAE: Symphoricarpos albus<sup>133</sup>; ERICACEAE: Phyllodoce empetriformis<sup>3,59</sup>; OROBANCHAECE-AE: Pedicularis bracteosa var. latifolia<sup>59</sup>; ROSACEAE: Potentilla gracilis<sup>133</sup>
- 14. Andrena (Andrena) saccata Viereck, 1904. County records: Clallam<sup>1,2,3,11</sup>, Grays Harbor<sup>3,11</sup>, King<sup>1,2,3,11,117</sup>, Pacific<sup>3,11</sup>, Pierce<sup>1,2,3</sup>, Snohomish<sup>2,3</sup>, Walla Walla<sup>1,2,3</sup>. Seasonality: Apr<sup>117</sup>, May<sup>1,2</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>2,3</sup> (1975<sup>1,2,3</sup>). Collections: BBSL, INHS, OSUC
- 15. † Andrena (Andrena) schuhi LaBerge, 1980. County records: Spokane<sup>1,2</sup>, Whitman<sup>1,2,3,7</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>7</sup>, May<sup>1,2,7</sup> (2011<sup>1,2</sup>). Collections: BBSL, SEMC, WSUC
- 16. Andrena (Andrena) thaspii Graenicher, 1903. County records: Chelan<sup>3,11</sup>, Clallam<sup>3,11</sup>, Columbia<sup>1,2,3,11</sup>, Garfield<sup>11</sup>, Island<sup>11</sup>, Jefferson<sup>1,2,3,11</sup>, King<sup>1,2,3,11</sup>, Kittitas<sup>2,3</sup>, Pierce<sup>11</sup>, San Juan<sup>11</sup>, Skagit<sup>1,2,3,11</sup>, Snohomish<sup>2,3</sup>, Thurston<sup>1,2,3,11,117,133</sup>, Whitman<sup>3,11</sup>, Yakima<sup>3,11</sup>. Seasonality: Jun<sup>1,2,3,117,133</sup>, Jul<sup>1,2,3</sup>, Aug<sup>2,3</sup> (2020<sup>133</sup>). Collections: AMNH, ANSP, BBSL, INHS, NMNH. [= Andrena clypeoporaria Viereck, 1904]. Holotype. USA, Washington, Thurston County, Olympia; 12 June 1895; PANS 10290. [= Andrena indotata Viereck, 1904]. Holotype. USA, Washington State; PANS 10295. Floral records: CAPRIFOLIACEAE: Symphoricarpos albus<sup>133</sup>; FA-BACEAE: Lupinus albicaulis<sup>133</sup>
- 17. Andrena (Andrena) topazana Cockerell, 1906. County records: Asotin<sup>3,11</sup>, Columbia<sup>3,11</sup>, Okanogan<sup>1,2,3,59</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>7</sup>. Seasonality: Jun<sup>1,2,3</sup>, Jul<sup>1,2,7</sup>, Aug<sup>1,2,3</sup> (2004<sup>1,2,3,59</sup>). Collections: BBSL, WSUC. Floral records: ASTER-ACEAE: Achillea millefolium<sup>59</sup>, Cirsium arvense<sup>8</sup>; ROSACEAE: Potentilla gracilis<sup>59</sup>, Rosa nutkana ssp. nutkana<sup>3,59</sup>

- 18. Andrena (Andrena) vicinoides Viereck, 1904. County records: Asotin<sup>3,11</sup>, Clallam<sup>3,11</sup>, Island<sup>7</sup>, King<sup>3,11</sup>, Kitsap<sup>3,7,11</sup>, Okanogan<sup>1,2,3,59</sup>, Pacific<sup>3,11</sup>, Pierce<sup>3,7,11</sup>, San Juan<sup>1,2,11,124,136</sup>, Skagit<sup>1,2,3,11,124</sup>, Thurston<sup>3,11,117</sup>, Whitman<sup>3,11</sup>. Seasonality: May<sup>1,2,7</sup>, Jun<sup>1,2,3,117</sup>, Jul<sup>1,2,3,7</sup> (2017<sup>136</sup>). Collections: BBSL, PWRC, WSUC. Floral records: FABACEAE: Lupinus sericeus<sup>59</sup>; ROSACEAE: Potentilla gracilis<sup>59</sup>, Rosa nutkana<sup>136</sup>
- 19. Andrena (Andrena) washingtoni Cockerell, 1901. County records: Clallam<sup>3</sup>, Douglas<sup>1,2,3</sup>, King<sup>3,11,117</sup>, Pierce<sup>1,2,3,11</sup>, Skamania<sup>3,11</sup>, Thurston<sup>1,3,11,117</sup>. Seasonality: Apr<sup>117</sup>, May<sup>1,2,3,117</sup>, Jun<sup>1,3,11,117</sup>, Jul<sup>3</sup> (2014<sup>3</sup>). Collections: BBSL, INHS, JRYA, NMNH. Holotype. USA, Washington, Thurston County, Olympia; 2 June 1895; Type No. 18938, USNM ENT 00533758
- 20. ‡ Andrena (Callandrena sensu lato) helianthi Robertson, 1891. County records: Whitman<sup>8</sup>. Seasonality: (1962–1963<sup>8</sup>). Collections: WSUC. Floral records: ASTERACEAE: Helianthus annuus<sup>8</sup>, Solidago canadensis<sup>8</sup>. Comments: Phylogenetic analyses (Larkin et al. 2006; Pisanty et al. 2021) have found the subgenus Callandrena to be paraphyletic. Callandrena in its strict sense was found to be monophyletic (Larkin et al. 2006; Pisanty et al. 2021). The remaining species, including A. helianthi, belong to another separate unnamed group that is sometimes referred to as Callandrena sensu lato.
- **21.** † *Andrena* (*Cnemidandrena*) *colletina* Cockerell, 1906. County records: Klickitat<sup>2,3</sup>. Seasonality: Sep<sup>2,3</sup> (1989<sup>2,3</sup>). Collections: INHS
- 22. Andrena (Cnemidandrena) columbiana Viereck, 1917. County records: Benton<sup>7</sup>, Clallam<sup>3</sup>, Island<sup>3,85</sup>, Jefferson<sup>1,2</sup>, King<sup>3,85</sup>, Okanogan<sup>1,2,3,59</sup>, Pacific<sup>1,2,3,85</sup>, Pend Oreille<sup>3,85</sup>, San Juan<sup>3,85</sup>, Snohomish<sup>2,3</sup>, Thurston<sup>7</sup>, Whatcom<sup>3,85</sup>, Yakima<sup>3,85</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2,85</sup>, Jul<sup>1,2,85</sup>, Aug<sup>1,2,3,85</sup> (2015<sup>1,2,3</sup>). Collections: BBSL, INHS, JRYA, WSUC. Floral records: ASTERACEAE: Anaphalis margaritacea<sup>3,59</sup>
- **23.** Andrena (Cnemidandrena) nubecula Smith, 1853. County records: Pend Oreille<sup>3,85</sup>, Walla Walla<sup>2,3</sup>, Whitman<sup>3,85</sup>, Yakima<sup>3,85</sup>. Seasonality: Aug<sup>2</sup> (1988<sup>2,3</sup>). Collections: INHS
- 24. Andrena (Cnemidandrena) scutellinitens Viereck, 1916. County records: Okanogan<sup>1,2,3,59</sup>. Seasonality: Aug<sup>1,2,3</sup> (2004<sup>1,2,3,59</sup>). Collections: BBSL. Floral records: ASTERACEAE: Achillea millefolium<sup>59</sup>, Anaphalis margaritacea<sup>59</sup>, Erigeron speciosus<sup>3,59</sup>
- 25. Andrena (Cnemidandrena) sulcata Donovan, 1977. County records: Adams<sup>1,3,85</sup>, Benton<sup>2,3,7</sup>, Chelan<sup>3,85</sup>, Yakima<sup>2,3</sup>. Seasonality: Sep<sup>1,2,3,7</sup>, Oct<sup>2</sup> (1991<sup>2</sup>). Collections: INHS, NMNH, WSUC. Holotype. USA, Washington, Adams County, Ritzville; 9 September 1920; RC Shannon; Type No. 71075, USNM ENT 00533741. Paratype. USA, Washington, Chelan County, Wenatchee; 25 September 1938; J Standish
- **26.** *Andrena* (*Cnemidandrena*) *surda* Cockerell, 1910. County records: Kittitas<sup>2,3,85</sup>, Pacific<sup>3,85</sup>, Yakima<sup>3,85</sup>. Seasonality: Sep<sup>2,3</sup> (1989<sup>2,3</sup>). Collections: INHS
- 27. † Andrena (Cremnandrena) anisochlora Cockerell, 1936. County records: Clark<sup>1,2</sup>. Seasonality: May<sup>1,2</sup> (2020<sup>1,2</sup>). Collections: iNaturalist
- 28. Andrena (Dactylandrena) berberidis Cockerell, 1905. County records: King<sup>3,16</sup>, Kittitas<sup>2,3</sup>, Pierce<sup>16</sup>, Thurston<sup>133</sup>, Whitman<sup>3,16</sup>. Seasonality: Apr<sup>2</sup>, May<sup>2,3,133</sup>, June<sup>133</sup> (2020<sup>133</sup>). Collections: INHS. Floral records: ASPARAGACEAE:

*Camassia quamash*<sup>133</sup>; ASTERACEAE: *Eriophyllum lanatum*<sup>133</sup>; CAPRIFOLI-ACEAE: *Plectritis congesta*<sup>133</sup>

- 29. Andrena (Dactylandrena) porterae Cockerell, 1900. County records: King<sup>1,2,117</sup>, Kittitas<sup>2,3</sup>. Seasonality: Feb<sup>2,3</sup>, Apr<sup>1,2,117</sup> (1994<sup>2</sup>). Collections: INHS, NMNH. [= Andrena neurona Viereck, 1904]. Holotype. USA, Washington, King County, Seattle; 17 April 1896
- **30.** Andrena (Dasyandrena) cristata Viereck, 1916. County records: Pierce<sup>3,17</sup>
- 31. Andrena (Dasyandrena) obscuripostica Viereck, 1916. County records: Pierce<sup>17</sup>
- **32.** *Andrena* (*Diandrena*) *chalybioides* (Viereck, 1904). Collections: NMNH. [= *Andrena* (*Parandrena*) *perchalybia* Viereck, 1916]. Holotype. USA, Washington State; HK Morrison
- **33.** *Andrena* (*Diandrena*) *cuneilabris* Viereck, 1926. County records: Thurston<sup>133</sup>. Seasonality: May<sup>133</sup> (2020<sup>133</sup>). Floral records: RANUNCULACEAE: *Ranunculus occidentalis*<sup>133</sup>
- **34.** *Andrena* (*Diandrena*) *evoluta* Linsley and MacSwain, 1961. County records: Adams<sup>3,62</sup>, Okanogan<sup>1,2,3,4,59</sup>, Whitman<sup>3,7,62</sup>. Seasonality: Apr<sup>7</sup>, Jun<sup>1,2,3,4</sup>, Jul<sup>1,2,23</sup> (2004<sup>1,2,3,4,59</sup>). Collections: BBSL, WSUC. Floral records: ASTERACEAE: *Arnica sororia*<sup>59</sup>, *Crepis atrabarba*<sup>3,59</sup>; LILIACEAE: *Calochortus lyallii*<sup>59</sup>
- 35. Andrena (Diandrena) nothocalaidis (Cockerell, 1905). County records: Adams<sup>3,62</sup>, Benton<sup>1,2,7</sup>, Chelan<sup>3,62</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>3,7,62</sup>, Pierce<sup>62</sup>, Spokane<sup>1,2</sup>, Whitman<sup>62</sup>, Yakima<sup>3,62</sup>. Seasonality: Mar<sup>1,2</sup>, May<sup>1,2</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL, WSUC
- **36.** † *Andrena* (*Diandrena*) *subchalybea* Viereck, 1916. County records: Kittitas<sup>2</sup>. Seasonality: Apr<sup>2</sup>, May<sup>2</sup> (1989<sup>2</sup>). Collections: INHS
- 37. Andrena (Geissandrena) trevoris Cockerell, 1897. County records: Asotin<sup>2,3,20</sup>, Columbia<sup>3,20</sup>, Island<sup>3,20</sup>, Jefferson<sup>3,20</sup>, King<sup>1,3,20</sup>, Kitsap<sup>3,20</sup>, Klickitat<sup>3,20</sup>, Pierce<sup>3,20</sup>, San Juan<sup>2,3,20,136</sup>, Thurston<sup>1,2,3,20,133</sup>, Walla Walla<sup>1,2,3,20</sup>, Whatcom<sup>3</sup>, Whitman<sup>2,3,20</sup>. Seasonality: Jun<sup>1,2,20</sup>, Jul<sup>1,2,133</sup>, Aug<sup>3</sup> (2017<sup>133,136</sup>). Collections: BBSL, INHS, JRYA, NMNH, WSUC. [= Andrena semipolita Viereck, 1904]. Holotype. USA, Washington, Thurston County, Olympia; 12 June 1895; Type No. 18952, USNM ENT 00533746. Floral records: CAPRIFOLIACEAE: Symphoricarpos albus<sup>133,136</sup>
- 38. Andrena (Gonandrena) flocculosa LaBerge and Ribble, 1972. County records: Kittitas<sup>2,3</sup>, Pierce<sup>3,20</sup>, Thurston<sup>133</sup>, Whitman<sup>3,7,20</sup>, Yakima<sup>1,2,3,7,20</sup>. Seasonality: May<sup>1,2,3,20,133</sup> (2017<sup>133</sup>). Collections: INHS, NMNH, WSUC. Holotype. USA, Washington, Yakima County, North Yakima; 20 May 1903; E Jenne. Lectotype. USA, Washington, Pierce County, Parkland; 14 May 1962; R. Tentineh. Floral records: ASPARAGACEAE: Camassia quamash<sup>133</sup>
- **39.** Andrena (Holandrena) cressonii infasciata Lanham, 1949. County records: Benton<sup>1,3,16</sup>, King<sup>3,16</sup>, Kittitas<sup>2,3</sup>, Pierce<sup>3,16</sup>, Walla Walla<sup>1,2,16</sup>, Whitman<sup>1,2,3,7,8,16</sup>, Yakima<sup>3,16</sup>. Seasonality: Apr<sup>1,3,7</sup>, May<sup>1,2,3,7</sup>, Jun<sup>1,2,3,7</sup> (2003<sup>2</sup>). Collections: BBSL, INHS, UCRC, WSUC
- 40. † Andrena (Larandrena) miserabilis Cresson, 1872. County records: Benton<sup>7</sup>, Kittitas<sup>2,3</sup>, Okanogan<sup>7</sup>, Whitman<sup>7</sup>. Seasonality: May<sup>2,3</sup> (1989<sup>2,3</sup>). Collections: INHS, WSUC. Floral records: ROSACEAE: *Physocarpus malvaceus*<sup>8</sup>

- 41. Andrena (Leucandrena) barbilabris (Kirby, 1802) County records: Benton<sup>1,2,7</sup>, Chelan<sup>7</sup>, Clallam<sup>1,2,3,15</sup>, Island<sup>3,15</sup>, King<sup>3,7,15,117</sup>, Pacific<sup>3,15</sup>, Pierce<sup>1,3</sup>, Snohom-ish<sup>1,2,3,15</sup>, Thurston<sup>3,15,117</sup>, Whitman<sup>3,7,15</sup>, Yakima<sup>7</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>1,2,3,7,117</sup>, May<sup>1,3,7</sup>, Jun<sup>1,117</sup>, Jul<sup>1,2</sup>, Aug<sup>1</sup>, Sep<sup>1</sup> (2015<sup>1,2</sup>). Collections: AMNH, BBSL, INHS, UCRC, WSUC. [= Andrena macgillivrayi Cockerell, 1897]. [= Andrena placida Smith, 1853]
- **42.** ‡ *Andrena* (*Melandrena*) *carlini* Cockerell, 1901. County records: King<sup>1,2,3,117</sup>. Seasonality: Apr<sup>117</sup>, May<sup>1,2,3</sup> (1919<sup>1,2,3</sup>). Collections: OSUC. Floral records: GROSSULARIACEAE: *Ribes*<sup>117</sup>
- **43.** *Andrena* (*Melandrena*) *cerasifolii* Cockerell, 1896. County records: Stevens<sup>3,15</sup>, Whitman<sup>3,15</sup>
- 44. ‡ *Andrena (Melandrena) commoda* Smith, 1879. County records: Columbia<sup>18</sup>, Klickitat<sup>3,18</sup>, Pierce<sup>3,18</sup>, Walla Walla<sup>3,18</sup>, Whitman<sup>1,2,3,7,18</sup>, Yakima<sup>3,18</sup>. Seasonality: May<sup>3,7</sup>, Jun<sup>1,2,3</sup> (1969<sup>1,2,3</sup>). Collections: BBSL, UCRC, WSUC
- 45. † Andrena (Melandrena) cyanura Cockerell, 1916. County records: Benton<sup>7</sup>, Kittitas<sup>7</sup>. Collections: WSUC
- **46.** † *Andrena (Melandrena) erythrogaster* (Ashmead, 1890). County records: Kittitas<sup>2,3</sup>. Seasonality: May<sup>2,3</sup> (1989<sup>2,3</sup>). Collections: INHS
- 47. Andrena (Melandrena) hallii Dunning, 1898. County records: Whitman<sup>1,2,3,21,117</sup>.
  Collections: NMNH. Lectotype. USA, Washington, Whitman County, Pullman; CV Piper; USNM ENT 00533619
- **48.** Andrena (Melandrena) lupinorum Cockerell, 1906. County records: King<sup>3,18</sup>, Thurston<sup>133</sup>, Whitman<sup>3,18</sup>. Seasonality: April<sup>133</sup>, May<sup>133</sup>, June<sup>133</sup> (2020<sup>133</sup>). Floral records: ASPARAGACEAE: Camassia quamash<sup>133</sup>; CAPRIFOLIACEAE: Plectritis congesta<sup>133</sup>, Symphoricarpos albus<sup>133</sup>; ERICACEAE: Arctostaphylos uva-ursi<sup>133</sup>; LILIACEAE: Fritillaria affinis<sup>133</sup>; ROSACEAE: Potentilla gracilis<sup>133</sup>
- 49. Andrena (Melandrena) nivalis Smith, 1853. County records: Asotin<sup>3,18</sup>, Benton<sup>3,7,18</sup>, Garfield<sup>3,18</sup>, Jefferson<sup>1,2</sup>, King<sup>3,18</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,59</sup>, Pierce<sup>3,18</sup>, San Juan<sup>1,2,3,22,124</sup>, Spokane<sup>1,2</sup>, Thurston<sup>1,2,3,18,117,133</sup>, Walla Walla<sup>3,18</sup>, Whitman<sup>1,2,3,7,18,117</sup>. Seasonality: Apr<sup>1,2,133</sup>, May<sup>1,2,7,18,117,133</sup>, Jul<sup>1,2</sup> (2020<sup>133</sup>). Collections: BBSL, NMNH, PWRC, WSUC. [= Andrena compactiscopa Viereck, 1904]. Holotype. USA, Washington, Whitman County, Pullman; CV Piper. [= Andrena junonia Viereck, 1904]. Holotype. USA, Washington, Whitman County, Pullman; May 1895; CV Piper. [= Andrena pluvialis Cockerell, 1901]. Holotype. USA, Washington, Thurston County, Olympia; 1 May 1894; T Kincaid; Type No. 18939, USNM ENT 00533694. [= Andrena solidula Viereck, 1904]. Holotype. USA, Washington, Whitman County, Pullman; CV Piper. Floral records: APIACEAE: Lomatium utriculatum<sup>133</sup>; ASPARAGACEAE: Camassia quamash<sup>133</sup>; ASTERACEAE: Taraxacum officinale<sup>133</sup>; ERICACEAE: Arcostaphylos uva-ursi<sup>133</sup>; ONAGRACEAE: Chamerion angustifolium<sup>133</sup>; ROSACEAE: Physocarpus malvaceus<sup>8</sup>, Potentilla gracilis<sup>133</sup>, Rosa nutkana ssp. nutkana<sup>3,59</sup>
- 50. Andrena (Melandrena) perplexa Smith, 1853. County records: Cowlitz<sup>1,2,3</sup>, Garfield<sup>135</sup>, Kittitas<sup>2,3</sup>, Thurston<sup>133</sup>, Whitman<sup>2,3,7,21,117</sup>. Seasonality: Apr<sup>117</sup>,

May<sup>1,2,3,7,117,133,135</sup>, Jun<sup>7,133</sup> (2023<sup>135</sup>). Collections: BBSL, INHS, NMDG. [= *Andrena viburnella* Graenicher, 1903]. Floral records: BRASSICACEAE: *Tees- dalia nudicaulis*<sup>133</sup>; ROSACEAE: *Potentilla gracilis*<sup>133</sup>

- **51.** Andrena (Melandrena) pertristis carliniformis Viereck and Cockerell, 1914. County records: Chelan<sup>3,18</sup>, San Juan<sup>5</sup>, Yakima<sup>3,18</sup>. Seasonality: Apr<sup>5</sup>, May<sup>5</sup> (2009<sup>5</sup>). Floral records: APIACEAE: Heracleum sphondylium ssp. montanum<sup>5</sup>; ASPARAGACEAE: Camassia quamash<sup>5</sup>; GERANIACEAE: Geranium molle<sup>5</sup>; RANUNCULACEAE: Ranunculus californicus × occidentalis<sup>5</sup>
- 52. † Andrena (Melandrena) sola Viereck, 1916. County records: Klickitat<sup>1,2</sup>, San Juan<sup>1,2,3,6,124</sup>, Spokane<sup>1,2</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2</sup>, Jun<sup>6</sup> (2017<sup>6</sup>). Collections: BBSL, PWRC, WSDA
- **53.** *Andrena* (*Melandrena*) *subaustralis* Cockerell, 1898. County records: Benton<sup>2,3,7</sup>, Kittitas<sup>2,3</sup>, Thurston<sup>133</sup>, Whitman<sup>1,3,7,21,117</sup>, Yakima<sup>3,21</sup>. Seasonality: Apr<sup>1,2,3,7,133</sup>, May<sup>7</sup> (2017<sup>133</sup>). Collections: INHS, WSUC. Floral records: ASTER-ACEAE: *Balsamorhiza sagittata*<sup>8</sup>, *Taraxacum officinale*<sup>133</sup>
- **54.** *Andrena* (*Melandrena*) *subtilis* Smith, 1879. County records: Island<sup>3,21</sup>, Kittitas<sup>2,3,21</sup>, San Juan<sup>5,136</sup>, Spokane<sup>1,2,3,21</sup>, Walla Walla<sup>3,21</sup>, Whitman<sup>1,2,3,7,8,21,117</sup>, Yakima<sup>3,21</sup>. Seasonality: Apr<sup>1,2,5,7</sup>, May<sup>2,3,5,7</sup>, Jun<sup>1,7</sup> (2017<sup>136</sup>). Collections: BBSL, INHS, WSUC. Floral records: BRASSICACEAE: *Teesdalia nudicaulis*<sup>5</sup>; GERA-NIACEAE: *Geranium molle*<sup>5</sup>; RANUNCULACEAE: *Ranunculus californicus* × *occidentalis*<sup>5</sup>; ROSACEAE: *Rosa*<sup>8</sup>, *Rosa nutkana*<sup>136</sup>
- **55.** *Andrena* (*Melandrena*) *transnigra* Viereck, **1904**. County records: Jefferson<sup>1,2</sup>, King<sup>1,2,18,117</sup>, Kitsap<sup>2,3,18</sup>, Kittitas<sup>2,3,7</sup>, Klickitat<sup>1,2</sup>, Pierce<sup>1,2,3,18</sup>, Skagit<sup>2</sup>, Spokane<sup>3,18</sup>, **Stevens**<sup>1,2</sup>, Thurston<sup>7,133</sup>. Seasonality: Mar<sup>7</sup>, Apr<sup>1,2,3,7,18,117,133</sup>, May<sup>1,2,3,7</sup>, Jun<sup>1,2,7</sup> (2017<sup>133</sup>). Collections: BBSL, BugGuide, INHS, NMNH, PCYU, WSUC. Holotype. USA, Washington, King County, Seattle; 17 April 1896; T Kincaid. Floral records: ERICACEAE: *Arctostaphylos uva-ursi*<sup>133</sup>. Comments: Sheffield (2020) resurrected *Andrena cyanura* from synonymy with *Andrena transnigra*. We did not inspect all of the recorded specimens, and it is possible that some of these records represent *A. cyanura*.
- 56. Andrena (Melandrena) vicina Smith, 1853. County records: King<sup>3,18,117</sup>, Kittitas<sup>2,3</sup>, San Juan<sup>1,2,3,124,136</sup>, Snohomish<sup>1,2,3,23</sup>, Stevens<sup>1,3,18</sup>, Thurston<sup>3,18,117,133</sup>, Whitman<sup>8</sup>. Seasonality: Jan<sup>1,3</sup>, Mar<sup>2,133</sup>, Apr<sup>117</sup>, May<sup>1,2,3</sup>, Jun<sup>1,117</sup>, Jul<sup>1,2</sup>, Aug<sup>1,2</sup>, Nov<sup>2,3</sup>, Dec<sup>2</sup> (2017<sup>133,136</sup>). Collections: INHS, PWRC, WSUC. Floral records: ASPARAGACE-AE: Camassia quamash<sup>133</sup>; ASTERACEAE: Taraxacum officinale<sup>136</sup>; BERBERI-DACEAE: Berberis aquifolium<sup>136</sup>; GERANIACEAE: Geranium viscosissimum<sup>8</sup>; ROSACEAE: Holodiscus discolor<sup>8</sup>, Physocarpus malvaceus<sup>8</sup>, Rosa<sup>8</sup>, Rubus parviflorus<sup>8</sup>
- **57.** ‡ *Andrena (Micrandrena) candidiformis* Viereck and Cockerell, 1914. County records: Spokane<sup>3,7,63</sup>. Seasonality: Jun<sup>7</sup> (1912<sup>7</sup>). Collections: WSUC
- 58. Andrena (Micrandrena) chlorogaster Viereck, 1904. County records: Chelan<sup>7</sup>, Kittitas<sup>2,3</sup>, Klickitat<sup>1,2</sup>, Thurston<sup>133</sup>, Walla Walla<sup>3,63</sup>, Whitman<sup>3,7,63</sup>, Yakima<sup>2,3,7</sup>. Seasonality: Apr<sup>1,2,3,7,133</sup>, May<sup>1,3,7,133</sup>, Jun<sup>133</sup> (2020<sup>133</sup>). Collections: AMNH, INHS, WSUC. Floral records: APIACEAE: Lomatium pugetensis<sup>133</sup>, L. utriculatum<sup>133</sup>;

ASTERACEAE: Leucanthemum vulgare<sup>133</sup>; OROBANCHACEAE: Castilleja levisecta<sup>133</sup>; RANUNCULACEAE: Ranunculus occidentalis<sup>133</sup>; ROSACEAE: Fragaria virginiana<sup>133</sup>, Physocarpus malvaceus<sup>8</sup>, Potentilla<sup>8</sup>, P. gracilis<sup>133</sup>; SALI-CACEAE: Salix<sup>7</sup>

- **59.** Andrena (Micrandrena) illinoiensis Robertson, 1891. County records: Grant<sup>3,7,63</sup>, Thurston<sup>133</sup>, Whitman<sup>3,7,63,117</sup>, Yakima<sup>2,3</sup>. Seasonality: Apr<sup>2,3,7,117</sup>, May<sup>3,7,133</sup>, Jul<sup>7</sup> (2017<sup>133</sup>). Collections: INHS, UCRC, WSUC. Floral records: ROSACEAE: Fragaria virgniana<sup>133</sup>
- **60.** *Andrena* (*Micrandrena*) *melanochroa* Cockerell, 1898. County records: Chelan<sup>3,63</sup>, Pierce<sup>7</sup>, Spokane<sup>1,2</sup>, Thurston<sup>1,2,3,63,117</sup>, Whitman<sup>3,7,8,63</sup>. Seasonality: May<sup>1,2,7,117</sup>, Jun<sup>1,2</sup> (2011<sup>1,2</sup>). Collections: BBSL, NMNH, WSUC. Holotype. USA, Washington, Thurston County, Olympia; 25 May 1894; T Kincaid; Type No. 18917, USNM ENT 00533649. Floral records: APIACEAE: *Lomatium*<sup>8</sup>; GROSSULARIACEAE: *Ribes aureum*<sup>8</sup>; ROSACEAE: *Malus domestica*<sup>8</sup>
- **61.** *Andrena* (*Micrandrena*) *microchlora* Cockerell, 1922. County records: Benton<sup>1,2,3,7</sup>, Kittitas<sup>7</sup>, Klickitat<sup>1,2,3,63</sup>, Lincoln<sup>7</sup>, Spokane<sup>1,2</sup>, Thurston<sup>133</sup>, Whitman<sup>1,3,6,7,61,63</sup>, Yakima<sup>2,3</sup>. Seasonality: Mar<sup>1,2,7,61</sup>, Apr<sup>1,2,3,7,61,133</sup>, May<sup>1,2,6,7</sup>, Jun<sup>7</sup> (2018<sup>133</sup>). Collections: BBSL, INHS, WSDA, WSUC. Floral records: APIACE-AE: *Lomatium utriculatum*<sup>133</sup>
- **62.** ‡ *Andrena (Micrandrena) nigrae* Robertson, 1905. County records: Asotin<sup>63</sup>, Whitman<sup>3,7,63</sup>. Seasonality: May<sup>7</sup> (1920<sup>7</sup>). Collections: WSUC
- 63. Andrena (Micrandrena) piperi Viereck, 1904. County records: Asotin<sup>3,63,135</sup>, Benton<sup>1,2,3,7,63</sup>, Chelan<sup>3,7,63</sup>, Kittitas<sup>2,3</sup>, Spokane<sup>1,2</sup>, Walla Walla<sup>7</sup>, Whitman<sup>1,2,3,7,63,117</sup>, Yakima<sup>2,3</sup>. Seasonality: Mar<sup>135</sup>, Apr<sup>1,2,3,63</sup>, May<sup>1,2,3,63</sup> (2021<sup>135</sup>). Collections: BBSL, INHS, NMDG, WSUC. Holotype. USA, Washington, Whitman County, Pullman; CV Piper
- 64. ‡ Andrena (Micrandrena) salictaria Robertson, 1905. County records: Spokane<sup>3,7,63</sup>, Whitman<sup>3,7,63</sup>. Seasonality: Apr<sup>7</sup>, May<sup>7</sup>, Jun<sup>7</sup>, Jul<sup>7</sup> (1930<sup>7</sup>). Collections: WSUC
- **65.** *Andrena* (*Onagrandrena*) *raveni* Linsley and MacSwain, 1961. County records: Adams<sup>86</sup>, Benton<sup>7</sup>. Seasonality: Apr<sup>7</sup> (1995<sup>7</sup>). Collections: WSUC
- 66. Andrena (Parandrena) andrenoides (Cresson, 1878). County records: Garfield<sup>135</sup>, Thurston<sup>117</sup>, Yakima<sup>2,3</sup>. Seasonality: Apr<sup>2,3</sup>, May<sup>117,135</sup> (2023<sup>135</sup>). Collections: INHS, NMDG. [= Parandrena andrenoides (Cresson, 1878)]
- **67.** ‡ *Andrena (Parandrena) nevadensis* (Cresson, 1879). County records: Thurston<sup>3,20</sup>, Whitman<sup>3,7,20</sup>, Yakima<sup>3,20</sup>. Seasonality: Apr<sup>7</sup> (1936<sup>7</sup>). Collections: WSUC
- 68. Andrena (Plastandrena) crataegi Robertson, 1893. County records: Asotin<sup>7</sup>, King<sup>3,19</sup>, Kittitas<sup>2,3</sup>, Okanogan<sup>7</sup>, Pierce<sup>1,3,19</sup>, Spokane<sup>7</sup>, Stevens<sup>3,7,19</sup>, Thurston<sup>133</sup>, Walla Walla<sup>1,2</sup>, Whitman<sup>1,2,3,7</sup>, Yakima<sup>3,7</sup>. Seasonality: Jan<sup>1</sup>, Apr<sup>2,3</sup>, May<sup>2,7,133</sup>, Jun<sup>1,2,3,7</sup>, Jul<sup>1,2</sup> (2017<sup>133</sup>). Collections: BBSL, INHS, UCRC, WSUC. Floral records: APIACEAE: Lomatium pugetensis<sup>133</sup>; ROSACEAE: Physocarpus malvaceus<sup>8</sup>
- **69.** *Andrena* (*Plastandrena*) *prunorum prunorum* Cockerell, 1896. County records: Adams<sup>7</sup>, Asotin<sup>7</sup>, Benton<sup>1,2,3,7</sup>, Chelan<sup>1,2,3,7</sup>, Clallam<sup>1,2</sup>, Ferry<sup>2</sup>, Franklin<sup>1,2,3,7,19,117</sup>,

Grant<sup>1,2,3,7</sup>, Island<sup>3,7,19</sup>, Jefferson<sup>1,2</sup>, King<sup>1,2,3,7,117</sup>, Kitsap<sup>2,23,134</sup>, Kittitas<sup>1,2,3,7</sup>, Klickitat<sup>1,2,3</sup>, Lincoln<sup>7</sup>, Mason<sup>7</sup>, Okanogan<sup>1,2,3,7,59</sup>, Pierce<sup>7</sup>, San Juan<sup>1,2,3,5,6,19,22,124</sup>, **Skagit**<sup>1,2</sup>, Snohomish<sup>1,2,3,23</sup>, **Spokane**<sup>1,2,3,7</sup>, **Stevens**<sup>1,7</sup>, Thurston<sup>1,2,3,6,19,117,133</sup>, Walla Walla<sup>1,2,3,7,71</sup>, Whitman<sup>1,2,3,6,7,8,117</sup>, Yakima<sup>1,2,3,7,23</sup>. Seasonality: Mar<sup>1,23,7</sup>, Apr<sup>1,2,3,7,23</sup>, May<sup>1,2,3,5,7,19,23,117,133</sup>, Jun<sup>1,2,3,5,6,7,19,117,133</sup>, Jul<sup>1,2,3,6,7,23,133</sup>, Aug<sup>1,2,3,6,7</sup>, Sep<sup>2</sup>, Oct<sup>7</sup> (2022<sup>1,2</sup>). Collections: AMNH, BBSL, BugGuide, iNaturalist, INHS, NMNH, PCYU, PWRC, SEMC, WSDA, WSUC. [= Andrena kincaidii Cockerell, 1897]. Holotype. USA, Washington, Thurston County, Olympia; 2 June 1894; Type No. 3698, USNM ENT 00533636. [= Andrena pascoensis Cockerell, 1897]. Holotype. USA, Washington, Franklin County, Pasco; 25 May 1896; Type No. 18936, USNM ENT 00533683. Floral records: APIACEAE: Chaerophyllum temulum<sup>3</sup>, Lomatium<sup>8</sup>; ASPARAGACEAE: Camassia quamash<sup>133</sup>; ASTER-ACEAE: Anaphalis margaritacea<sup>3,59</sup>; BRASSICACEAE: Sisymbrium altissimum<sup>8</sup>, Teesdalia nudicaulis<sup>133</sup>; CACTACEAE: Pediocactus nigrispinus<sup>7</sup>; CARYOPHYL-LACEAE: Cersatium arvense133; GERANIACEAE: Geranium viscosissimum8; HY-DRANGEACEAE: *Philadelphus lewisit*<sup>8,23</sup>; ONAGRACEAE: *Clarkia amoena*<sup>133</sup>; ROSACEAE: Fragaria virginiana<sup>133</sup>, Holodiscus discolor<sup>8</sup>, Physocarpus malvaceus<sup>8</sup>, Potentilla gracilis<sup>133</sup>; SALICACEAE: Salix<sup>7</sup>

- 70. Andrena (Ptilandrena) astragali Viereck and Cockerell, 1914. County records: Jefferson<sup>1,2</sup>, Kittitas<sup>3,14</sup>, Okanogan<sup>1,2,3,59</sup>, San Juan<sup>5</sup>, Spokane<sup>1,2</sup>, Thurston<sup>133</sup>, Whitman<sup>7</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,5,133</sup>, Jun<sup>1,2,3,5,7,133</sup> (2023<sup>7</sup>). Collections: BBSL, WSUC. Floral records: APIACEAE: Lomatium pugetensis<sup>133</sup>; ASPARAGACEAE: Triteleia hyacinthina<sup>133</sup>; ASTERACEAE: Balsamorhiza deltoidea<sup>133</sup>, Eriophyllum lanatum<sup>133</sup>, Hypochaeris radicata<sup>133</sup>, Leucanthemum vulgare<sup>133</sup>, Solidago simplex<sup>133</sup>; CAPRIFOLIACEAE: Plectritis congesta<sup>133</sup>, Symphoricarpos albus<sup>133</sup>; CARYOPHYL-LACEAE: Cerastrium arvense<sup>133</sup>; FABACEAE: Lupinus albicaulis<sup>133</sup>; MELANTHI-ACEAE: Toxicoscordion venenosus<sup>133</sup>, T. venenosum var. venenosum<sup>5</sup>; RANUNCU-LACEAE: Ranunculus occidentalis<sup>133</sup>; ROSACEAE: Potentilla gracilis<sup>133</sup>
- 71. Andrena (Ptilandrena) auricoma Smith, 1879. County records: Garfield<sup>135</sup>, Kittitas<sup>2,3</sup>, Walla Walla<sup>3,14</sup>, Whitman<sup>7</sup>. Seasonality: Apr<sup>2</sup>, May<sup>135</sup>, Jun<sup>7</sup>, Jul<sup>7</sup> (2023<sup>135</sup>). Collections: INHS, NMDG, WSUC. Floral records: ASTERACEAE: Achillea millefolium<sup>8</sup>; ROSACEAE: Physocarpus malvaceus<sup>8</sup>, Potentilla<sup>8</sup>
- 72. Andrena (Ptilandrena) caerulea Smith, 1879. County records: Island<sup>3,7</sup>, Kittitas<sup>1,2,3,7</sup>, Klickitat<sup>1,2</sup>, Lewis<sup>7</sup>, Pierce<sup>14</sup>, Thurston<sup>1,2,3,14,117,133</sup>, Whitman<sup>7,8</sup>. Seasonality: Apr<sup>3,7,133</sup>, May<sup>1,2,7,14,117,133</sup>, Jun<sup>1,2,133</sup>, Jul<sup>1,2</sup> (2020<sup>133</sup>). Collections: BBSL, NMNH, SEMC, UCRC, WSUC. [= Andrena coerulea var. territa Cockerell, 1898]. Holotype. USA, Washington, Thurston County, Olympia; 20 May 1894; Type No. 18943, USNM ENT 00533743. [= Pterandrena acrypta Viereck, 1904]. [= Pterandrena erigenoides Viereck, 1904]. Floral records: ASPARA-GACEAE: Camassia quamash<sup>133</sup>; ASTERACEAE: Microseris laciniata<sup>133</sup>; CAR-YOPHYLLACEAE: Cerastium arvense<sup>133</sup>; CAPRIFOLIACEAE: Symphoricarpos albus<sup>133</sup>; RANUNCULACEAE: Ranunculus<sup>8</sup>, R. occidentalis<sup>133</sup>; ROSACEAE: Prunus virginiana<sup>8</sup>

- **73.** *Andrena (Ptilandrena) chlorura* Cockerell, 1916. County records: King<sup>3,14</sup>, Thurston<sup>133</sup>, Whitman<sup>3,14</sup>. Seasonality: May<sup>133</sup> (2017<sup>133</sup>). Floral records: ROSACEAE: *Fragaria virginiana*<sup>133</sup>
- 74. Andrena (Ptilandrena) lawrencei Viereck and Cockerell, 1914. County records: Benton<sup>1,2,7</sup>, Kittitas<sup>2,3,7,14</sup>, Okanogan<sup>14</sup>, Spokane<sup>1,2</sup>, Whitman<sup>3,14</sup>, Yakima<sup>3,14</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>1,2,3,7</sup>, May<sup>1,2,7</sup> (2015<sup>1,2</sup>). Collections: BBSL, INHS, WSUC
- **75.** Andrena (Ptilandrena) nigrihirta (Ashmead, 1890). County records: Clallam<sup>3,14</sup>, Grays Harbor<sup>3,14</sup>, King<sup>3,14</sup>, Pierce<sup>1,3,14</sup>, **Spokane**<sup>1,2</sup>, Thurston<sup>133</sup>, Whitman<sup>3,7,14,114,117</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,7,14,117</sup>, Jun<sup>133</sup>, Jul<sup>1,3</sup> (2018<sup>133</sup>). Collections: BBSL, INHS, WSUC. [= Andrena decussata Viereck, 1904]. Holotype. USA, Washington, Whitman County, Pullman. Floral records: CAPRIFOLI-ACEAE: Symphoricarpos albus<sup>133</sup>
- 76. Andrena (Ptilandrena) nigrocaerulea Cockerell, 1897. County records: Chelan<sup>7,130</sup>, Clallam<sup>3,14</sup>, Columbia<sup>14</sup>, Island<sup>7</sup>, King<sup>1,2,3,14,117</sup>, Kittitas<sup>3,14</sup>, Klickitat<sup>1,2</sup>, Pierce<sup>3,14</sup>, San Juan<sup>1,2,124</sup>, Spokane<sup>1,2</sup>, Thurston<sup>3,14,117,133</sup>, Walla Walla<sup>1,2,3,14</sup>, Whitman<sup>1,2,3,6,7,8,14,61,117</sup>, Yakima<sup>3,14</sup>. Seasonality: Apr<sup>1,2,7,61,133</sup>, May<sup>1,2,7,14,117,133</sup>, Jun<sup>1,2,3,6,7,117,133</sup>, Jul<sup>1,2,7</sup> (2020<sup>133</sup>). Collections: BBSL, NMNH, PWRC, WSDA, WSUC. [= Andrena seattlensis Viereck, 1904]. Holotype. USA, Washington, King County, Seattle; 17 May 1896. [= Pterandrena nigrocaerulea Viereck, 1904]. Floral records: ASPARAGACEAE: Camassia quamash133; ASTERACEAE: Balsamorhiza deltoidea<sup>133</sup>, Crepis capillaris<sup>133</sup>, Eriophyllum lanatum<sup>133</sup>, Hypochaeris radicata<sup>133</sup>, Leucanthemum vulgare<sup>133</sup>, Microseris laciniata<sup>133</sup>, Taraxacum officinale<sup>133</sup>; BOR-AGINACEAE: Hackelia venusta<sup>130</sup>; BRASSICACEAE: Teesdalia nudicaulis<sup>133</sup>; CAMPANULACEAE: Campanula rotundifolia<sup>133</sup>; CAPRIFOLIACEAE: Plectritis congesta<sup>133</sup>; CARYOPHYLLACEAE: Cerastium arvense<sup>133</sup>; ERICACEAE: Arctostaphylos uva-ursi<sup>133</sup>; FABACEAE: Vicia sativa<sup>133</sup>; GERANIACEAE: Geranium viscosissimum<sup>8</sup>; IRIDACEAE: Sisyrinchium idahoense<sup>133</sup>; PLANTAGINACEAE: Collinsia grandiflora<sup>133</sup>; PLUMBAGINACEAE: Armeria maritima<sup>133</sup>; RANUN-CULACEAE: Ranunculus occidentalis<sup>133</sup>; ROSACEAE: Potentilla gracilis<sup>133</sup>
- 77. Andrena (Ptilandrena) pallidiscopa (Viereck, 1904). County records: Benton<sup>7</sup>, Kittitas<sup>7</sup>, Klickitat<sup>3,15</sup>, Walla Walla<sup>3,15</sup>, Whitman<sup>3,7,15</sup>. Seasonality: Apr<sup>7</sup>, May<sup>7</sup> (2023<sup>7</sup>). Collections: WSUC
- 78. Andrena (Ptilandrena) ribblei LaBerge, 1977. County records: Okanogan<sup>1,2,3,59</sup>, Pierce<sup>3,17</sup>. Seasonality: Jul<sup>1,2,3,17</sup>, Aug<sup>17</sup> (2004<sup>1,2,3,59</sup>). Collections: BBSL. Floral records: BRASSICACEAE: Smelowskia calycina<sup>59</sup>; POLEMONIACEAE: Polemonium pulcherrimum<sup>3,59</sup>; ROSACEAE: Potentilla gracilis<sup>59</sup>
- 79. Andrena (Scaphandrena) chapmanae Viereck, 1904. County records: Adams<sup>7</sup>, Chelan<sup>1,2,3</sup>, Garfield<sup>1,2,3,10,46</sup>, Klickitat<sup>1,2,7</sup>, Whitman<sup>7</sup>. Seasonality: Mar<sup>7</sup>, Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jun<sup>7</sup> (2012<sup>1,2</sup>). Collections: BBSL, WSUC
- 80. Andrena (Scaphandrena) gordoni Ribble, 1974. County records: Benton<sup>1,2</sup>, Whitman<sup>60</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>1,2</sup>, May<sup>60</sup> (2015<sup>1,2</sup>). Collections: AMNH, BBSL. Paratype. USA, Washington, Whitman County, Pullman; May; AL Melander; WSU No. 402.

- 81. Andrena (Scaphandrena) merriami Cockerell, 1901. County records: Asotin<sup>3,60</sup>, Benton<sup>1,2,3,7</sup>, Kittitas<sup>2,3,60</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>7</sup>, Spokane<sup>1,2</sup>, Walla Walla<sup>3,60</sup>, Whitman<sup>1,2,3,6,7,8,60,117</sup>, Yakima<sup>3,60</sup>. Seasonality: Mar<sup>1,7</sup>, Apr<sup>1,2,3,7,117</sup>, May<sup>1,2,3,7,117</sup>, Jul<sup>6</sup> (2015<sup>1,2</sup>). Collections: BBSL, INHS, WSDA, WSUC. [= Andrena pullmani Viereck, 1904]. Holotype. USA, Washington, Whitman County, Pullman. Floral records: APIACEAE: Lomatium<sup>8</sup>; ROSACEAE: Prunus avium<sup>8</sup>
- **82.** *Andrena* (*Scaphandrena*) *scurra* Viereck, 1904. County records: Adams<sup>3,7,60</sup>, Benton<sup>1,2,3,7,60</sup>, Chelan<sup>1,2,3,7,60</sup>, Garfield<sup>1,2,3,4,46</sup>, Grant<sup>3,7,60</sup>, Kittitas<sup>3,60</sup>, Okanogan<sup>3,7,60</sup>, Spokane<sup>1,2,3,60</sup>, *Walla Walla*<sup>1,2,3</sup>, Whitman<sup>1,2,3,4,7,60</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>1,2,3,7</sup>, May<sup>1,2,3,4,7</sup>, Jun<sup>1,2,3,7</sup>, Jul<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL, FMNH, INHS, PCYU, SEMC, WSUC
- **83.** *Andrena* (*Scaphandrena*) *shoshoni* Ribble, 1974. County records: Whitman<sup>32</sup>. Seasonality: May<sup>32</sup> (2013<sup>32</sup>)
- 84. Andrena (Scaphandrena) sladeni Viereck, 1924. County records: Asotin<sup>3,60</sup>, Benton<sup>7</sup>, Kittitas<sup>3,60</sup>, Whitman<sup>7,61</sup>, Yakima<sup>7</sup>. Seasonality: Mar<sup>7,61</sup>, Apr<sup>7,61</sup> (1991<sup>61</sup>). Collections: WSUC
- **85.** ‡ *Andrena* (*Scaphandrena*) *walleyi* Cockerell, 1932. County records: Spokane<sup>3,60</sup>, Whitman<sup>7</sup>. Seasonality: May<sup>7</sup> (1918<sup>7</sup>). Collections: WSUC
- 86. Andrena (Simandrena) angustitarsata Viereck, 1904. County records: Asotin<sup>2,3,7,13</sup>, Ferry<sup>1,2,3</sup>, King<sup>1,2,3,7,13</sup>, Kittitas<sup>2</sup>, Klickitat<sup>1,2,3,13</sup>, Lewis<sup>3,7,13</sup>, Pierce<sup>3,7,13</sup>, Spokane<sup>1,2,3,13</sup>, Thurston<sup>133</sup>, Walla Walla<sup>1,2,3,13</sup>, Whitman<sup>1,2,3,6,7,8,13,61,117</sup>. Seasonality: Mar<sup>3,7,61</sup>, Apr<sup>1,2,7,133</sup>, May<sup>1,2,3,7,133</sup>, Jun<sup>1,2,6,7,133</sup> (2020<sup>133</sup>). Collections: AMNH, BBSL, INHS, NMNH, SEMC, UCDC, UCRC, WSDA, WSUC. [Andrena (Simandrena) angustitarsata Viereck, 1904]. Holotype. USA, Washington Territory. [= Andrena mustelicolor Viereck, 1904]. Holotype. USA, Washington, Whitman County, Pullman; CV Piper. Floral records: APIACEAE: Lomatium<sup>8</sup>, L. pugetensis<sup>133</sup>, L. utriculatum<sup>133</sup>; ASTERACEAE: Achillea millefolium<sup>133</sup>, Balsamorhiza deltoidea<sup>133</sup>, Eriophyllum lanatum<sup>133</sup>; BRASSICACEAE: Lepidium campestre<sup>133</sup>, Teesdalia nudicaulis<sup>133</sup>; CAPRIFOLIACEAE: Plectritis congesta<sup>133</sup>; RANUNCU-LACEAE: Ranunculus<sup>8</sup>; ROSACEAE: Malus domestica<sup>8</sup>, Physocarpus malvaceus<sup>8</sup>, Potentilla gracilis<sup>133</sup>, Prunus virginiana<sup>8</sup>, Sorbus scopulina<sup>8</sup>, Rosa<sup>8</sup>, Rubus parviflorus<sup>8</sup>
- **87.** *Andrena* (*Simandrena*) *orthocarpi* Cockerell, 1936. County records: Klickitat<sup>1,2,3,13</sup>, Thurston<sup>133</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>133</sup> (2020<sup>133</sup>). Collections: AMNH. Floral records: APIACEAE: *Lomatium pugetensis*<sup>133</sup>, *L. utriculatum*<sup>133</sup>
- **88.** *Andrena* (*Simandrena*) *pallidifovea* (Viereck, 1904). County records: Benton<sup>1,3,7,13</sup>, Chelan<sup>1,2,3</sup>, Kittitas<sup>2,3</sup>, Spokane<sup>1,2,3,13</sup>, Thurston<sup>133</sup>, Walla Walla<sup>1,2,3,13</sup>, Whitman<sup>3,7,8,13,117</sup>, Yakima<sup>3,7,13</sup>. Seasonality: May<sup>1,2,3,7</sup>, Jun<sup>1,2,7,133</sup>, Jul<sup>1</sup> (2019<sup>133</sup>). Collections: BBSL, INHS, WSUC. [= *Pterandrena pallidifovea* Viereck, 1904]. Floral records: ASTERACEAE: *Eriophyllum lanatum*<sup>8,133</sup>, *Solidago simplex*<sup>133</sup>
- 89. †\* Andrena (Taeniandrena) wilkella (Kirby, 1802). County records: Whitman<sup>7</sup>. Seasonality: May<sup>7</sup>, Jun<sup>7</sup> (2023<sup>7</sup>). Collections: WFBM, WSUC
- **90.** Andrena (*Thysandrena*) candida Smith, 1879. County records: Adams<sup>3,17</sup>, Asotin<sup>3,17</sup>, Benton<sup>2,3,7</sup>, Clark<sup>3,17</sup>, Island<sup>2,3,7,17</sup>, King<sup>1,2,3,17,117</sup>, Kitsap<sup>2,3</sup>, Pacific<sup>3,17</sup>,

Pierce<sup>1,2,3,7,17</sup>, San Juan<sup>3,17</sup>, Skagit<sup>1,2,3,17</sup>, **Spokane**<sup>1,2</sup>, Thurston<sup>117,133</sup>, Walla Walla<sup>1,2,3,17</sup>, Whatcom<sup>1,3,17</sup>, Whitman<sup>3,7,8,17,117</sup>, Yakima<sup>3,7,17</sup>. Seasonality: Feb<sup>2</sup>, Mar<sup>2,3,7,117</sup>, Apr<sup>1,2,3,7,117</sup>, May<sup>1,2,7,133</sup>, Jun<sup>1,2,117,133</sup>, Jul<sup>1,2,3,7</sup> (2020<sup>133</sup>). Collections: AMNH, BBSL, INHS, NMNH, UCDC, UCRC, WSUC. [= *Andrena subcandida* Viereck, 1904]. **Holotype**. USA, Washington, King County, Seattle; 14 March 1896; T Kincaid. Floral records: APIACEAE: *Lomatium*<sup>8</sup>, *L. utriculatum*<sup>133</sup>; ASTERACEAE: *Balsamorhiza sagittata*<sup>8</sup>; LAMIACEAE: *Prunella vulgaris*<sup>133</sup>; ROSACEAE: *Prunus avium*<sup>8</sup>

- **91.** *Andrena* (*Thysandrena*) *knuthiana* Cockerell, 1901. County records: Clallam<sup>3</sup>, King<sup>3,17</sup>, Okanogan<sup>1,2,3,59</sup>, Pierce<sup>3,17</sup>, San Juan<sup>3,5,17</sup>, Snohomish<sup>7</sup>, Walla Walla<sup>3,17</sup>, Whitman<sup>3,7,17</sup>. Seasonality: Apr<sup>5,7</sup>, Jul<sup>1,2,3,7</sup> (2014<sup>3</sup>). Collections: BBSL, JRYA, WSUC
- **92.** *Andrena* (*Thysandrena*) *medionitens* Cockerell, 1902. County records: Franklin<sup>1,2,3,17,117</sup>, Grant<sup>7</sup>, Kittitas<sup>1,2,3,17</sup>, Pierce<sup>3,17</sup>, Spokane<sup>7</sup>, Walla Walla<sup>1,2,3,17</sup>, Whitman<sup>1,2,3,17</sup>. Seasonality: May<sup>1,2,7,17,117</sup>, Jun<sup>1</sup>, Jul<sup>1,2</sup> (2003<sup>2</sup>). Collections: BBSL, INHS, NMNH, SEMC, WSUC. Holotype. USA, Washington, Franklin County, Pasco; 25 May 1896; Type No. 18921, USNM ENT 00533648
- **93.** ‡ *Andrena* (*Thysandrena*) *trizonata* (Ashmead, 1890). County records: Pierce<sup>1,3</sup>, Whitman<sup>3,17</sup>. Seasonality: Mar<sup>1</sup>, Apr<sup>1,3</sup> (1946<sup>1,3</sup>). Collections: INHS. Floral records: ROSACEAE: *Physocarpus malvaceus*<sup>8</sup>
- **94.** *Andrena* (*Thysandrena*) *vierecki* Cockerell, 1904. County records: King<sup>3,17</sup>, Kittitas<sup>2,3</sup>, Klickitat<sup>17</sup>, Thurston<sup>133</sup>, Whitman<sup>3,7,17</sup>, Yakima<sup>3,17</sup>. Seasonality: Apr<sup>2,3</sup>, May<sup>7</sup>, Jun<sup>133</sup> (2018<sup>133</sup>). Collections: INHS, WSUC. Floral records: CAPRIFO-LIACEAE: *Symphoricarpos albus*<sup>133</sup>
- 95. Andrena (Thysandrena) w-scripta Viereck, 1904. County records: Asotin<sup>3,17</sup>, Benton<sup>7</sup>, Chelan<sup>3,17</sup>, Clallam<sup>3</sup>, Ferry<sup>1,2,3,17</sup>, King<sup>2,3,17</sup>, Kitsap<sup>2,3</sup>, Kittitas<sup>2,3</sup>, Klickitat<sup>1,2</sup>, Pierce<sup>3,17</sup>, Snohomish<sup>1,3</sup>, Spokane<sup>1,2</sup>, Thurston<sup>133</sup>, Walla Walla<sup>3,17</sup>, Whitman<sup>2,3,7,17</sup>, Yakima<sup>2,3</sup>. Seasonality: Mar<sup>7</sup>, Apr<sup>2,3,7</sup>, May<sup>1,2,3,7,133</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2</sup>, Nov<sup>1,3</sup> (2020<sup>133</sup>). Collections: BBSL, INHS, JRYA, SEMC, WSUC. Floral records: APIACEAE: Lomatium pugetensis<sup>133</sup>
- 96. Andrena (Trachandrena) amphibola (Viereck, 1904). County records: Asotin<sup>3,12</sup>, Benton<sup>1,2</sup>, Chelan<sup>3,12</sup>, Island<sup>3,7,12</sup>, Jefferson<sup>3,12</sup>, King<sup>2,3,12</sup>, Kitsap<sup>3,12</sup>, Kittitas<sup>3</sup>, Klickitat<sup>1,2</sup>, Mason<sup>3,12</sup>, Pacific<sup>1,2,7</sup>, San Juan<sup>1,2,3,12</sup>, Thurston<sup>3,7,12,133</sup>, Whitman<sup>3,7,8,12</sup>. Seasonality: Apr<sup>1,2,3,7</sup>, May<sup>1,7,133</sup>, Jun<sup>7</sup>, Jul<sup>1,7</sup> (2019<sup>133</sup>). Collections: BBSL, EMEC, INHS, NMNH, UCRC, WSUC. [= *Trachandrena crassihirta* Viereck, 1904]. Holotype. USA, Washington State (presumably)<sup>12,116</sup>. [= *Trachandrena hadra* Viereck, 1904]. Holotype. USA, Washington Territory. Floral records: ASPARA-GACEAE: Camassia quamash<sup>133</sup>; LAMIACEAE: Agastache urticifolia<sup>8</sup>
- **97.** ‡ *Andrena* (*Trachandrena*) *cleodora cleodora* (Viereck, 1904). County records: King<sup>2,3,12</sup>, Kitsap<sup>3,12</sup>, Klickitat<sup>3,12</sup>, Pierce<sup>3,12</sup>, Stevens<sup>3,12</sup>, Whitman<sup>3,12</sup>, Yakima<sup>3,12</sup>. Seasonality: Jul<sup>3</sup> (1927<sup>3</sup>). Collections: INHS, UCRC
- 98. Andrena (Trachandrena) cupreotincta Cockerell, 1901. County records: Benton<sup>1,2,3,7</sup>, Ferry<sup>3,12</sup>, Island<sup>3,12</sup>, King<sup>1,2,3,12</sup>, Kittitas<sup>2,3</sup>, Lincoln<sup>3,7,12</sup>, Mason<sup>1,2,3,12,116</sup>, Pacific<sup>3,12</sup>, Pierce<sup>3,12</sup>, San Juan<sup>3,12</sup>, Snohomish<sup>3,12</sup>, Spokane<sup>3,12</sup>, Stevens<sup>3,12</sup>

Thurston<sup>3,12,133</sup>, Walla Walla<sup>3,12</sup>, Whitman<sup>3,7,12</sup>. Seasonality: Apr<sup>1,2,3,7,12</sup>, May<sup>1,2,3,7,12,133</sup>, Jun<sup>2,7</sup> (2017<sup>133</sup>). Collections: AMNH, BBSL, INHS, NMNH, UCDC, WSUC. **Holotype**. USA, Washington, Mason County, Skokomish River; 26 April 1892; T Kincaid; Type No. 18937, USNM ENT 00532972. [= *Trachandrena ochreopleura* Viereck, 1904]. **Holotype**. USA, Washington, Mason County, Skokomish River; 5 May 1912; USNM Type No 28535. Floral records: PLUMBAGINACEAE: *Armeria maritima*<sup>133</sup>

- **99.** ‡ *Andrena* (*Trachandrena*) *cyanophila* Cockerell, 1906. County records: Spokane<sup>1,2,3,12</sup>, Whitman<sup>3,7,12</sup>. Seasonality: May<sup>7</sup>, Jun<sup>7</sup>, Jul<sup>1,2</sup> (1945<sup>1,2</sup>). Collections: INHS, WSUC
- 100. ‡ Andrena (Trachandrena) forbesii Robertson, 1891. County records: Spokane<sup>3</sup>, Whitman<sup>1,3,7,12</sup>. Seasonality: Apr<sup>7</sup>, May<sup>1,3,7</sup>, Jun<sup>1,7</sup> (1924<sup>3</sup>). Collections: BBSL, INHS, UCRC, WSUC
- 101. Andrena (Trachandrena) fuscicauda (Viereck, 1904). County records: King<sup>1,2,3,12</sup>, Kitsap<sup>3,12</sup>, Pacific<sup>7</sup>, Pierce<sup>1,2,3</sup>, Thurston<sup>133</sup>. Seasonality: Apr<sup>1,2,3,7</sup>, May<sup>1,2,133</sup> (2018<sup>133</sup>). Collections: INHS, NMNH, UCDC, WSUC. [= Trachandrena fuscicauda Viereck, 1904]. Holotype. USA, Washington Territory; PANS 10293. Floral records: ASPARAGACEAE: Camassia quamash<sup>133</sup>
- 102. †# Andrena (Trachandrena) hippotes Robertson, 1895. County records: Benton<sup>7</sup>, Pierce<sup>3</sup>, Whitman<sup>1,3,7</sup>, Yakima<sup>1,3</sup>. Seasonality: Apr<sup>1,3,7</sup>, May<sup>1,7</sup>, Jun<sup>3,7</sup> (1966<sup>3</sup>). Collections: CUIC, INHS, WSUC
- 103. Andrena (Trachandrena) mariae Robertson, 1891. County records: Lincoln<sup>7</sup>, Thurston<sup>133</sup>, Whitman<sup>3,7,12</sup>. Seasonality: Apr<sup>133</sup>, May<sup>133</sup>, Jun<sup>7</sup> (2017<sup>133</sup>). Collections: WSUC. Floral records: APIACEAE: Lomatium utriculatum<sup>133</sup>; CARYO-PHYLLACEAE: Cersatium arvense<sup>133</sup>
- 104. Andrena (Trachandrena) miranda Smith, 1879. County records: Asotin<sup>3,12</sup>, Columbia<sup>12</sup>, King<sup>3,12</sup>, Kitsap<sup>3,12</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,59</sup>, Pend Oreille<sup>3,12</sup>, Pierce<sup>3,12</sup>, Spokane<sup>1,2</sup>, Stevens<sup>3,12</sup>, Thurston<sup>1,2,3,12,133</sup>, Walla Walla<sup>3,12</sup>, Whatcom<sup>6</sup>, Whitman<sup>2,3,7,12</sup>. Seasonality: May<sup>7,133</sup>, Jun<sup>1,2,3,6,7,12,133</sup>, Jul<sup>1,2,3,7</sup>, Aug<sup>1,2</sup> (2020<sup>133</sup>). Collections: BBSL, CUIC, INHS, NMNH, WSDA, WSUC. [= Andrena grandior Cockerell, 1897]. Holotype. USA, Washington, Thurston County, Olympia; 18 June 1895; Type No. 18954, USNM ENT 00533617. Floral records: APIACEAE: Lomatium utriculatum<sup>133</sup>; ASPARAGACEAE: Camassia quamash<sup>133</sup>; ASTERACEAE: Achillea millefolium<sup>133</sup>; BRASSICACEAE: Lepidium campestre<sup>133</sup>; CAPRIFOLIACEAE: Symphoricarpos albus<sup>133</sup>; ROSACEAE: Potentilla gracilis<sup>3,59</sup>, Rubus parviflorus<sup>3,59</sup>
- **105.** Andrena (Trachandrena) quintiliformis Viereck, 1916. County records: Okanogan<sup>1,2,3,59</sup>, Whitman<sup>3,7,12</sup>, Yakima<sup>3,12</sup>. Seasonality: May<sup>7</sup>, Jun<sup>1,2,3,7</sup>, Jul<sup>1,2,3,7</sup>, Aug<sup>1,2,3</sup> (2004<sup>1,2,3</sup>). Collections: BBSL, WSUC. Floral records: ROSACEAE: *Potentilla gracilis*<sup>3,59</sup>
- 106. Andrena (Trachandrena) salicifloris Cockerell, 1897. County records: Clallam<sup>3,12</sup>, Grays Harbor<sup>3,12</sup>, Island<sup>3,12</sup>, Jefferson<sup>1,2,3</sup>, King<sup>2,3,7,12,116</sup>, Kitsap<sup>2,3,12</sup>, Klickitat<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Pacific<sup>3,12</sup>, Pierce<sup>1,2,3,12</sup>, Skagit<sup>10</sup>, Snohomish<sup>1,2,3,12</sup>,

**Spokane**<sup>1,2</sup>, **Stevens**<sup>1,2</sup>, Thurston<sup>1,2,3,12,116,133</sup>, Whitman<sup>1,3,7,12</sup>. Seasonality: Apr<sup>1,2,3,7,12,116</sup>, May<sup>1,2,3,7,12,116,133</sup>, Jun<sup>1,2,3,7</sup>, Jul<sup>1,3</sup>, Aug<sup>2</sup>, Sep<sup>1</sup>, Nov<sup>1,3</sup> (2017<sup>133</sup>). Collections: AMNH, BBSL, INHS, NMNH, OSUC, UCMC, WSUC, WWUC. [= *Trachandrena auricauda* Viereck, 1904]. **Holotype**. USA, Washington State. Floral records: ASPARAGACEAE: *Camassia quamash*<sup>133</sup>; GROSSULARIACE-AE: *Ribes*<sup>116</sup>; ROSACEAE: *Rosa nutkana* ssp. *nutkana*<sup>3,59</sup>; SALICACEAE: *Salix*<sup>116</sup>

- 107. Andrena (Trachandrena) semipunctata Cockerell, 1902. County records: King<sup>1,2,3,12</sup>, Kittitas<sup>2,3</sup>, Lincoln<sup>3,12</sup>, Yakima<sup>2,3,12</sup>. Seasonality: Apr<sup>1,2,3,12</sup>, Jun<sup>1,2</sup> (1989<sup>2,3</sup>). Collections: INHS, NMNH. Holotype. USA, Washington, King County, Seattle; 5 April 1896; T Kincaid; Type No. 18922, USNM ENT 00533728
- 108. Andrena (Trachandrena) sigmundi Cockerell, 1902. County records: Kit-sap<sup>2,3</sup>, Thurston<sup>133</sup>, Whitman<sup>3,12</sup>. Seasonality: Apr<sup>2,3</sup>, May<sup>133</sup> (2019<sup>133</sup>). Collections: INHS. Floral records: ASPARAGACEAE: Camassia quamash<sup>133</sup>
- 109. Andrena (Trachandrena) striatifrons Cockerell, 1897. County records: Benton<sup>7</sup>, King<sup>3,12</sup>, Kittitas<sup>2,3</sup>, Pacific<sup>3,12</sup>, Pierce<sup>3,12</sup>, Thurston<sup>1,2,3,12</sup>, Whitman<sup>1,2,3,7,12</sup>, Yakima<sup>2,3,7,12</sup>. Seasonality: Apr<sup>1,2,3,7,12</sup>, May<sup>7</sup>, Jun<sup>3,7</sup> (1989<sup>2,3</sup>). Collections: INHS, NMNH, WSUC. Holotype. USA, Washington, Thurston County, Olympia; 19 April 1894; T Kincaid; Type No. 18945, USNM ENT 533735. [= *Trachandrena pernuda* Viereck, 1904]. Holotype. USA, Washington, Whitman County, Pullman; CV Piper.

## Panurginae: Calliopsini

## Genus Calliopsis Smith

- 110. *Calliopsis* (*Nomadopsis*) *edwardsii* Cresson, 1878. County records: Klickitat<sup>1,2</sup>, Spokane<sup>3</sup>. Seasonality: Jul<sup>1,2,3</sup>, Aug<sup>1,2</sup>, Sep<sup>1,2</sup> (2011<sup>1,2</sup>). Collections: BBSL, UCRC
- 111. Calliopsis (Nomadopsis) personata Cockerell, 1897. County records: Adams<sup>3</sup>, Benton<sup>1,2,3</sup>, Franklin<sup>1,2,118,123</sup>, Walla Walla<sup>1,2,3</sup>. Seasonality: May<sup>1,2,3,118,123</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup> (1995<sup>1,2,3</sup>). Collections: AMNH, BBSL, NMNH, UCRC. Holotype. USA, Washington, Franklin County, Pasco; 25 May 1896; Type No. 18985, USNM ENT 00533826.
- **112.** †**‡** *Calliopsis* (*Nomadopsis*) *scutellaris* Fowler, 1899. County records: Adams<sup>3</sup>. Seasonality: Jul<sup>3</sup> (1920<sup>3</sup>). Collections: UCRC
- 113. ‡ Calliopsis (Nomadopsis) xenus (Rozen, 1958). County records: Pierce<sup>123</sup> (Yakima<sup>1,2,3</sup>). Seasonality: Jul<sup>1,2,3,123</sup> (1949<sup>1,2,3,123</sup>). Collections: SEMC. Paratype. USA, Washington, Chinook Pass; 29 July 1949; RH Beamer. Floral records: BORAGINACEAE: Mertensia paniculata<sup>1,2</sup>; HYDROPHYLLACEAE: Phacelia hastata var. hastata<sup>1,2</sup>. Comments: The paratype label describes the locality as only Chinook Pass, Wash., which is located on the Pierce and Yakima County line. Rozen (1958) reports the paratype as being collected in Pierce County. Discover Life and GBIF report the paratype as being collected in Yakima County. It is unclear which county is correct, so both counties are being presented here with preference given to Rozen (1958).

## Panurgini

## Genus Panurginus Nylander

- 114. Panurginus atriceps (Cresson, 1878). County records: Clark<sup>1,2</sup>, Cowlitz<sup>1,2,3</sup>, King<sup>34,118</sup>, Skagit<sup>1,2,3</sup>, Thurston<sup>87</sup>, Whitman<sup>1,2,3</sup>, Yakima<sup>1,2,3</sup>. Seasonality: May<sup>1,2,118</sup>, Jun<sup>1,2,3,118</sup>, Jul<sup>1,2,3,118</sup>, Aug<sup>1,2,3</sup> (2014<sup>3</sup>). Collections: BBSL, JRYA, NMNH, PWRC, SEMC. Floral records: ROSACEAE: Rubus ursinus<sup>118</sup>
- 115. *Panurginus ineptus* Cockerell, 1922. County records: Clallam<sup>3</sup>, Pierce<sup>1,2,3,48</sup>, Skagit<sup>3</sup>. Seasonality: Jul<sup>1,2,3,48</sup>, Aug<sup>1,2,3</sup> (2014<sup>3</sup>). Collections: AMNH, BBSL, JRYA, OSUC
- 116. † *Panurginus nigrellus* Crawford, 1926. County records: Klickitat<sup>7</sup>. Seasonality: Jun<sup>7</sup> (1975<sup>7</sup>). Collections: WSUC

## Perditini

## Genus Perdita Smith

- **117.** *Perdita* (*Cockerellia*) *albipennis* Cresson, 1868. Comments: Viereck et al. (1905) indicate that *P. albipennis* is present in Washington, but do not provide a locality.
- **118.** *Perdita* (*Cockerellia*) *lingualis* Cockerell, 1896. County records: Whitman<sup>1,2,3,8</sup>. Seasonality: Sep<sup>1,2,3</sup> (1982<sup>1,2,3</sup>). Collections: BBSL, WSUC. Floral records: ASTERACEAE: *Helianthus annuus*<sup>8</sup>; GERANIACEAE: *Geranium viscosissimum*<sup>8</sup>; ROSACEAE: *Rosa*<sup>8</sup>
- 119. ‡ *Perdita* (*Perdita*) *ciliata* Timberlake, 1958. County records: Chelan<sup>2,67,112</sup>. Seasonality: Aug<sup>2,67</sup> (1941<sup>2,67,112</sup>). Collections: LACM. [= *Perdita crassihirta* Timberlake, 1968]. Holotype. USA, Washington, Chelan County, Wenatchee; 21 August 1941; J Roberds; LACM ENT 164669. Conservation status: Data Deficient (National Research Council 2007)
- 120. Perdita (Perdita) oregonensis Timberlake, 1929. County records: Benton<sup>7</sup>, Franklin<sup>66</sup>. Seasonality: Sep<sup>66</sup>, Oct<sup>7</sup> (1994<sup>7</sup>). Collections: WSUC
- 121. Perdita (Perdita) salicis imperialis Cockerell, 1925. County records: Asotin<sup>89</sup>, Benton<sup>7</sup>, Spokane<sup>89</sup>, Walla Walla<sup>89</sup>, Whitman<sup>89</sup>. Seasonality: May<sup>7,89</sup>, Jun<sup>89</sup>, Jul<sup>89</sup> (1994<sup>7</sup>). Collections: WSUC
- 122. §‡ Perdita (Perdita) similis pascoensis Timberlake, 1958. County records: Franklin<sup>1,2,3,66,112</sup>. Seasonality: Sep<sup>1,2,3,66</sup> (1904<sup>1,2,3,66</sup>). Collections: NMNH. Holotype. USA, Washington, Franklin County, Pasco; 11 September 1904; ESG Titus; Type No. 64325, USNM ENT 00532871. Conservation status: Vulnerable (National Research Council 2007)
- 123. † *Perdita (Perdita) zonalis* Cresson, 1879. County records: Whitman<sup>1,2,3</sup>. Seasonality: Sep<sup>1,2,3</sup> (1982<sup>1,2,3</sup>)
- 124. ‡ *Perdita (Pygoperdita) nevadensis nevadensis* Cockerell, 1896. County records: Chelan<sup>1,2,3,88</sup>, Spokane<sup>1,2,3</sup>. Seasonality: Jul<sup>1,2,3,88</sup> (1949<sup>1,2,88</sup>). Collections: BBSL, INHS, SEMC, UCRC

- 125. Perdita (Pygoperdita) wyomingensis Cockerell, 1922. County records: Whitman<sup>3</sup>. Seasonality: Jun<sup>3</sup> (1962<sup>3</sup>). Collections: UCRC
- 125a. § Perdita (Pygoperdita) wyomingensis sculleni Timberlake, 1956. County records: Whitman<sup>8,88</sup>, Yakima<sup>6</sup>. Seasonality: Jun<sup>88</sup>, Jul<sup>6,88</sup> (2022<sup>6</sup>). Collections: WSDA, WSUC. Conservation status: Vulnerable (National Research Council 2007). Floral records: ASTERACEAE: Achillea millefolium<sup>8</sup>; ROSACEAE: Holodiscus discolor<sup>8</sup>
- 125b. † *Perdita (Pygoperdita) wyomingensis segona* Timberlake, 1956. County records: Benton<sup>1,2</sup>, Spokane<sup>1,2</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL

### Apidae: Anthophorinae: Anthophorini

#### Genus Anthophora Latreille

- 126. Anthophora (Clisodon) terminalis Cresson, 1869. County records: Benton<sup>1,2</sup>, Okanogan<sup>1,2,3</sup>, Pierce<sup>1,2,3,6</sup>, San Juan<sup>1,2,3,124,136</sup>, Spokane<sup>1,2</sup>, Thurston<sup>1,2,118</sup>, Whatcom<sup>6</sup>, Whitman<sup>1,2,3</sup>. Seasonality: Jun<sup>1,2,3</sup>, Jul<sup>1,2,3,6,118</sup>, Aug<sup>6</sup> (2021<sup>1,2</sup>). Collections: BBSL, iNaturalist, NMNH, PWRC, SEMC, WSDA. [= Podalirius syringae Cockerell, 1898]. Holotype. USA, Washington, Thurston County, Olympia; 2 July 1896; Type No. 20234, USNM ENT 00534169. Conservation status: G5 Secure globally (NatureServe 2024). Floral records: CONVOLVULACEAE: Calystegia soldanella<sup>136</sup>
- 127. Anthophora (Lophanthophora) affabilis Cresson, 1878. County records: Whitman<sup>32</sup>. Seasonality: Jun<sup>32</sup> (2013<sup>32</sup>). Conservation status: G5 Secure globally (NatureServe 2024)
- **128.** †§ *Anthophora* (*Lophanthophora*) *neglecta* Timberlake and Cockerell, 1936. County records: Benton<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2,3</sup> (1995<sup>1,2,3</sup>). Collections: BBSL. Conservation status: G3 – Vulnerable globally (NatureServe 2024)
- 129. Anthophora (Lophanthophora) pacifica Cresson, 1878. County records: Benton<sup>1,2,3</sup>, Chelan<sup>1,2,3</sup>, King<sup>1,2</sup>, Kittitas<sup>2,3</sup>, Okanogan<sup>1,2,3</sup>, Spokane<sup>1,2</sup>, Whitman<sup>1,2,3,8,61</sup>, Yakima<sup>1,2,3,121</sup>. Seasonality: Feb<sup>1,2</sup>, Mar<sup>1,2</sup>, Apr<sup>1,2,3,61</sup>, May<sup>1,2,3,121</sup> (2022<sup>1,2</sup>). Collections: BBSL, iNaturalist, INHS, SEMC, WSUC. Conservation status: G4 – Apparently Secure globally (NatureServe 2024). Floral records: API-ACEAE: Lomatium<sup>8</sup>; ASTERACEAE: Balsamorhiza sagittata<sup>8</sup>; FABACEAE: Astragalus columbianus<sup>3</sup>, A. sinuatus<sup>3</sup>; GROSSULARIACEAE: Ribes<sup>3</sup>, R. aureum<sup>8</sup>; LAMIACEAE: Salvia dorrit<sup>3</sup>; OLEACEAE; Syringa<sup>8</sup>; ROSACEAE: Malus domestica<sup>8</sup>, Prunus armeniaca<sup>8</sup>
- 130. Anthophora (Lophanthophora) porterae Cockerell, 1900. County records: Benton<sup>1,2,3</sup>, Chelan<sup>136</sup>, Garfield<sup>1,2,3,46</sup>, Walla Walla<sup>1,2</sup>, Whitman<sup>1,2</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2,3</sup>, May<sup>1,2,3</sup> (2012<sup>1,2</sup>). Collections: BBSL, SEMC. Conservation status: G4 – Apparently Secure globally (NatureServe 2024). Floral records: FA-BACEAE: Astragalus<sup>3</sup>, A. columbianus<sup>3</sup>, A. speirocarpus<sup>3</sup>

- 131. Anthophora (Lophanthophora) ursina Cresson, 1869. County records: Adams<sup>3</sup>, Garfield<sup>1,2,3,46</sup>, Okanogan<sup>1,2,3,59</sup>, Spokane<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,8</sup>, Yakima<sup>2,121</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>1,2,3</sup>, May<sup>1,2,3,121</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL, SEMC, UCRC, WSUC. [= Anthophora simillima Cresson, 1879]. Conservation status: G4 – Apparently Secure globally (NatureServe 2024). Floral records: FABACEAE: Astragalus<sup>3</sup>, Vicia villosa<sup>8</sup>; ROSACEAE: Rosa nutkana ssp. nutkana<sup>3,59</sup>
- 132. Anthophora (Melea) bomboides Kirby, 1837. County records: Chelan<sup>1,2,3</sup>, Clallam<sup>1,2</sup>, Garfield<sup>1,2,3,46</sup>, Island<sup>2,3,106</sup>, Jefferson<sup>1,2</sup>, King<sup>1,2,106</sup>, Kittitas<sup>1,2</sup>, Pierce<sup>1,2,6</sup>, San Juan<sup>1,2,3,5,6,22,106,136</sup>, Spokane<sup>1,2</sup>, Thurston<sup>1,2,106</sup>, Walla Walla<sup>1,2</sup>, Whatcom<sup>2,106</sup>, Whitman<sup>8,106</sup>, Yakima<sup>1,2,3,121</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3,121</sup>, Jun<sup>1,2,3,5,6</sup>, Jul<sup>1,2,6</sup>, Aug<sup>2,3,6</sup> (2020<sup>1,2,6</sup>). Collections: BBSL, iNaturalist, PMNH, PWRC, SEMC, UCRC, WSDA, WSUC. [= Anthophora sodalis Cresson, 1879]. [= Anthophora bomboides solitaria Ritsema, 1880]. [= Anthophora bomboides stanfordiana Cockerell, 1904]. Conservation status: G5 Secure globally (NatureServe 2024). Floral records: ASPARAGACEAE: Brodiaea coronaria<sup>5</sup>; ASTERACEAE: Balsamorhiza<sup>3</sup>; BRASSICACEAE: Cakile maritima<sup>136</sup>; CAPRIFOLIACEAE: Symphoricarpos albus<sup>136</sup>; CONVOLVULACEAE: Calystegia soldanella<sup>136</sup>; FABACEAE: Astragalus podolobus<sup>3</sup>; ROSACEAE: Rosa nutkana<sup>136</sup>, Rubus bifrons<sup>136</sup>
- 133. \$ Anthophora (Melea) occidentalis Cresson, 1869. County records: Chelan<sup>1,2</sup>, King<sup>1,2</sup>, Whitman<sup>1,2</sup>, Yakima<sup>1,2,106</sup>. Seasonality: Apr<sup>2</sup>, May<sup>1,2</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2</sup> (1982<sup>1,2</sup>). Collections: SEMC. Conservation status: G3 – Vulnerable globally (NatureServe 2024)
- **134.** *Anthophora (Micranthophora) albata* Cresson, **1876**. County records: Benton<sup>1,2,107</sup>, Chelan<sup>107</sup>, **Douglas**<sup>2,3</sup>. Seasonality: Jun<sup>1,2,107</sup>, Aug<sup>2,107</sup> (1995<sup>1,2,107</sup>). Collections: BBSL, SEMC. Conservation status: G4 Apparently Secure globally (NatureServe 2024)
- **135.** † *Anthophora (Micranthophora) curta* **Provancher, 1895.** County records: Walla Walla<sup>1,2,107</sup>. Seasonality: Jun<sup>1,2,107</sup>, Jul<sup>107</sup> (2012<sup>1,2,107</sup>). Collections: BBSL. Conservation status: G5 Secure globally (NatureServe 2024)
- 136. ‡ Anthophora (Micranthophora) exigua Cresson, 1879. County records: Adams<sup>7</sup>, Grant<sup>7</sup>, Kittitas<sup>1,107</sup>. Seasonality: Jun<sup>7</sup>, Jul<sup>1,107</sup>, Sep<sup>7</sup>, Aug<sup>7</sup> (1949<sup>1,107</sup>). Collections: SEMC, WSUC. Conservation status: G4 – Apparently Secure globally (NatureServe 2024)
- 137. † Anthophora (Micranthophora) peritomae Cockerell, 1905. County records: Benton<sup>7</sup>. Seasonality: Aug<sup>7</sup> (1994<sup>7</sup>). Collections: WSUC
- **138.** *Anthophora (Mystacanthophora) urbana* Cresson, 1878. County records: Benton<sup>1,2,3,71</sup>, Chelan<sup>1,2</sup>, Douglas<sup>1,2</sup>, Grant<sup>1,2</sup>, Jefferson<sup>1,2</sup>, Kittias<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,59</sup>, Walla Walla<sup>1,2,3,71</sup>, Whitman<sup>2,3</sup>, Yakima<sup>121</sup>. Seasonality: Jun<sup>1,2,3,121</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2</sup> (2021<sup>1,2</sup>). Collections: BBSL, iNaturalist, SEMC. Conservation status: G5 – Secure globally (NatureServe 2024). Floral records: HYDROPHYLLACEAE: *Phacelia hastata*<sup>3</sup>; PLANTAGINACEAE: *Penstemon washingtonensis*<sup>3,59</sup>

- 139. § Anthophora (Pyganthophora) crotchii Cresson, 1878. County records: Adams<sup>1,2,3</sup>, Benton<sup>1,2</sup>, Franklin<sup>1,2,3,118</sup>, Grant<sup>1,2,3</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3</sup>, Yakima<sup>2,121</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>1,2,3,121</sup>, May<sup>1,2,3,118,121</sup>, Jun<sup>1,2,3</sup> (2022<sup>1,2</sup>). Collections: AMNH, BBSL, iNaturalist, SEMC, UCRC. [= Anthophora washingtoni Cockerell, 1905]. Holotype. USA, Washington, Franklin County, Pasco; 25 May 1896; T Kincaid. Conservation status: G3 Vulnerable globally (NatureServe 2024)
- 140. ‡ Anthophora (Pyganthophora) edwardsii Cresson, 1878. County records: Douglas<sup>3</sup>, Garfield<sup>46</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3</sup>, Yakima<sup>1,2,3,121</sup>. Seasonality: Apr<sup>1,2,121</sup>, May<sup>1,2,3,121</sup>, Jun<sup>1,2</sup> (1937<sup>1,2</sup>). Collections: SEMC, UCRC. Conservation status: G4 – Apparently Secure Globally (NatureServe 2024)

#### Genus Habropoda Smith

- 141. Habropoda cineraria (Smith, 1879). County records: Adams<sup>2</sup>, Asotin<sup>2</sup>, Benton<sup>1,2,3</sup>, Chelan<sup>1,2,3</sup>, Franklin<sup>1,2</sup>, King<sup>1</sup>, Kittitas<sup>2,3</sup>, Spokane<sup>1,2</sup>, Whitman<sup>1,2,3,8</sup>, Yakima<sup>1,2,3,121</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>1,2,3,121</sup>, May<sup>1,2,3</sup> (2015<sup>1,2</sup>). Collections: BBSL, INHS, SEMC, WSUC. Conservation status: G5 Secure globally (NatureServe 2024). Floral records: GROSSULARIACEAE: *Ribes<sup>3</sup>*, *R. aureum<sup>8</sup>*; LAMIACEAE; Salvia dorrii<sup>3</sup>; ROSACEAE: Malus domestica<sup>8</sup>, Prunus armeniaca<sup>8</sup>, Rosa<sup>8</sup>
- 142. † *Habropoda cressonii* (Dalla Torre, 1896). County records: Whitman<sup>2</sup>. Seasonality: Apr<sup>2</sup> (1973<sup>2</sup>). Collections: SEMC
- 143. †§ *Habropoda miserabilis* (Cresson, 1878). County records: Jefferson<sup>1,2</sup>, King<sup>1,2</sup>, Okanogan<sup>1,2,3</sup>, Pacific<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2,3</sup>, May<sup>1,2,3</sup> (2022<sup>1,2</sup>). Collections: BBSL, iNaturalist, SEMC. Conservation status: G2 – Imperiled globally (NatureServe 2024)
- 144. Habropoda morrisoni (Cresson, 1878). County records: Benton<sup>1,2,3</sup>, Franklin<sup>1,2,118</sup>. Seasonality: Apr<sup>1,2,3</sup>, May<sup>1,2</sup> (1995<sup>1,2</sup>). Collections: BBSL, NMNH, SEMC. [= Emphoropsis floridana var. pascoensis Cockerell, 1878]. [= Habropoda floridana var. pascoensis Cockerell, 1878]. Holotype. USA, Washington, Franklin County, Pasco; 25 May 1896; Type No. 58047, USNM ENT 00534175. Conservation status: G4 Apparently Secure globally (NatureServe 2024)

#### Apinae: Apini

#### Genus Apis Linnaeus

145. \* Apis mellifera Linnaeus, 1758. County records: Adams<sup>1,2</sup>, Asotin<sup>1,2,3</sup>, Benton<sup>1,2,3,6,71</sup>, Chelan<sup>1,2,3</sup>, Clallam<sup>1,2,3,6</sup>, Clark<sup>1,2,3</sup>, Columbia<sup>1,2</sup>, Cowlitz<sup>1,2,3</sup>, Douglas<sup>1,2</sup>, Franklin<sup>1,2,6</sup>, Garfield<sup>1,2,46</sup>, Grant<sup>1,2,3,6</sup>, Grays Harbor<sup>1,2,6</sup>, Island<sup>1,2</sup>, Jefferson<sup>1,2,6</sup>, King<sup>1,2,3,6</sup>, Kitsap<sup>1,2,6</sup>, Kittitas<sup>1,2</sup>, Klickitat<sup>1,2,3</sup>, Lewis<sup>1,2,3</sup>, Lincoln<sup>1,2</sup>, Mason<sup>1,2,3</sup>, Okanogan<sup>1,2,3</sup>, Pacific<sup>1,2,3,6</sup>, Pierce<sup>1,2,3,6</sup>, San Juan<sup>1,2,3,5,6,124</sup>, Skagit<sup>1,2,3,6,10</sup>, Skamania<sup>1,2,3</sup>, Snohomish<sup>1,2,3,6</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2,3</sup>, Thurston<sup>1,2,3,6,130,133</sup>, Wahkiakum<sup>1,2,3</sup>, Walla Walla<sup>1,2,3,6,71</sup>, Whatcom<sup>1,2,3,6,33</sup>, Whitman<sup>1,2,3</sup>, Yakima<sup>1,2,3,6</sup>

Seasonality: Jan<sup>1,2</sup>, Feb<sup>1,2</sup>, Mar<sup>1,2,3</sup>, Apr<sup>1,2,3</sup>, May<sup>1,2,3,5,6,133</sup>, Jun<sup>1,2,3,5,6,133</sup>, Jul<sup>1,2,3,6,133</sup>, Aug<sup>1,2,3,6,33</sup>, Sep<sup>1,2,3,6</sup>, Oct<sup>1,2,3,6</sup>, Nov<sup>1,2,6</sup> (2022<sup>1,2,6</sup>). Collections: BBSL, EMEC, FMNH iNaturalist, JRYA, NMNH, OSUC, PWRC, SEMC, UNM, WSDA. Floral records: APIACEAE: *Heracleum sphondylium* ssp. *Montanum*<sup>5</sup>; APOC-YNACEAE: *Apocynum androsaemifolium*<sup>133</sup>; ASPARAGACEAE: *Camassia quamash*<sup>133</sup>, *Triteleia hyacinthina*<sup>133</sup>; ASTERACEAE: *Balsamorhiza deltoidea*<sup>133</sup>, *Crepis capillaris*<sup>133</sup>, *Cirsium arvense*<sup>133</sup>, *Eriophyllum lanatum*<sup>133</sup>, *Hypochaeris radicata*<sup>133</sup>, *Leucanthemum vulgare*<sup>133</sup>, *Solidago simplex*<sup>133</sup>; CAPRIFOLIACEAE: *Plectritis congesta*<sup>133</sup>, *Symphoricarpos albus*<sup>5,133</sup>; ERICACEAE: *Arctostaphylos uva-ursi*<sup>133</sup>; FABACEAE: *Lupinus albicaulis*<sup>133</sup>, *L. bicolor*<sup>133</sup>, *L. lepidus*<sup>133</sup>, *Trifolium repens*<sup>133</sup>, *Vicia hirsuta*<sup>133</sup>, V. sativa<sup>133</sup>; HYPERICACEAE: *Collinsia grandiflora*<sup>133</sup>; LAMI-ACEAE: *Salvia dorrii*<sup>3</sup>; PLANTAGINACEAE: *Collinsia grandiflora*<sup>133</sup>; PLUM-BAGINACEAE: *Armeria maritima*<sup>133</sup>; POLEMONIACEAE: *Gilia capitata*<sup>133</sup>. Comments: Due to its ubiquitous use in commercial agriculture, it is assumed that *A. mellifera* occurs in Ferry and Pend Oreille counties as well.

## Bombini

### Genus Bombus Latreille

- 146. †§ Bombus (Alpinobombus) kirbiellus Curtis, 1835. County records: Okanogan<sup>1,2,3</sup>. Seasonality: Aug<sup>1,2,3</sup> (2019<sup>1,2,3</sup>). Collections: BOMBUS, iNaturalist, NMNH. Conservation status: Data Deficient (Hatfield et al. 2016a); G4 Apparently Secure globally, S1 Critically Imperiled in Washington (NatureServe 2024)
- 147. Bombus (Bombias) nevadensis Cresson, 1874. County records: Adams<sup>1,2</sup>, Asotin<sup>1,2,3</sup>, Benton<sup>1,2,3</sup>, Chelan<sup>1,2,3</sup>, Clark<sup>1,2</sup>, Columbia<sup>1,2</sup>, Douglas<sup>1,2</sup>, Ferry<sup>1,2</sup>, Franklin<sup>1,2</sup>, Garfield<sup>1,2,3,46</sup>, Grant<sup>1,2,3</sup>, Island<sup>1,2,3</sup>, King<sup>1,2,3</sup>, Kitsap<sup>1,2,3</sup>, Kittitas<sup>1,2,</sup>, Klickitat<sup>1,2,3</sup>, Lincoln<sup>1,2</sup>, Okanogan<sup>1,2</sup>, Pend Oreille<sup>1,2</sup>, Pierce<sup>1,2</sup>, San Juan<sup>1,2,3</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2,3</sup>, Thurston<sup>1,2,3</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3,8</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2,3</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2,3</sup>, Oct<sup>1,2</sup> (2021<sup>1,2</sup>). Collections: AMNH, BBSL, BOMBUS, CNC, EMEC, iNaturalist, INHS, NMNH, PMNH, UCRC, WSUC. Conservation status: Least Concern (Hatfield et al. 2015a); G4 Apparently Secure globally, S4 Apparently Secure in Washington (NatureServe 2024). Floral records: ASPARAGACEAE: Triteleia grandiflora<sup>8</sup>; ASTERACEAE: Balsamorhiza sagittata<sup>8</sup>, Cirsium vulgare<sup>8</sup>, Solidago<sup>8</sup>; DIPSACACEAE: Dipsacus fullonum<sup>8</sup>; FABACEAE: Astragulus<sup>8</sup>, Medicago sativa<sup>8</sup>, Trifolium pratense<sup>3</sup>, T. repens<sup>8</sup>, Vicia villosa<sup>8</sup>; HYDROPHYLLACEAE: Phacelia<sup>8</sup>; LAMIACEAE: Agastache urticifolia<sup>8</sup>; PLANTAGINACEAE: Penstemon<sup>8</sup>; ROSACEAE: Malus domestica<sup>8</sup>
- 148. § Bombus (Bombus) occidentalis Greene, 1858. County records: Asotin<sup>1,2,3</sup>, Benton<sup>1,2,3</sup>, Chelan<sup>1,2,3</sup>, Clallam<sup>1,2,3,124</sup>, Columbia<sup>1,2,3</sup>, Cowlitz<sup>1,3</sup>, Douglas<sup>1,2</sup>, Ferry<sup>1,2,3</sup>, Franklin<sup>1,2</sup>, Garfield<sup>1,2,3,46</sup>, Grant<sup>1,2,3</sup>, Grays Harbor<sup>1,2,3</sup>, Island<sup>1,2,3,6</sup>, Jefferson<sup>1,2,3,124</sup>, King<sup>1,2,3</sup>, Kitsap<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,3</sup>, Lewis<sup>1,2,3</sup>

Lincoln<sup>1,2,3</sup>, Mason<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Pacific<sup>1,2,3</sup>, Pend Oreille<sup>1,2,3</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>1,2,3</sup>, Skagit<sup>1,2,3</sup>, Skamania<sup>1,2,3</sup>, Snohomish<sup>1,2,3,6</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2,3</sup>, Thurston<sup>1,2,3,130</sup>, Wahkiakum<sup>1,2,3</sup>, Walla Walla<sup>1,2,3</sup>, Whatcom<sup>1,2,3,6</sup>, Whitman<sup>1,2,3,8</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Jan<sup>2</sup>, Feb<sup>1,2</sup>, Mar<sup>1,2</sup>, Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3,6</sup>, Aug<sup>1,2,3,6</sup>, Sep<sup>1,2,3</sup>, Oct<sup>1,2</sup>, Dec<sup>1,2</sup> (2021<sup>1,2,6</sup>). Collections: AMNH, BBSL, BOMBUS, CNC, CSCA, EMEC, FMNH, iNaturalist, INHS, JRYA, LACM, NMNH, PMNH, SEMC, TAMU, UCMC, UCRC, WSDA, WSUC. Conservation status: Vulnerable (National Research Council 2007; Hatfield et al. 2015b); G3 – Vulnerable globally, S2 – Imperiled in Washington (NatureServe 2024). Floral records: ASPARAGACEAE: Triteleia grandiflora<sup>8</sup>; ASTERACEAE: Arnica cordifolia<sup>59</sup>, Balsamorhiza sagittata<sup>8</sup>, Cirsium vulgare<sup>8</sup>, Erigeron speciosus<sup>59</sup>; FABACEAE: Lupinus polyphyllus<sup>8</sup>; Medicago sativa<sup>8</sup>, Trifolium repens<sup>8</sup>, Vicia villosa<sup>8</sup>; HYDROPHYLLACEAE: Phacelia<sup>8</sup>; IRIDACEAE: Sisyrinchium<sup>8</sup>; ONA-GRACEAE: Chamerion angustifolium ssp. Angustifolium<sup>8</sup>; PLANTAGINACE-AE: *Penstemon*<sup>8</sup>; RANUNCULACEAE: *Aconitum columbianum*<sup>8</sup>; ROSACEAE: Malus domestica<sup>8</sup>, Rosa<sup>8</sup>, Rubus parviflorus<sup>8</sup>

- 149. Bombus (Cullumanobombus) griseocollis (DeGeer, 1773). County records: Adams<sup>1,2</sup>, Asotin<sup>1,2</sup>, Benton<sup>1,2,3</sup>, Chelan<sup>1,2,3</sup>, Clark<sup>1,2,3,124</sup>, Douglas<sup>1,2</sup>, Franklin<sup>1,2,3</sup>, Garfield<sup>1,2,46</sup>, Grant<sup>1,2,3</sup>, Kittitas<sup>1,2</sup>, Klickitat<sup>1,2</sup>, Lincoln<sup>1,2</sup>, Okanogan<sup>1,2,3</sup>, Pierce<sup>3</sup>, Spokane<sup>1,2,3</sup>, Thurston<sup>130</sup>, Walla Walla<sup>1,2,3,71</sup>, Whitman<sup>1,2,3,6,8</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Jan<sup>1,2</sup>, Apr<sup>1,2,3</sup>, May<sup>1,2,3,6</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2,3</sup>, Oct<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: BBSL, BOMBUS, BugGuide, EMEC, iNaturalist, INHS, LACM, NMNH, UCDC, UCRC, WSDA, WSUC. Conservation status: Least Concern (Hatfield et al. 2015d); G5 – Secure globally, S5 – Secure in Washington (NatureServe 2024). Floral records: ASTERACEAE: Balsamorhiza sagittata<sup>8</sup>, Helianthus annuus<sup>8</sup>, Solidago<sup>8</sup>; FABACEAE: Lupinus polyphyllus<sup>8</sup>, Medicago sativa<sup>8</sup>, Vicia villosa<sup>8</sup>; HYDROPHYLLACEAE: Phacelia<sup>8</sup>; IRIDACEAE: Sisyrinchium<sup>8</sup>; ONAGRACEAE: Chamerion angustifolium ssp. Angustifolium<sup>8</sup>; PLANTAGI-NACEAE: Penstemon<sup>8</sup>; ROSACEAE: Rosa<sup>8</sup>
- 150. § Bombus (Cullumanobombus) morrisoni Cresson, 1878. County records: Adams<sup>1,2</sup>, Asotin<sup>2,3</sup>, Benton<sup>1,2</sup>, Chelan<sup>1,2,3</sup>, Franklin<sup>1,2</sup>, Grant<sup>1,2,3</sup>, Grays Harbor<sup>1,2</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Pierce<sup>1,2,3</sup>, Spokane<sup>1,2,3</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3</sup>, Yakima<sup>1,2</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1</sup>, Oct<sup>1</sup> (2021<sup>1,2</sup>). Collections: AMNH, BBSL, iNaturalist, INHS, NMNH, UCMC. Conservation status: Vulnerable (Hatfield et al. 2014a); G3 – Vulnerable globally, S4 – Apparently Secure in Washington (NatureServe 2024). Floral records: FABACEAE: Trifolium pratense<sup>3</sup>; PLANTAGINACEAE: Penstemon washingtonensis<sup>59</sup>
- 151. Bombus (Cullumanobombus) rufocinctus Cresson, 1863. County records: Asotin<sup>1,2,3</sup>, Benton<sup>1,2,3</sup>, Chelan<sup>1,2,3</sup>, Clallam<sup>1,2,3</sup>, Clark<sup>1,2,3</sup>, Columbia<sup>1,2,3</sup>, Douglas<sup>1,2</sup>, Ferry<sup>1,2,3</sup>, Garfield<sup>1,2,3</sup>, Island<sup>124</sup>, Jefferson<sup>1,2</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Lewis<sup>1,2,4</sup>, Lincoln<sup>1,2,3</sup>, Mason<sup>1,2</sup>, Okanogan<sup>1,2,3,59</sup>, Pend Oreille<sup>1,2,3</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>1,2,3,5,124</sup>, Skamania<sup>1,2,3</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2,3</sup>, Thurston<sup>133</sup>, Walla Walla<sup>1,2</sup>

Whatcom<sup>1,2,3</sup>, Whitman<sup>1,2,3,6,8</sup>, Yakima<sup>1,2</sup>. Seasonality: May<sup>1,2,3,4,5,133</sup>, Jun<sup>1,2,3,5,6</sup>, Aug<sup>1,2,3,5</sup>, Sep<sup>1,2,3</sup>, Oct<sup>1,2,3</sup> (2021<sup>1,2</sup>). Collections: BBSL, BOMBUS, Bug-Guide, EMEC, FMNH, iNaturalist, INHS, JRYA, LACM, PCYU, PMNH, PWRC, SEMC, UCRC, WSDA, WSUC. Conservation status: Least Concern (Hatfield et al. 2015e); G5 – Secure globally, S4 – Apparently Secure in Washington (NatureServe 2024). Floral records: ASPARAGACEAE: *Triteleia grandiflora*<sup>8</sup>; ASTERACEAE: *Cirsium arvense*<sup>3</sup>, *Erigeron speciosus*<sup>3,59</sup>, *Eriophyllum lanatum*<sup>133</sup>, *Crepis capillaris*<sup>5</sup>, *Jacobaea vulgaris*<sup>5</sup>, *Solidago simplex*<sup>133</sup>; GERANIACEAE: *Geranium viscosissimum*<sup>8</sup>; HYDROPHYLLACEAE: *Phacelia*<sup>3,5,8</sup>, *P. hastata*<sup>3</sup>; IRI-DACEAE: *Sisyrinchium*<sup>8</sup>; ONAGRACEAE: *Chamerion angustifolium* ssp. *Angustifolium*<sup>8</sup>; ROSACEAE: *Rosa nutkana*<sup>5</sup>, *Rubus ulmifolius*<sup>5</sup>, *R. ursinus*<sup>5</sup>

- 152. § Bombus (Psithyrus) flavidus Eversmann, 1852. County records: Chelan<sup>1,2,3</sup>, Clallam<sup>1,2,3</sup>, Columbia<sup>1,2</sup>, Grays Harbor<sup>1,2,3</sup>, Island<sup>2,3</sup>, Jefferson<sup>1,2,3</sup>, King<sup>1,2,3</sup>, Kitsap<sup>1,2,3</sup>, Kittias<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Mason<sup>1,2</sup>, Okanogan<sup>1,2,3,59</sup>, Pacific<sup>1,2</sup>, Pend Oreille<sup>1,2</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>1,2,3,124</sup>, Skagit<sup>1,2,3</sup>, Skamania<sup>1,2,3</sup>, Snohomish<sup>1,2</sup>, Thurston<sup>1,2</sup>, Whatcom<sup>1,2,3,4</sup>, Whitman<sup>1,2,3</sup>, Yakima<sup>1,2</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3,4</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2,3</sup>, Oct<sup>1,2</sup> (2021<sup>1,2</sup>). Collections: BBSL, BugGuide, CNC, LACM, NMNH, PMNH, PWRC, SEMC, TAMU, UCRC, WSDA. [= Bombus fernaldae (Franklin, 1911)]. [= Psithyrus tricolor Franklin, 1911]. Conservation status: Data Deficient (Hatfield et al. 2016d); G5 Secure Globally, S3 Vulnerable in Washington (NatureServe 2024). Floral records: ASTERACEAE: Centaurea<sup>3</sup>, Cirsium<sup>3</sup>; BRASSICACEAE: Smelowskia calycina<sup>359</sup>
- 153. § Bombus (Psithyrus) insularis (Smith, 1861). County records: Asotin<sup>1,2,3</sup>, Chelan<sup>1,2,3</sup>, Clallam<sup>1,2</sup>, Clark<sup>1,2</sup>, Columbia<sup>1,2,3</sup>, Ferry<sup>1,2</sup>, Garfield<sup>1,2,3</sup>, Grays Harbor<sup>1,2,3</sup>, Jefferson<sup>1,2,3</sup>, King<sup>1,2,3</sup>, Kitsap<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2,3</sup>, Lewis<sup>1,2</sup>, Lincoln<sup>1,2,3</sup>, Mason<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Pend Oreille<sup>1,2,3</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>1,2,3</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2,3</sup>, Whatcom<sup>1,2,3</sup>, Whitman<sup>1,2,3,8</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Jan<sup>1,2</sup>, Mar<sup>1,2</sup>, Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2,3</sup>, Oct<sup>1,2</sup> (20201,2). Collections: AMNH, BBSL, BOMBUS, CNC, EMEC, iNaturalist, INHS, JRYA, LACM, NMNH, NMSU, OSUC, PMNH, SEMC, UCRC, WSUC. Conservation status: Least Concern (Hatfield et al. 2014b); G3 - Vulnerable globally, S5 – Secure in Washington (NatureServe 2024). Floral records: ASTERACEAE: Achillea millefolium<sup>59</sup>, Agoseris glauca var. dasycephala<sup>59</sup>, Anaphalis margaritacea<sup>59</sup>, Cirsium arvense<sup>3</sup>, C. hookerianum<sup>59</sup>, C. vulgare<sup>59</sup>, Erigeron speciosus<sup>59</sup>, Microseris nutans<sup>59</sup>, Senecio triangularis<sup>59</sup>, Taraxacum officinale<sup>3,59</sup>; BRAS-SICACEAE: Smelowskia calycina<sup>59</sup>; CRASSULACEAE: Sedum lanceolatum<sup>59</sup>; DIPSACACEAE: Dipsacus fullonum<sup>8</sup>; FABACEAE: Melilotus albus<sup>59</sup>, Trifolium repens<sup>3</sup>, Vicia<sup>3</sup>; LAMIACEAE: Agastache urticifolia<sup>8</sup>; ONAGRACEAE: Chamerion angustifolium ssp. Angustifolium<sup>8</sup>, Epilobium<sup>3</sup>; PLANTAGINACEAE: Penstemon confertus<sup>59</sup>, P. washingtonensis<sup>59</sup>
- 154. †§ Bombus (Psithyrus) suckleyi Greene, 1860. County records: Chelan<sup>1,2</sup>, Clallam<sup>1,2</sup>, Columbia<sup>1,2</sup>, Douglas<sup>1,2</sup>, Ferry<sup>1,2</sup>, Jefferson<sup>1,2,3</sup>, King<sup>1,2,3</sup>, Kitsap<sup>1,2,3</sup>, Kittitas<sup>1,2</sup>, Lewis<sup>1,2,3</sup>, Mason<sup>1,2,3</sup>, Pend Oreille<sup>1,2,3</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>1,2,3</sup>, Skamania<sup>1,2</sup>,

Snohomish<sup>1,2</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2,3</sup>, Thurston<sup>1,2,3</sup>, Walla Walla<sup>1,2</sup>, Whitman<sup>1,2,3</sup>, Yakima<sup>1,2</sup>. Seasonality: Jan<sup>1</sup>, Apr<sup>1</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2,3</sup> (1998<sup>1,2</sup>). Collections: AMNH, BBSL, CNC, EMEC, FMNH, INHS, LACM, NMNH, PMNH, SEMC, UCRC, WSUC. Conservation status: Critically Endangered (Hatfield et al. 2015f); G2 – Imperiled globally, S1 – Critically Imperiled in Washington (NatureServe 2024). Floral records: ASPARAGACEAE: *Triteleia grandiflora*<sup>8</sup>; ASTERACEAE: *Senecio*<sup>8</sup>; IRIDACEAE: *Sisyrinchium*<sup>8</sup>; LAMIACEAE: *Agastache urticifolia*<sup>8</sup>; ONAGRACEAE: *Chamerion angustifolium* ssp. *Angustifolium*<sup>8</sup>

- 155. § Bombus (Pyrobombus) caliginosus (Frison, 1927). County records: Clallam<sup>1,2,3,124</sup>, Clark<sup>1,2</sup>, Cowlitz<sup>1,2,3</sup>, Grays Harbor<sup>1,2,3,6,70</sup>, Jefferson<sup>1,2,3</sup>, King<sup>2,3</sup>, Kitsap<sup>1,2,3</sup>, Lewis<sup>1,2,3</sup>, Mason<sup>1,2,3</sup>, Pacific<sup>1,2,3,6</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>2,3</sup>, Skamania<sup>1,2,3</sup>, Thurston<sup>1,2,3,6,133</sup>, Whatcom<sup>1,2,3</sup>. Seasonality: May<sup>1,2,133</sup>, Jun<sup>1,2,133</sup>, Jul<sup>1,2,3,6</sup>, Aug<sup>1,2,3,6</sup>, Sep<sup>6</sup> (2021<sup>6</sup>). Collections: BBSL, BOMBUS, EMEC, iNaturalist, INHS, JRYA, LACM, NMNH, PMNH, SEMC, WSDA. Conservation status: Vulnerable (Hatfield et al. 2014c); G2 Imperiled globally, S3 Vulnerable in Washington (NatureServe 2024). Floral records: ASTERACEAE: *Microseris laciniata*<sup>133</sup>; CAPRIFOLIACEAE: Symphoricarpos albus<sup>133</sup>; FABACEAE: Lathyrus odoratus<sup>3</sup>, Lupinus albicaulis<sup>133</sup>; LAMIACEAE: Prunella vulgaris<sup>133</sup>
- 156. Bombus (Pyrobombus) centralis Cresson, 1864. County records: Adams<sup>1,2,3</sup>, Asotin<sup>1,2,3</sup>, Benton<sup>1,2,3</sup>, Chelan<sup>1,2,3</sup>, Columbia<sup>1,2</sup>, Douglas<sup>1,2</sup>, Ferry<sup>1,2,3</sup>, Garfield<sup>1,2,3,46</sup>, Grant<sup>1,2,3</sup>, King<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2,3</sup>, Lincoln<sup>1,2</sup>, Mason<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Pend Oreille<sup>1,2</sup>, San Juan<sup>1,2,3</sup>, Skagit<sup>1,2,3</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2,3</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3,6,8</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Mar<sup>1,2,3</sup>, Apr<sup>1,2,3</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3,6</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2</sup>, Nov<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: AMNH, BBSL, BOMBUS, EMEC, iNaturalist, INHS, NMNH, PMNH, PWRC, SEMC, UCRC, WSDA, WSUC. Conservation status: Least Concern (Hatfield et al. 2014d); G5 – Secure globally, S4 – Apparently Secure in Washington (NatureServe 2024). Floral records: ASPARAGACEAE: Triteleia grandiflora8; ASTERACEAE: Anaphalis margaritacea<sup>8</sup>, Balsamorhiza sagittata<sup>8</sup>, Erigeron speciosus<sup>59</sup>, Rudbeckia occidentalis<sup>8</sup>; BORAGINACEAE: Mertensia paniculata<sup>8</sup>; CAPRI-FOLIACEAE: Lonicera<sup>3</sup>, Symphoricarpos albus<sup>3</sup>; DIPSACACEAE: Dipsacus fullonum<sup>8</sup>; FABACEAE: Astragalus sinuatus<sup>3</sup>, Lupinus polyphyllus<sup>8</sup>, L. sericeus<sup>3,59</sup>, Trifolium repens<sup>8</sup>, Vicia villosa<sup>8</sup>; GERANIACEAE: Geranium viscosissimum<sup>8</sup>; HY-DROPHYLLACEAE: Phacelia hastata<sup>3</sup>, P. leptosepala<sup>59</sup>; IRIDACEAE: Sisyrinchium<sup>8</sup>; LAMIACEAE: Agastache urticifolia<sup>8</sup>; ONAGRACEAE: Chamerion angusti*folium* ssp. *angustifolium*<sup>8</sup>, *Clarkia pulchella*<sup>3</sup>, *Epilobium*<sup>3</sup>; OROBANCHACEAE: Orthocarpus tenuifolius<sup>3,59</sup>; PLANTAGINACEAE: Collinsia parviflora<sup>8</sup>, Penstemon<sup>8</sup>, P. confertus<sup>3,59</sup>, P. washingtonensis<sup>59</sup>; ROSACEAE: Malus domestica<sup>8</sup>, Rosa<sup>8</sup>, *R. nutkana* ssp. *nutkana*<sup>59</sup>, *Rubus parviflorus*<sup>8</sup>
- 157. Bombus (Pyrobombus) flavifrons Cresson, 1864. County records: Asotin<sup>1,2,3</sup>, Chelan<sup>1,2,3,124</sup>, Clallam<sup>1,2,3,47,124</sup>, Clark<sup>1,2,3</sup>, Columbia<sup>1,2,3</sup>, Cowlitz<sup>1,2</sup>, Ferry<sup>1,2</sup>, Garfield<sup>1,2</sup>, Grays Harbor<sup>1,2,3,6,70</sup>, Island<sup>1,2,3,124</sup>, Jefferson<sup>1,2,3,47,124</sup>, King<sup>1,2,3</sup>, Kitsap<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Lewis<sup>1,2,3,47</sup>, Lincoln<sup>1,2</sup>, Mason<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>

Pacific<sup>1,2</sup>, Pend Oreille<sup>1,2</sup>, Pierce<sup>1,2,3,47</sup>, San Juan<sup>1,2,3,5,6,47,124,136</sup>, Skagit<sup>1,2,3,6,10,47,70,124</sup>, Skamania<sup>1,2,3</sup>, Snohomish<sup>1,2,3</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2,3</sup>, Thurston<sup>1,2,3,6,130,133</sup>, Wahkiakum<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>, Whatcom<sup>1,2,3,6,47,124</sup>, Whitman<sup>1,2,3,8</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Jan<sup>1,2</sup>, Feb<sup>1,2</sup>, Mar<sup>1,2</sup>, Apr<sup>1,2,3,5</sup>, May<sup>1,2,3,5,133</sup>, Jun<sup>1,2,3,6,133</sup>, Jul<sup>1,2,3,5,6,47,133</sup>, Aug<sup>1,2,3,6,47</sup>, Sep<sup>1,2,3</sup>, Nov<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: AMNH, BBSL, BOMBUS, CNC, EMEC, iNaturalist, INHS, JRYA, LACM, NMNH, OSUC, PMNH, PWRC, SEMC, UCRC, WSDA, WSUC. Conservation status: Least Concern (Hatfield et al. 2015g); G5 – Secure globally, S5 – Secure in Washington (NatureServe 2024). Floral records: ASTERACEAE: Balsamorhiza deltoidea<sup>133</sup>, Cirsium arvense<sup>8,133</sup>, Erigeron speciosus<sup>59</sup>, Eriophyllum lanatum<sup>133</sup>, Helianthus annuus<sup>8</sup>, Microseris nutans<sup>59</sup>, Solidago simplex<sup>133</sup>, Taraxacum officinale<sup>5,136</sup>; BORAGINACEAE: Mertensia<sup>3</sup>; CAMPANULACEAE: Campanula rotundifolia<sup>133</sup>; CAPRIFOLIACEAE: Plectritis congesta<sup>133</sup>, Symphoricarpos albus<sup>5,59,133,136</sup>; CARYOPHYLLACEAE: Cerastium arvense<sup>133</sup>; DIPSACACEAE: Dipsacus fullonum<sup>8</sup>; ERICACEAE: Gaultheria shallon<sup>3</sup>, Rhododendron<sup>5</sup>; FABACEAE: Astragalus miser var. serotinus<sup>59</sup>, Lathyrus japonicus<sup>136</sup>, L. nevadensis<sup>5</sup>, L. odoratus<sup>3</sup>, Lupinus albicaulis<sup>133</sup>, L. lepidus<sup>133</sup>, L. littoralis<sup>136</sup>, Trifolium pratense<sup>133</sup>, T. repens<sup>3,5,59</sup>, Vicia americana<sup>133</sup>, V. sativa<sup>133</sup>, V. villosa<sup>8</sup>; GERA-NIACEAE: Geranium dissectum<sup>133</sup>; GROSSULARIACEAE: Ribes divaricatum<sup>136</sup>; HYDROPHYLLACEAE: Phacelia leptosepala<sup>59</sup>; HYPERICACEAE: Hypericum perforatum<sup>133</sup>; IRIDACEAE: Sisyrinchium<sup>8</sup>; LAMIACEAE: Agastache urticifolia<sup>8</sup>, Prunella vulgaris<sup>133</sup>; ONAGRACEAE: Chamerion angustifolium ssp. angustifo*lium*<sup>3,8</sup>; OROBRANCHACEAE: *Castilleja*<sup>8</sup>, *C. miniata*<sup>59</sup>, *Parentucellia viscosa*<sup>133</sup>; PLANTAGINACEAE: Collinsia grandiflora<sup>133</sup>, Penstemon<sup>8</sup>, P. confertus<sup>59</sup>, P. washingtonensis<sup>59</sup>; POLEMONIACEAE: Gilia capitata<sup>133</sup>; RANUNCULACEAE: Delphinium nuttallianum<sup>59,133</sup>; ROSACEAE: Potentilla gracilis<sup>133</sup>, Rubus bifrons<sup>136</sup>

- 158. § Bombus (Pyrobombus) frigidus Smith, 1854. County records: Chelan<sup>1,2,3</sup>, Clallam<sup>1,2</sup>, Cowlitz<sup>1,2</sup>, Jefferson<sup>1,2</sup>, King<sup>1,2,3</sup>, Kitsap<sup>1,2,3</sup>, Okanogan<sup>1,2,3</sup>, Thurston<sup>1,2</sup>, Whatcom<sup>1,2</sup>, Yakima<sup>1,2</sup>. Seasonality: Jun<sup>1,2</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2,3</sup> (2010<sup>1,2</sup>). Collections: BBSL, CNC, NMNH, SEMC. Conservation status: Least Concern (Hatfield et al. 2014e); G5 Secure globally, S2 Imperiled in Washington (NatureServe 2024). Floral records: CAPRIFOLIACEAE: Symphoricarpos albus<sup>3</sup>; FABACEAE: Lupinus<sup>3</sup>; ONAGRACEAE: Epilobium<sup>3</sup>
- 159. Bombus (Pyrobombus) huntii Greene, 1860. County records: Adams<sup>1,2,3</sup>, Asotin<sup>1,2</sup>, Benton<sup>1,2,3</sup>, Chelan<sup>1,2,3</sup>, Douglas<sup>1,2,3</sup>, Ferry<sup>1,2,3</sup>, Garfield<sup>46</sup>, Grant<sup>1,2,3</sup>, King<sup>1,2,3</sup>, Kittias<sup>1,2,3</sup>, Klickitat<sup>1,2,3</sup>, Lincoln<sup>1,2,3</sup>, Okanogan<sup>1,2,3</sup>, Pierce<sup>1,2,3</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2</sup>, Thurston<sup>1,2,3</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>1,2,3</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2,3</sup>, Nov<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: AMNH, BOMBUS, BugGuide, EMEC, iNaturalist, INHS, LACM, NMNH, SEMC, UCRC. Conservation status: Least Concern (Hatfield et al. 2015h); G5 Secure globally, S4 Apparently Secure in Washington (Nature-Serve 2024). Floral records: CAPRIFOLIACEAE: Symphoricarpos albus<sup>3</sup>
- **160.** \* *Bombus* (*Pyrobombus*) *impatiens* Cresson, 1863. County records: King<sup>1,2</sup>, Skagit<sup>1,2</sup>, Whatcom<sup>1,2,3,6,33</sup>. Seasonality: Apr<sup>1,2,33</sup>, May<sup>1,2,6,33</sup>, Jul<sup>1,2,6</sup>, Aug<sup>1,2,6,33</sup>,

Sep<sup>1,6</sup>, Oct<sup>1,2,3,6</sup>, Dec<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: BOMBUS, BugGuide, iNaturalist, WSDA. Conservation status: Least Concern (Hatfield et al. 2014f); G5 – Secure globally (NatureServe 2024)

- 161. \$ Bombus (Pyrobombus) lapponicus sylvicola Kirby, 1837. County records: Chelan<sup>1,2,3,124</sup>, Clallam<sup>1,2,3,47,69,124</sup>, Jefferson<sup>1,2,3,47,69,124</sup>, King<sup>1,2,3</sup>, Kittitas<sup>1,2</sup>, Lewis<sup>1,2,47,124</sup>, Lincoln<sup>1,2</sup>, Mason<sup>1,2,3</sup>, Okanogan<sup>1,2</sup>, Pierce<sup>1,2,3,47,124</sup>, San Juan<sup>1,2,3,124</sup>, Skagit<sup>1,2,3,47,124</sup>, Whatcom<sup>1,2,3,47</sup>, Yakima<sup>1,2</sup>, Seasonality: Jun<sup>1,2</sup>, Jul<sup>1,2,3,47</sup>, Aug<sup>1,2,3,47</sup>, Sep<sup>1,2,3</sup> (2018<sup>1,2</sup>). Collections: BBSL, BOMBUS, iNaturalist, JRYA, LACM, NMNH, OSUC, PMNH, PWRC, UCDC. Conservation status: Least Concern (Hatfield et al. 2015j); G5 – Secure globally, S3 – Vulnerable in Washington (NatureServe 2024)
- 162. Bombus (Pyrobombus) melanopygus Nylander, 1848. County records: Chelan<sup>1,2,3,124</sup>, Clallam<sup>1,2,3,47,124</sup>, Clark<sup>1,2,3</sup>, Cowlitz<sup>1,2</sup>, Douglas<sup>1,2</sup>, Ferry<sup>1,2</sup>, Franklin<sup>1,2</sup>, Gravs Harbor<sup>1,2,3</sup>, Island<sup>1,2</sup>, Jefferson<sup>1,2,3,47,124</sup>, King<sup>1,2,3</sup>, Kitsap<sup>1,2,3</sup>, Kittitas<sup>1,2</sup>, Lewis<sup>1,2,3</sup>, Mason<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Pacific<sup>1,2,3</sup>, Pend Oreille<sup>1,2,3</sup>, Pierce<sup>1,2,3,47,124</sup>, San Juan<sup>1,2,3,5,6,22,47,124,136</sup>, Skagit<sup>1,2,3,10,124</sup>, Skamania<sup>1,2,3</sup>, Snohomish<sup>1,2,3,6</sup>, Spokane<sup>1,2,3</sup>, Thurston<sup>1,2,3,130,133</sup>, Walla Walla<sup>1,2,3</sup>, Whatcom<sup>1,2,3,6,33,47,124</sup>, Whitman<sup>1,2,3</sup>, Yakima<sup>1,2,3</sup>. Seasonality:  $Jan^{1,2}$ ,  $Feb^{1,2}$ ,  $Mar^{1,2}$ ,  $Apr^{1,2,3,5,133}$ , May<sup>1,2,3,5,33,133</sup>, Jun<sup>1,2,3,5,133</sup>, Jul<sup>1,2,3,6,47</sup>, Aug<sup>1,2,3,6,47</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2</sup>, Nov<sup>1,2</sup>, Dec<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: AMNH, BBSL, BOMBUS, CNC, EMEC, FMNH, iNaturalist, INHS, LACM, NMNH, OSUC, PMNH, PWRC, SEMC, UCDC, UCRC, WSDA. Conservation status: Least Concern (Hatfield et al. 2014g); G5 - Secure globally, S4 - Apparently Secure in Washington (NatureServe 2024). Floral records: ASPARAGACEAE: Camassia quamash133; ASTERACEAE: Achillea millefolium<sup>59,133</sup>, Anaphalis margaritacea<sup>59</sup>, Erigeron speciosus<sup>59</sup>, Grindelia integrifolia<sup>5</sup>, Hypochaeris radicata<sup>133</sup>, Microseris nutans<sup>59</sup>, Senecio integerrimus<sup>3,59</sup>, Solidago simplex<sup>133</sup>, Taraxacum officinale<sup>5,59</sup>; BORAGINACEAE: Myosotis laxa<sup>59</sup>; CAPRIFOLIACEAE: Symphoricarpos albus<sup>136</sup>; CARYOPHYLLACEAE: Eremogone capillaris var. capillaris<sup>59</sup>; CUCURBITACEAE: Marah oregana<sup>5</sup>; ERICACE-AE: Arctostaphylos uva-ursi<sup>133</sup>, Heather<sup>5</sup>, Rhododendron<sup>5</sup>; FABACEAE: Lupinus albicaulis<sup>133</sup>, L. lepidus<sup>133</sup>, Trifolium repens<sup>3,59</sup>, Vicia sativa<sup>133</sup>; GROSSULARI-ACEAE: Ribes divaricatum<sup>5</sup>; HYDROPHYLLACEAE: Phacelia leptosepala<sup>59</sup>; OROBRANCHACEAE: Castilleja miniata<sup>59</sup>, Parentucellia viscosa<sup>133</sup>; PLAN-TAGINACEAE: Collinsia grandiflora<sup>133</sup>, Penstemon confertus<sup>59</sup>; ROSACEAE: Rubus<sup>3,59</sup>; VALERIANACEAE: Plectritis congesta<sup>5</sup>; VIOLACEAE: Viola adunca<sup>133</sup>
- 163. Bombus (Pyrobombus) mixtus Cresson, 1879. County records: Asotin<sup>1,2,3</sup>, Chelan<sup>1,2,3,124</sup>, Clallam<sup>1,2,3,47,124</sup>, Clark<sup>1,2,3</sup>, Columbia<sup>1,2,3</sup>, Cowlitz<sup>1,2,3</sup>, Douglas<sup>1,2,3</sup>, Ferry<sup>1,2,3</sup>, Garfield<sup>1,2</sup>, Grays Harbor<sup>1,2,3,6,70</sup>, Island<sup>1,2,3,6</sup>, Jefferson<sup>1,2,3,47,124</sup>, King<sup>1,2,3</sup>, Kitsap<sup>1,2,3</sup>, Kittias<sup>1,2,3</sup>, Klickitat<sup>1,2,3</sup>, Lewis<sup>1,2,3,124</sup>, Mason<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Pacific<sup>1,2,3</sup>, Pend Oreille<sup>1,2,3</sup>, Pierce<sup>1,2,3,6,47</sup>, San Juan<sup>1,2,3,5,6,22,47,124,136</sup>, Skagit<sup>1,2,3,6,10,47,70,124</sup>, Skamania<sup>1,2</sup>, Snohomish<sup>1,2,3,6</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2,3</sup>, Thurston<sup>1,2,3,6,130,133</sup>, Wahkiakum<sup>1,2,3</sup>, Walla Walla<sup>1,2,3</sup>, Whatcom<sup>1,2,3,6,47,124</sup>, Whitman<sup>1,2,3,8</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Jan<sup>1,2</sup>, Feb<sup>1,2</sup>, Mar<sup>1,2</sup>, Apr<sup>1,2,5,133</sup>, May<sup>1,2,3,5,133</sup>,

Jun<sup>1,2,3,5,6,133</sup>, Jul<sup>1,2,3,5,6,47,133</sup>, Aug<sup>1,2,3,5,6,47</sup>, Sep<sup>1,2,6</sup>, Oct<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: AMNH, BBSL, BOMBUS, CNC, CSCA, EMEC, iNaturalist, INHS, JRYA, LACM, NMNH, OSUC, PMNH, PWRC, SEMC, UCRC, WFBM, WSDA, WSUC. Conservation status: Least Concern (Hatfield et al. 2014h); G5 – Secure globally, S5 - Secure in Washington (NatureServe 2024). Floral records: APOC-YNACEAE: Apocynum androsaemifolium<sup>133</sup>; ASPARAGACEAE: Camassia quamash<sup>133</sup>; ASTERACEAE: Achillea millefolium<sup>59</sup>, Arnica cordifolia<sup>8,59</sup>, Balsamorhiza deltoidea<sup>133</sup>, Cirsium arvense<sup>133</sup>, Crepis capillaris<sup>133</sup>, Erigeron speciosus<sup>59</sup>, Eriophyllum lanatum<sup>133</sup>, Hypochaeris radicata<sup>133</sup>, Jacobaea vulgaris<sup>5</sup>, Leucanthemum vulgare<sup>133</sup>, Microseris laciniata<sup>133</sup>, Rudbeckia occidentalis<sup>8</sup>, Senecio jacobaea<sup>133</sup>, S. triangularis<sup>59</sup>, Solidago simplex<sup>133</sup>, Taraxacum officinale<sup>5,59,136</sup>; BORAGINACEAE: Mertensia<sup>3</sup>, M. paniculata<sup>8</sup>; BRASSICACEAE: Brassica rapa<sup>5</sup>, Cakile maritima<sup>136</sup>; CAPRIFOLIACEAE: Lonicera involucrata<sup>3,59</sup>, Plectritis congesta<sup>133</sup>, Symphoricarpos albus<sup>133,136</sup>; ERICACEAE: Arctostaphylos uva-ursi<sup>133</sup>, Phyllodoce empetriformis<sup>59</sup>; FABACEAE: Astragalus miser var. serotinus<sup>59</sup>, Lupinus<sup>59</sup>, L. albicaulis<sup>133</sup>, L. bicolor<sup>133</sup>, L. lepidus<sup>133</sup>, L. littoralis<sup>136</sup>, L. polyphyllus<sup>8</sup>, Vicia hirsuta<sup>133</sup>, V. sativa<sup>133</sup>; GERANIACEAE: Geranium dissectum<sup>133</sup>, G. molle<sup>5,136</sup>; GROSSULARIACEAE: Ribes<sup>3</sup>, R. divaricatum<sup>5,136</sup>; HYDROPHYLLACEAE: Phacelia<sup>8</sup>, P. leptosepala<sup>59</sup>; HYPERICACEAE: Hypericum perforatum<sup>133</sup>; IRIDACEAE: Sisyrinchium<sup>8</sup>; LA-MIACEAE: Prunella vulgaris<sup>133</sup>; ONAGRACEAE: Chamerion angustifolium ssp. angustifolium<sup>8</sup>, Clarkia amoena<sup>133</sup>; OROBRANCHACEAE: Pedicularis bracteosa var. latifolia<sup>59</sup>; PAPAVERACEAE: Eschscholzia californica<sup>5</sup>; PLANTAGINACE-AE: Collinsia grandiflora<sup>133</sup>, C. parviflora<sup>8</sup>, Penstemon confertus<sup>59</sup>, P. washingtonensis<sup>59</sup>; POLEMONIACEAE: Gilia capitata<sup>133</sup>; RANUNCULACEAE: Delphinium nuttallianum<sup>59</sup>; ROSACEAE: Potentilla gracilis<sup>133</sup>, Rosa nutkana ssp. nutkana<sup>59</sup>, Rubus<sup>59</sup>, R. bifrons<sup>136</sup>, R. ulmifolius<sup>5</sup>, R. parviflorus<sup>59</sup>, R. ursinus<sup>5</sup>; VALERIAN-ACEAE: *Plectritis congesta*<sup>5</sup>

164. Bombus (Pyrobombus) sitkensis Nylander, 1848. County records: Chelan<sup>1,2,3</sup>, Clallam<sup>1,2,3</sup>, Clark<sup>1,2,3</sup>, Columbia<sup>1,2,3</sup>, Cowlitz<sup>1,2</sup>, Grant<sup>3</sup>, Grays Harbor<sup>1,2,3</sup>, Island<sup>1,2,3</sup>, Jefferson<sup>1,2,3</sup>, King<sup>1,2,3</sup>, Kitsap<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Lewis<sup>1,2,3</sup>, Mason<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Pacific<sup>1,2,3</sup>, Pend Oreille<sup>1,2</sup>, Pierce<sup>1,2,3,6</sup>, San Juan<sup>1,2,3,6,22,124,136</sup>, Skagit<sup>1,2,3,6,10</sup>, Skamania<sup>1,2</sup>, Snohomish<sup>1,2,3</sup>, Spokane<sup>1,2</sup>, Thurston<sup>1,2,3,6,130,133</sup>, **Whatcom**<sup>1,2,3,6</sup>, **Whitman**<sup>1,2,3</sup>, **Yakima**<sup>1,2,3</sup>. Seasonality: Jan<sup>1,2</sup>, Mar<sup>1,2</sup>, Apr<sup>1,2</sup>, May<sup>1,2,3,133</sup>, Jun<sup>1,2,3,6,133</sup>, Jul<sup>1,2,3,6,133</sup>, Aug<sup>1,2,3,6</sup>, Sep<sup>1,2,6</sup>, Oct<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: AMNH, BBSL, BOMBUS, CNC, CSCA, EMEC, FMNH, iNaturalist, INHS, JRYA, LACM, NMNH, OSUC, PMNH, PWRC, SEMC, UCDC, UCRC, WSDA. Conservation status: Least Concern (Hatfield et al. 2015i); G4 - Apparently Secure globally, S4 - Apparently Secure in Washington (NatureServe 2024). Floral records: ASPARAGACEAE: Camassia quamash<sup>133</sup>; ASTERACEAE: Balsamorhiza deltoidea<sup>133</sup>, Cirsium arvense<sup>133</sup>, Hypochaeris radicata<sup>133</sup>; CAPRIFO-LIACEAE: Plectritis congesta<sup>133</sup>, Symphoricarpos albus<sup>133,136</sup>; FABACEAE: Lathyrus<sup>3</sup>, Lupinus<sup>3</sup>, L. albicauilis<sup>133</sup>, Vicia hirsuta<sup>136</sup>; GROSSULARIACEAE: Ribes divaricatum<sup>136</sup>; HYDROPHYLLACEAE: Phacelia leptosepala<sup>59</sup>; LAMIACEAE: Agastache<sup>3</sup>, *Prunella vulgaris*<sup>133</sup>; OROBANCHACEAE: *Parentucellia viscosa*<sup>133</sup>; PRIMULA-CEAE: *Dodecatheon hendersonii*<sup>133</sup>; RANUNCULACEAE: *Delphinium nuttallii*<sup>133</sup>

- 165. § Bombus (Pyrobombus) vagans Smith, 1854. County records: Chelan<sup>1,2</sup>, Ferry<sup>1,2</sup>, Lincoln<sup>1,2</sup>, Okanogan<sup>1,2,3</sup>, Pend Oreille<sup>1,2,3</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2,3</sup>, Thurston<sup>133</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2,3</sup>, May<sup>1,2,3,133</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2</sup> (2021<sup>1,2</sup>). Collections: BBSL, BOMBUS, BugGuide, EMEC, iNaturalist, UCRC, WSUC. Conservation status: Least Concern (Hatfield et al. 2015k); G4 – Apparently Secure globally, S2 – Imperiled in Washington (NatureServe 2024). Floral records: CAPRIFOLIACEAE: Plectritis congesta<sup>133</sup>; IRIDACEAE: Sisyrinchium<sup>8</sup>
- 166. Bombus (Pyrobombus) vancouverensis Cresson, 1879. County records: Asotin<sup>1,2,3</sup>, Benton<sup>1,2,3</sup>, Chelan<sup>1,2,3,124</sup>, Clallam<sup>1,2,3,124</sup>, Columbia<sup>1,2,3</sup>, Douglas<sup>1,2,3</sup>, Ferry<sup>1,2,3</sup>, Garfield<sup>1,2,3,46</sup>, Grant<sup>1,2,3</sup>, Jefferson<sup>1,2,3,124</sup>, King<sup>1,2,3</sup>, Kitsap<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2,3</sup>, Lewis<sup>1,2,124</sup>, Lincoln<sup>1,2,3</sup>, Mason<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Pend Oreille<sup>1,2,3</sup>, Pierce<sup>1,2,3,124</sup>, San Juan<sup>1,2,3,5,6,22,124,136</sup>, Skagit<sup>124</sup>, Skamania<sup>1,2,3</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2,3</sup>, Thurston<sup>1,2,3</sup>, Walla Walla<sup>1,2,3</sup>, Whatcom<sup>1,2,3,124</sup>, Whitman<sup>1,2,3,8</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Jan<sup>1,2</sup>, Mar<sup>1,2</sup>, Apr<sup>1,2,3</sup>, May<sup>1,2,3,5</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3,5,6</sup>, Aug<sup>1,2,3,5,6</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2</sup> (2019<sup>1,2,6</sup>). Collections: AMNH, BBSL, BOMBUS, CNC, CSCA, EMEC, FMNH, iNaturalist, INHS, JRYA, LACM, NMNH, PMNH, PWRC, OSUC, SEMC, UCRC, WSDA, WSUC. Conservation status: G5 - Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Achillea millefolium<sup>59</sup>, Agoseris glauca var. dasycephala<sup>59</sup>, Anaphalis margaritacea<sup>8,59</sup>, Arnica cordifolia<sup>59</sup>, A. sororia<sup>59</sup>, Cirsium arvense<sup>8</sup>, Erigeron speciosus<sup>59</sup>, Hypochaeris radicata<sup>136</sup>, Jacobaea vulgaris<sup>5</sup>, Microseris nutans<sup>59</sup>, Rudbeckia occidentalis<sup>8</sup>, Senecio integerrimus<sup>59</sup>, S. triangularis<sup>59</sup>, Taraxacum officinale<sup>59,136</sup>; BRASSI-CACEAE: Sisymbrium altissimum<sup>59</sup>; CAPRIFOLIACEAE: Symphoricarpos albus<sup>59,136</sup>; CUCURBITACEAE: Marah oregana<sup>5</sup>; FABACEAE: Astragalus miser var. serotinus<sup>59</sup>, Lupinus<sup>59</sup>, L. littoralis<sup>136</sup>, L. polyphyllus<sup>8</sup>, L. sericeus<sup>59</sup>, Melilotus albus<sup>59</sup>, Trifolium pratense<sup>59</sup>, T. repens<sup>59</sup>, Vicia villosa<sup>8</sup>; GERANIACEAE: Geranium viscosissimum var. viscosissimum<sup>59</sup>; GROSSULARIACEAE: *Ribes divaricatum*<sup>136</sup>; HYDROPHYLLACEAE: Phacelia<sup>8</sup>, P. leptosepala<sup>59</sup>; IRIDACEAE: Sisyrinchium<sup>8</sup>; ONAGRACEAE: Chamerion angustifolium ssp. angustifolium<sup>8,59</sup>; OROBANCHACEAE: Orthocarpus tenuifolius<sup>59</sup>; PLANTAGINACEAE: Collinsia parviflora<sup>8</sup>, Penstemon<sup>8</sup>, P. confertus<sup>59</sup>, P. washingtonensis<sup>59</sup>; POLEMONIACEAE: Polemonium pulcherrimum<sup>59</sup>; ROSACEAE: Potentilla gracilis<sup>59</sup>, Rubus bifrons<sup>136</sup>, L. parviflorus<sup>59</sup>
- 166a. Bombus (Pyrobombus) vancouverensis nearcticus Handlirsch, 1888. County records: Chelan<sup>1,2</sup>, Kittitas<sup>1,2</sup>, Klickitat<sup>1,2</sup>, Lewis<sup>68</sup>, Okanogan<sup>1,2</sup>, Pend Oreille<sup>1,2</sup>, Pierce<sup>1,2,68</sup>, Skamania<sup>1,2</sup>, Spokane<sup>1,2</sup>, Stevens<sup>1,2</sup>, Whatcom<sup>1,2</sup>, Whitman<sup>1,2</sup>, Yakima<sup>1,2</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2</sup>, Aug<sup>1,2</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: iNaturalist
- **166b.** *Bombus* (*Pyrobombus*) *vancouverensis vancouverensis* Cresson, 1879. County records: San Juan<sup>1,2,68</sup>, **Skagit**<sup>1,2</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>1,2,3</sup>, May<sup>1,2,3</sup>, Aug<sup>1,2</sup> (2020<sup>1,2</sup>). Collections: iNaturalist
- 167. § *Bombus (Pyrobombus) vandykei* (Frison, 1927). County records: Chelan<sup>1,2,3</sup>, Clallam<sup>3,124</sup>, Douglas<sup>1,2</sup>, Grays Harbor<sup>1,2</sup>, Jefferson<sup>1,69,124</sup>, King<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>,

Klickitat<sup>1,2</sup>, Mason<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>124</sup>, Snohomish<sup>1,2,3</sup>, Thurston<sup>1,2,3</sup>, Whatcom<sup>1,2</sup>, Whitman<sup>1,2,3</sup>, Yakima<sup>1,2,3,105</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2</sup> (2021<sup>1,2</sup>). Collections: AMNH, BBSL, BOMBUS, CAS, EMEC, iNaturalist, INHS, JRYA, LACM, NMNH, PMNH, UCRC. [= *Bombus flavifrons* var. *vandykei* Frison, 1927]. Holotype. USA, Washington, Yakima County, Mt. Adams, Yakima Indian Forest Reservation; CAS #2437. [= *Pyrobombus cascadensis* Milliron, 1970]. Conservation status: Least Concern (Hatfield et al. 2015l); G4 – Apparently Secure globally, S3 – Vulnerable in Washington (NatureServe 2024). Floral records: FABACEAE: *Lupinus*<sup>3,59</sup>; HYDROPHYLLACEAE: *Phacelia leptosepala*<sup>59</sup>

- 168. Bombus (Pyrobombus) vosnesenskii Radoszkowski, 1862. County records: Benton<sup>1,2,3</sup>, Chelan<sup>1,2</sup>, Clallam<sup>1,2,3,6,124</sup>, Clark<sup>1,2,3,124</sup>, Cowlitz<sup>1,2,3</sup>, Douglas<sup>1,2</sup>, Garfield<sup>1,2,3</sup>, Grays Harbor<sup>1,2</sup>, Island<sup>1,2,3,124</sup>, Jefferson<sup>1,2,3,6,124</sup>, King<sup>1,2,3,6</sup>, Kitsap<sup>1,2,3</sup>, Kittitas<sup>1,2</sup>, Klickitat<sup>1,2</sup>, Lewis<sup>1,2,4</sup>, Lincoln<sup>1,2</sup>, Mason<sup>1,2,3</sup>, Okanogan<sup>1,2</sup>, Pacific<sup>1,2,3,6</sup>, Pierce<sup>1,2,3,6</sup>, San Juan<sup>1,2,3,5,6,136</sup>, Skagit<sup>1,2,3,6,10</sup>, Skamania<sup>1,2,3</sup>, Snohomish<sup>1,2,6</sup>, Stevens<sup>1,2</sup>, Thurston<sup>1,2,3,6,130,133</sup>, Wahkiakum<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>, Whatcom<sup>1,2,6,33</sup>, Whitman<sup>1,2</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Jan<sup>1,2</sup>, Feb<sup>1,2</sup>, Mar<sup>1,2</sup>, Apr<sup>1,2,5,33,133</sup>, May<sup>1,2,5,33,133</sup>, Jun<sup>1,2,3,5,133</sup>, Jul<sup>1,2,3,5,6,133</sup>, Aug<sup>1,2,6,33</sup>, Sep<sup>1,2,6</sup>, Oct<sup>1,2,3</sup>, Nov<sup>1,2</sup>, Dec<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: AMNH, BBSL, BOMBUS, BugGuide, CNC, CSCA, EMEC, FMNH, iNaturalist, INHS, LACM, NMNH, PCYU, PMNH, PWRC, SEMC, TAMU, UCRC, WSDA. Conservation status: Least Concern (Hatfield et al. 2015m); G5 – Secure globally, S5 – Secure in Washington (NatureServe 2024). Floral records: ASPARAGACEAE: Brodiaea coronaria<sup>133</sup>, Camassia quamash<sup>133</sup>; ASTERACEAE: Balsamorhiza deltoidea<sup>133</sup>, Cirsium arvense<sup>133</sup>, Crepis capillaris<sup>133</sup>, Erigeron speciosus<sup>133</sup>, Eriophyllum lanatum<sup>133</sup>, Grindelia integrifolia<sup>5</sup>, Hypochaeris radicata<sup>5,133</sup>, Leucanthemum vulgare<sup>133</sup>, Microseris laciniata<sup>133</sup>, Senecio jacobaea<sup>133</sup>, Solidago missouriensis<sup>133</sup>, S. simplex<sup>133</sup>, Taraxacum officinale<sup>133</sup>; BRAS-SICACEAE: Lepidium campestre<sup>133</sup>; CAPRIFOLIACEAE: Plectritis congesta<sup>133</sup>, Symphoricarpos albus<sup>133,136</sup>; CARYOPHYLLACEAE: Cerastrium arvense<sup>133</sup>; ERI-CACEAE: Arctostaphylos uva-ursi<sup>133</sup>; FABACEAE: Lathyrus japonicus<sup>136</sup>, Lupinus albicaulis<sup>133</sup>, L. bicolor<sup>133</sup>, L. lepidus<sup>133</sup>, L. littoralis<sup>136</sup>, Trifolium pratense<sup>133</sup>, T. repens<sup>133</sup>, Vicia americana<sup>133</sup>, V. hirsuta<sup>133</sup>, V. sativa<sup>133,136</sup>; GROSSULARIACEAE: Ribes<sup>5</sup>; HYPERICACEAE: Hypericum perforatum<sup>133</sup>; LAMIACEAE: Prunella vulgaris<sup>133</sup>; OROBANCHACEAE: Castilleja hispida<sup>133</sup>, C. levisecta<sup>133</sup>, Parentucellia viscosa<sup>133</sup>; PAPAVERACEAE: Eschscholzia californica<sup>5</sup>; PLANTAGI-NACEAE: Collinsia grandiflora<sup>133</sup>; PLUMBAGINACEAE: Armeria maritima<sup>133</sup>; POLEMONIACEAE: Gilia capitata<sup>133</sup>; PRIMULACEAE: Dodecatheon hendersonii<sup>133</sup>; RANUNCULACEAE: Delphinium nuttallii<sup>133</sup>; ROSACEAE: Potentilla gracilis<sup>133</sup>, Rubus bifrons<sup>136</sup>; SAPINACEAE: Acer macrophyllum<sup>5</sup>
- 169. § Bombus (Subterraneobombus) appositus Cresson, 1879. County records: Asotin<sup>1,2,3</sup>, Chelan<sup>1,2,3</sup>, Clallam<sup>1,2,3,124</sup>, Clark<sup>1,2,124</sup>, Columbia<sup>1,2,3</sup>, Ferry<sup>1,2</sup>, Franklin<sup>1,2,3</sup>, Garfield<sup>1,2,3</sup>, Grant<sup>3</sup>, King<sup>1,2</sup>, Kitsap<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2,3</sup>, Lincoln<sup>1,2</sup>, Mason<sup>3</sup>, Okanogan<sup>1,2,3,59</sup>, Pend Oreille<sup>1,2,3</sup>, San Juan<sup>1,2,3,5</sup>, Skagit<sup>3</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2,3</sup>, Thurston<sup>1,2,3</sup>, Walla Walla<sup>1,2,3</sup>, Whatcom<sup>1,2,3</sup>,

Whitman<sup>1,2,3,6,8</sup>, **Yakima**<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2,3</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3,5,6</sup>, Aug<sup>1,2,3,6</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2</sup>, Nov<sup>2,3</sup> (2022<sup>1,2</sup>). Collections: BBSL, BOMBUS, Bug-Guide, CNC, CSCA, FMNH, iNaturalist, INHS, JRYA, LACM, NMNH, PMNH, TAMU, UCRC, WSDA, WSUC. Conservation status: Least Concern (Hatfield et al. 2015n); G3 – Vulnerable globally, S4 – Apparently Secure in Washington (NatureServe 2024). Floral records: ASPARAGACEAE: *Triteleia grandiflora*<sup>8</sup>; ASTERACEAE: *Balsamorhiza sagittata*<sup>8</sup>, *Cirsium*<sup>3</sup>, *C. arvense*<sup>5</sup>; BO-RANGINACEAE: *Myosotis laxa*<sup>59</sup>; FABACEAE: *Lupinus*<sup>3</sup>, *Medicago sativa*<sup>3</sup>, *Vicia villosa*<sup>8</sup>; HYDROPHYLLACEAE: *Phacelia*<sup>8</sup>; LAMIACEAE: *Agastache urticifolia*<sup>8</sup>; OROBANCHACEAE: *Orthocarpus tenuifolius*<sup>3,59</sup>; PLANTAGINACEAE: *Penstemon confertus*<sup>3,59</sup>, *P. washingtonensis*<sup>3,59</sup>

170. § Bombus (Thoracobombus) fervidus (Fabricius, 1798) species complex. County records: Adams<sup>1,2,3</sup>, Asotin<sup>1,2,3</sup>, Benton<sup>1,2,3,71</sup>, Chelan<sup>1,2,3</sup>, Clallam<sup>1,2,3</sup>, Clark<sup>1,2</sup>, Columbia<sup>1,2</sup>, Cowlitz<sup>1,2,3</sup>, Douglas<sup>1,2</sup>, Ferry<sup>1,2</sup>, Franklin<sup>1,2,3</sup>, Garfield<sup>1,2,46</sup>, Grant<sup>1,2,3</sup>, Grays Harbor<sup>1,2,6,70</sup>, Island<sup>1,2,3</sup>, Jefferson<sup>1,2,3</sup>, King<sup>1,2,3</sup>, Kitsap<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2,3</sup>, Lewis<sup>1,2,3</sup>, Lincoln<sup>1,2</sup>, Mason<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Pacific<sup>1,2,3,6</sup>, Pend Oreille<sup>1,2</sup>, Pierce<sup>1,2,3,6</sup>, San Juan<sup>1,2,3</sup>, Skagit<sup>1,2,10,70</sup>, Skamania<sup>1,2</sup>, Snohomish<sup>1,2,3</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2</sup>, Thurston<sup>1,2,3,6,133</sup>, Wahkiakum<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>, Whatcom<sup>1,2,33</sup>, Whitman<sup>1,2,3,6,8</sup>, **Yakima**<sup>1,2,3</sup>. Seasonality: Jan<sup>1,2</sup>, Mar<sup>1,2</sup>, Apr<sup>1,2,3,133</sup>, May<sup>1,2,3,133</sup>, Jun<sup>1,2,3,133</sup>, Jul<sup>1,2,3,6</sup>, Aug<sup>1,2,3,6,33</sup>, Sep<sup>1,2,3,6</sup>, Oct<sup>1,2,3</sup>, Nov<sup>1,2</sup>, Dec<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: AMNH, BBSL, BOMBUS, BugGuide, CNC, EMEC, FMNH, iNaturalist, INHS, LACM, NMNH, PMNH, OSUC, SEMC, TAMU, UCDC, UCRC, WSDA, WSUC. Conservation status: Vulnerable (Hatfield et al. 2015p); G3 - Vulnerable globally, S4 - Apparently Secure in Washington (NatureServe 2024). Floral records: ASPARAGACEAE: Camassia quamash133, Triteleia grandiflora<sup>8</sup>; ASTERACEAE: Anaphalis margaritacea<sup>8</sup>, Balsamorhiza deltoidea<sup>133</sup>, B. sagittata<sup>8</sup>, Cirsium vulgare<sup>8</sup>, Hypochaeris radicata<sup>133</sup>, Leucanthemum vulgare<sup>133</sup>, Microseris laciniata<sup>133</sup>, Rudbeckia occidentalis<sup>8</sup>, Taraxacum officinale<sup>133</sup>; CAPRIFOLIACEAE: Plectritis congesta<sup>133</sup>, Symphoricarpos albus<sup>133</sup>; CONVOLVULACEAE: Ipomoea<sup>3</sup>; DIPSACACEAE: Dipsacus fullonum<sup>8</sup>,; FABACEAE: Astragalus sinuatus<sup>3</sup>, Lathyrus odoratus<sup>3</sup>, Lupinus albicaulis<sup>133</sup>, L. polyphyllus<sup>8</sup>, Medicago sativa<sup>8</sup>, Trifolium pratense<sup>133</sup>, T. repens<sup>3,59,133</sup>, Vicia americana<sup>133</sup>, V. sativa<sup>133</sup>, V. villosa<sup>8</sup>; GERANIACEAE: Geranium viscosissimum<sup>8</sup>; HYDROPHYLLACEAE: Phacelia leptosepala<sup>59</sup>; HY-PERICACEAE: Hypericum perforatum<sup>133</sup>; IRIDACEAE: Sisyrinchium<sup>8</sup>; LAMI-ACEAE: Agastache urticifolia<sup>8</sup>, Prunella vulgaris<sup>133</sup>; ONAGRACEAE: Chamerion angustifolium ssp. angustifolium<sup>8</sup>; OROBRANCHACEAE: Castilleja hispida<sup>133</sup>, C. levisecta<sup>133</sup>, C. miniata<sup>59</sup>, Parentucellia viscosa<sup>133</sup>; PLANTAGINACEAE: Collinsia grandiflora<sup>133</sup>, Penstemon washingtonensis<sup>59</sup>; RANUNCULACEAE: Delphinium nuttallii<sup>133</sup>; ROSACEAE: Malus domestica<sup>8</sup>, Rosa<sup>8</sup>. Comments: Bombus fervidus and B. californicus are morphologically identical, but molecular analysis by Koch et al. (2018) supports the existence of two distinct lineages. However, based on the original species description, it is unclear which name is attributed to which species, or if these names represent two variations of the same species (Koch et al. 2018). Records of both species are presented here as a single species complex.

## Eucerinae: Emphorini

## Genus Diadasia Patton

- 171. Diadasia (Coquillettapis) diminuta (Cresson, 1878). County records: Asotin<sup>36</sup>, Benton<sup>1,2,3</sup>, Chelan<sup>1,2,3</sup>, Walla Walla<sup>1,2</sup>, Whatcom<sup>3</sup>, Whitman<sup>36</sup>, Yakima<sup>7</sup>. Seasonality: May<sup>1,2,3</sup>, Jun<sup>1,2,3,7</sup>, Jul<sup>1,2,7</sup>, Aug<sup>3</sup> (2022<sup>1,2</sup>). Collections: BBSL, iNaturalist, JRYA, UCRC, WSUC
- 172. † *Diadasia* (*Coquillettapis*) *lutzi* Cockerell, 1924. County records: Benton<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: May<sup>7</sup> (2015<sup>7</sup>). Collections: WSUC
- 173. *Diadasia* (*Coquillettapis*) *nigrifrons* (Cresson, 1878). County records: Chelan<sup>1</sup>, Kittitas<sup>1,2,3</sup>, Whitman<sup>8,36</sup>, Yakima<sup>36</sup>. Seasonality: Jul<sup>1,2,3</sup> (2023<sup>1</sup>). Collections: SEMC, WSUC. Floral records: MALVACEAE: *Sidalcea oregana*<sup>8</sup>
- 174. ‡ *Diadasia* (*Coquillettapis*) *nitidifrons* Cockerell, 1905. County records: Chelan<sup>3</sup>, Yakima<sup>36</sup>. Seasonality: Jun<sup>1</sup> (1919<sup>1</sup>). Collections: UCRC
- 175. ‡ *Diadasia* (*Dasiapis*) *ochracea* (Cockerell, 1903). County records: Whitman<sup>36</sup>, Yakima<sup>7,36,121</sup>. Seasonality: Jun<sup>7,121</sup> (1903<sup>7,121</sup>). Collections: WSUC. Comments: Adlakha (1969) synonymizes *D. ochracea* with *D. olivacea*; however, Snelling (1994) determined these were separate species and notes Washington records as *D. ochracea*.
- 176. Diadasia (Diadasia) enavata (Cresson, 1872). County records: Asotin<sup>1,2</sup>, Benton<sup>1,2,3,7</sup>, Klickitat<sup>2,3</sup>, Walla Walla<sup>1,2,3,7,36,71</sup>, Whitman<sup>1,2,3,7,8,36</sup>, Yakima<sup>7</sup>. Seasonality: Jun<sup>1,2,7</sup>, Jul<sup>1,2,3,7</sup>, Aug<sup>1,2,3,7</sup>, Sep<sup>1,2</sup> (2012<sup>1,2</sup>). Collections: BBSL, BugGuide, INHS, TAMU, WSUC. Floral records: ASTERACEAE: Helianthus<sup>3,7</sup>, H. annuus<sup>8</sup>

## Eucerini

## Genus Epimelissodes Ashmead

- 177. *Epimelissodes (Epimelissodes) obliquus* (Say, 1837). County records: Yakima<sup>2</sup>. Seasonality: Jul<sup>2</sup> (2015<sup>2</sup>). Collections: BugGuide, iNaturalist
- 177a. *Epimelissodes (Epimelissodes) obliquus expurgatus* Cockerell, 1925. County records: Benton<sup>1,2,3</sup>, Grant<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>72</sup>, Yakima<sup>72</sup>. Seasonality: Jul<sup>1,2</sup>, Aug<sup>1,2,3</sup> (2020<sup>1,2</sup>). Collections: BBSL, iNaturalist

## Genus Eucera Scopoli

- 178. Eucera (Synhalonia) actuosa (Cresson, 1878). County records: Benton<sup>1,2,3</sup>, Chelan<sup>1,2,3</sup>, Garfield<sup>1,2,3,46</sup>, Spokane<sup>1,2</sup>, Whitman<sup>8,109</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>1,2,3</sup>, May<sup>1,2,3,109</sup>, Jun<sup>1,2,3,46</sup> (2015<sup>1,2</sup>). Collections: BBSL, SEMC, WSUC. Floral records: ASTERACEAE: Balsamorhiza careyana<sup>3</sup>, B. sagittata<sup>8</sup>; FABACEAE: Lupinus<sup>8</sup>, Onobrychis viciifolia<sup>3</sup>, Vicia villosa<sup>8</sup>; ROSACEAE: Malus domestica<sup>8</sup>, Prunus virginiana<sup>8</sup>
- 179. Eucera (Synhalonia) amsinckiae (Timberlake, 1969). County records: Benton<sup>1,2,3</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>109</sup>. Seasonality: Apr<sup>1,2,3</sup>, May<sup>1,2,3</sup> (2015<sup>1,2</sup>). Collections: BBSL

- 180. †‡ *Eucera (Synhalonia) angustifrons* (Timberlake, 1969). County records: Spokane<sup>2</sup>. Seasonality: Jun<sup>2</sup> (1957<sup>2</sup>). Collections: SEMC
- 181. *Eucera* (*Synhalonia*) *delphinii* (Timberlake, 1969). County records: Asotin<sup>1,2,3,109</sup>, Garfield<sup>46</sup>, Spokane<sup>1,2</sup>, Stevens<sup>1,2</sup>, Whitman<sup>1,2,3,109</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,109</sup>, Jul<sup>1,2,3,109</sup> (2015<sup>1,2</sup>). Collections: BBSL, SEMC
- 182. § Eucera (Synhalonia) douglasiana (Cockerell, 1906). County records: Benton<sup>1,2</sup>, Grant<sup>109,112,121</sup>. Seasonality: Apr<sup>1,2</sup>, Jul<sup>109,121</sup> (2015<sup>1,2</sup>). Collections: BBSL. [= Tetralonia douglasiana Cockerell, 1906]. Conservation status: Vulnerable (Shepherd 2005b; National Research Council 2007). Comments: Cockerell (1906b) and Timberlake (1969) note a record at Steamboat Rock, Grand Coulee in Douglas County; however, Steamboat Rock, Grand Coulee is located in Grant County.
- 183. Eucera (Synhalonia) edwardsii (Cresson, 1878). County records: Benton<sup>1,2,3</sup>, Chelan<sup>136</sup>, Franklin<sup>1,2,118</sup>, Garfield<sup>1,2,3,46</sup>, Grant<sup>6</sup>, Klickitat<sup>1,2</sup>, Spokane<sup>1,2,3</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3,6,8</sup>, Yakima<sup>1,2,3,6</sup>. Seasonality: Apr<sup>1,2,3</sup>, May<sup>1,2,3,118</sup>, Jun<sup>1,2,3,6</sup>, Jul<sup>1,2</sup> (2022<sup>6</sup>). Collections: BBSL, NMNH, SEMC, WSDA, WSUC. Floral records: DIPSACACEAE: Dipsacus fullonum<sup>8</sup>; FABACEAE: Astragalus bungeanus<sup>3</sup>, A. columbianus<sup>3</sup>, Lupinus polyphyllus<sup>8</sup>, Vicia villosa<sup>8</sup>
- 184. Eucera (Synhalonia) frater (Cresson, 1878). County records: Benton<sup>1,2</sup>, Chelan<sup>1,2,3</sup>, Garfield<sup>1,2,46</sup>, Jefferson<sup>1,2</sup>, Klickitat<sup>1,2</sup>, San Juan<sup>1,2,124,136</sup>, Stevens<sup>1,2,109</sup>, Thurston<sup>1,2,118</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3,6,8,61</sup>. Seasonality: Mar<sup>1</sup>, Apr<sup>1,2,109,118</sup>, May<sup>1,2,3,118</sup>, Jun<sup>1,2,3,6,46,118</sup>, Jul<sup>1,2,118</sup>, Aug<sup>1,2</sup> (2017<sup>136</sup>). Collections: BBSL, BugGuide, NMNH, PWRC, WSDA, WSUC. [= Synhalonia edwardsii latior Cockerell, 1897]. Floral records: ASPARAGACEAE: Triteleia grandiflora<sup>8</sup>; ASTERACEAE: Balsamorhiza sagittata<sup>8</sup>, Hypochaeris radicata<sup>136</sup>; FABACEAE: Astragalus sinuatus<sup>3</sup>, Lathyrus japonicus<sup>136</sup>, Lupinus<sup>3,118</sup>, Trifolium repens<sup>8</sup>, Vicia sativa<sup>136</sup>; OLEACEAE: Syringa<sup>8</sup>; PLANTAGINACEAE: Penstemon attenuatus<sup>8</sup>; ROSACEAE: Malus domestica<sup>8</sup>
- 184a. § Eucera (Synhalonia) frater lata (Provancher, 1888). County records: Asotin<sup>1,2,3,109</sup>, Chelan<sup>1,2,3</sup>, Garfield<sup>1,2,3</sup>, Island<sup>109</sup>, Jefferson<sup>1,2</sup>, King<sup>109</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>1,2,3,5,22,124</sup>, Whitman<sup>1,2,109</sup>. Seasonality: Apr<sup>1,2,3,5</sup>, May<sup>1,2,3,5,109</sup>, Jun<sup>1,2,3,5,109</sup>, Jul<sup>1,2,3,109</sup>, Aug<sup>109</sup> (2015<sup>1,2,22</sup>). Collections: BBSL, PWRC, SEMC. Conservation status: Vulnerable (Shepherd 2005c; National Research Council 2007). Floral records: ASPARAGACEAE: Camassia quamash<sup>5</sup>; ASTERACEAE: Taraxacum officinale<sup>5</sup>; BERBERIDACEAE: Berberis aquifolium<sup>5</sup>; FABACEAE: Astragalus bungeanus<sup>3</sup>, A. cicer<sup>3</sup>; HYDROPHYLLACEAE: Hydrophyllum<sup>109</sup>
- 185. Eucera (Synhalonia) fulvitarsis (Cresson, 1878). County records: Benton<sup>1,2,3,109</sup>, Chelan<sup>1,2,3,109</sup>, Douglas<sup>1,2</sup>, Garfield<sup>46</sup>, Walla Walla<sup>1,2</sup>, Yakima<sup>1,2,3,109,121</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>1,2,3,121</sup>, May<sup>1,2,3</sup> (2015<sup>1,2</sup>). Collections: BBSL, SEMC. [= Synhalonia yakimensis Cockerell, 1906]. Holotype. USA, Washington, Yakima County, Yakima. [= Tetralonia yakimensis Cockerell, 1906]. Floral records: FABACEAE: Astragalus columbianus<sup>3</sup>
- 186. Eucera (Synhalonia) hurdi (Timberlake, 1969). County records: Asotin<sup>2</sup>, Spokane<sup>1,2</sup>, Whitman<sup>3,109</sup>. Seasonality: Apr<sup>1,2,3,109</sup>, May<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL, SEMC
- **187.** † *Eucera* (*Synhalonia*) *speciosa* (Cresson, 1878). County records: Benton<sup>1,2,3</sup>. Seasonality: May<sup>1,2,3</sup>, Jun<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL
#### Genus Melissodes Latreille

- 188. Melissodes (Callimelissodes) glenwoodensis Cockerell, 1905. County records: Grant<sup>49</sup>
- 189. Melissodes (Callimelissodes) lupinus Cresson, 1878. County records: Benton<sup>1,2,7,71</sup>, Klickitat<sup>1,2</sup>, Walla Walla<sup>1,2,7,71</sup>, Whitman<sup>1,2,7,8,49</sup>, Yakima<sup>7</sup>. Seasonality: Jun<sup>1,2,7</sup>, Jul<sup>1,2,7</sup>, Aug<sup>1,2</sup>, Sep<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL, WSUC. Floral records: ASTERACEAE: Helianthus annuus<sup>8</sup>
- 190. ‡ *Melissodes* (*Callimelissodes*) *metenua* Cockerell, 1924. County records: Kittitas<sup>1,2</sup>, Whitman<sup>7,8</sup>, Yakima<sup>49</sup>. Seasonality: Jul<sup>1,2,7</sup>, Aug<sup>7</sup> (1962<sup>7</sup>). Collections: TAMU, WSUC. Floral records: ASTERACEAE: *Pyrrocoma liatriformis*<sup>8</sup>
- 191. ‡ Melissodes (Callimelissodes) plumosus LaBerge, 1961. County records: Yakima<sup>49</sup>. Seasonality: Jul<sup>49</sup>, Aug<sup>49</sup> (1941<sup>49</sup>)
- **192.** ‡ *Melissodes* (*Callimelissodes*) *stearnsi* Cockerell, 1905. County records: Kittitas<sup>1,2,49</sup>, Okanogan<sup>1,2,3</sup>, Seasonality: Jul<sup>1,2,3</sup> (1949<sup>1,2</sup>). Collections: BBSL, SEMC
- 193. Melissodes (Eumelissodes) agilis Cresson, 1878. County records: Adams<sup>7,49</sup>, Asotin<sup>1,2,49</sup>, Benton<sup>1,2,3,7,71</sup>, Chelan<sup>7,49</sup>, Douglas<sup>1,2</sup>, Garfield<sup>7</sup>, Grant<sup>1,2</sup>, Klickitat<sup>49</sup>, Spokane<sup>1,2</sup>, Walla Walla<sup>1,2,3,7,49,71</sup>, Whitman<sup>1,2,7,8,49</sup>, Yakima<sup>7,49</sup>. Seasonality: Jun<sup>1,2,3,7</sup>, Jul<sup>1,2,7</sup>, Aug<sup>1,2,3,7</sup>, Sep<sup>1,2,7</sup>, Oct<sup>1,2,7</sup> (2015<sup>7</sup>). Collections: BBSL, SEMC, TAMU, WSUC. Floral records: ASTERACEAE: Helianthus annuus<sup>8</sup>; GERANI-ACEAE: Geranium<sup>8</sup>
- 194. Melissodes (Eumelissodes) bimatris LaBerge, 1961. County records: Benton<sup>7</sup>, Franklin<sup>49</sup>, Grant<sup>49</sup>, Okanogan<sup>49</sup>, Walla Walla<sup>49</sup>, Whitman<sup>7</sup>, Yakima<sup>49</sup>. Seasonality: Sep<sup>7</sup> (1993<sup>7</sup>). Collections: WSUC
- 195. † Melissodes (Eumelissodes) brevipyga LaBerge, 1961. County records: Benton<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: Jul<sup>7</sup> (2015<sup>7</sup>). Collections: WSUC
- 196. Melissodes (Eumelissodes) grindeliae Cockerell, 1898. County records: Yakima<sup>49</sup>
- 197. Melissodes (Eumelissodes) lutulentus LaBerge, 1961. County records: Adams<sup>7,49</sup>, Benton<sup>7</sup>, Walla Walla<sup>7</sup>. Seasonality: Jun<sup>7</sup>, Aug<sup>7</sup> (2015<sup>7</sup>). Collections: WSUC
- **198.** *Melissodes* (*Eumelissodes*) *menuachus* Cresson, 1868. County records: Benton<sup>1,2</sup>, Grant<sup>49</sup>, Okanogan<sup>2,3</sup>, Walla Walla<sup>1,2,3,71</sup>. Seasonality: Aug<sup>1,2</sup>, Sep<sup>1,2,3</sup> (2015<sup>1,2</sup>). Collections: BBSL, SEMC
- 199. Melissodes (Eumelissodes) microstictus Cockerell, 1905. County records: Benton<sup>7</sup>, Chelan<sup>7</sup>, Island<sup>2,7,49</sup>, King<sup>1,2,49</sup>, Kitsap<sup>7,23, 134</sup>, Kittitas<sup>1,2</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,59</sup>, Pend Oreille<sup>49</sup>, Pierce<sup>1,2,49</sup>, San Juan<sup>1,2,7,49,124</sup>, Spokane<sup>1,2,49</sup>, Thurston<sup>1,2,49</sup>, Walla Walla<sup>1,2,7,49</sup>, Whatcom<sup>7,49</sup>, Whitman<sup>2,49</sup>, Yakima<sup>49</sup>. Seasonality: Apr<sup>1,2</sup>, Jun<sup>1,2,7</sup>, Jul<sup>1,2,7,134</sup>, Aug<sup>1,2,7,134</sup>, Sep<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL, FMNH, iNaturalist, INHS PWRC, SEMC, TAMU, WSUC. Floral records: ASTER-ACEAE: Anaphalis margaritacea<sup>59</sup>, Erigeron speciosus<sup>59</sup>, Hypochaeris radicata<sup>134</sup>
- 200. Melissodes (Eumelissodes) pallidisignatus Cockerell, 1905. County records: Benton<sup>1,2,7</sup>, Island<sup>2,3,49</sup>, Jefferson<sup>1,2</sup>, Kittitas<sup>2</sup>, Klickitat<sup>2</sup>, Okanogan<sup>1,2,59</sup>, Pend Oreille<sup>2,49</sup>, Stevens<sup>49</sup>, Walla Walla<sup>1,2,7,8,71</sup>, Whitman<sup>2</sup>, Yakima<sup>2</sup>. Seasonality: Jun<sup>1,2</sup>,

Jul<sup>1,2,7</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL, INHS, SEMC, UCRC, WSUC. Floral records: ASTERACEAE: *Achillea millefolium*<sup>59</sup>, *Erigeron speciosus*<sup>59</sup>, *Senecio triangularis*<sup>59</sup>; BRASSICACEAE: *Sisymbrium altissimum*<sup>59</sup>

- **201.** *Melissodes* (*Eumelissodes*) *paululus* LaBerge, 1961. County records: Benton<sup>7</sup>, Walla Walla<sup>1,2,71</sup>, Yakima<sup>49</sup>. Seasonality: Jun<sup>1,2</sup>, Jul<sup>1,2</sup>, Aug<sup>1,2</sup>, Sep<sup>1,2</sup> (1998<sup>1,2</sup>). Collections: BBSL, WSUC
- 202. Melissodes (Eumelissodes) robustior Cockerell, 1915. County records: Adams<sup>7</sup>, Asotin<sup>49</sup>, Benton<sup>1,2,7</sup>, Spokane<sup>7</sup>, Walla Walla<sup>1,2,3,7,49</sup>, Whitman<sup>1,2,3,7,8,49</sup>, Yakima<sup>7,49</sup>. Seasonality: Jun<sup>1,2,3,7</sup>, Jul<sup>2,3,7</sup>, Aug<sup>7</sup> (1995<sup>1,3</sup>). Collections: BBSL, INHS, SEMC, WSUC. Floral records: ASTERACEAE: Helianthus annuus<sup>8</sup>
- **203.** *Melissodes* (*Eumelissodes*) *saponellus* Cockerell, 1908. County records: Benton<sup>1,2,7</sup>, Grant<sup>49</sup>, Yakima<sup>7</sup>. Seasonality: May<sup>1,2,7</sup>, Jun<sup>1,2,7,49</sup>, Jul<sup>7</sup> (2015<sup>1,2,7</sup>). Collections: BBSL, WSUC. Holotype. USA, Washington, Grant County, Grand Coulee, Soap Lake; 29 June 1902
- **204.** *Melissodes* (*Eumelissodes*) *semilupinus* Cockerell, 1905. County records: Benton<sup>1,7</sup>, Chelan<sup>1</sup>, Walla Walla<sup>7,49</sup>, Whitman<sup>7</sup>, Yakima<sup>2,7</sup>. Seasonality: Jul<sup>7</sup>, Aug<sup>1,7</sup>, Sep<sup>1,2,7</sup>, Oct<sup>7</sup> (1995<sup>1</sup>). Collections: INHS, WSUC
- 205. Melissodes (Eumelissodes) subagilis Cockerell, 1905. County records: Adams<sup>7</sup>, Benton<sup>7</sup>, Grant<sup>7,49</sup>. Seasonality: Jul<sup>7</sup>, Aug<sup>7</sup>, Sep<sup>7</sup> (2015<sup>7</sup>). Collections: WSUC
- **206.** ‡ *Melissodes* (*Eumelissodes*) *verbesinarum* Cockerell, 1905. County records: Adams<sup>49</sup>, Yakima<sup>7</sup>. Seasonality: Aug<sup>7</sup> (1957<sup>7</sup>). Collections: WSUC
- 207. Melissodes (Eumelissodes) vernalis LaBerge, 1961. County records: Adams<sup>49</sup>, Benton<sup>7</sup>. Seasonality: Jun<sup>7</sup> (2014<sup>7</sup>). Collections: WSUC
- 208. *Melissodes* (*Heliomelissodes*) *rivalis* Cresson, 1872. County records: Adams<sup>7,108</sup>, Asotin<sup>108</sup>, Benton<sup>1,2,3,7,71</sup>, Columbia<sup>7</sup>, Garfield<sup>108</sup>, Grant<sup>7</sup>, King<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2,7</sup>, Lewis<sup>2,3,108</sup>, Lincoln<sup>108</sup>, San Juan<sup>1,2,3,124</sup>, Walla Walla<sup>1,2,7,71</sup>, Whitman<sup>7,8,108</sup>, Yakima<sup>7,108</sup>. Seasonality: Jun<sup>1,2,3,7</sup>, Jul<sup>1,2,3,7</sup>, Aug<sup>1,2,7</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2</sup> (2012<sup>1,2</sup>). Collections: BBSL, PWRC, SEMC, WSUC. Floral records: ASTERACEAE: *Cirsium vulgare*<sup>8</sup>
- **209.** *Melissodes* (*Melissodes*) *communis* Cresson, 1878. County records: Walla Walla<sup>1,2,3</sup>. Seasonality: Jul<sup>1,2,3</sup> (1998<sup>1,2,3</sup>). Collections: BBSL
- **209a.** *Melissodes* (*Melissodes*) *communis alopex* Cockerell, 1928. County records: Asotin<sup>2,3,72</sup>, Benton<sup>7</sup>, Yakima<sup>1,2,7,72</sup>. Seasonality: Jun<sup>2,3,7</sup>, Jul<sup>1,2,3,7</sup> (2015<sup>7</sup>). Collections: SEMC, WSUC
- **210.** *Melissodes* (*Tachymelissodes*) *dagosus* Cockerell, 1909. County records: Adams<sup>7,108</sup>, Benton<sup>7</sup>, Grant<sup>7,108</sup>, Lincoln<sup>7</sup>, Yakima<sup>7,108</sup>. Seasonality: Jun<sup>7</sup>, Jul<sup>7</sup> (1973<sup>7</sup>). Collections: WSUC

### Nomadinae: Ammobatini

### Genus Oreopasites Cockerell

**211.** *Oreopasites* (*Oreopasites*) *vanduzeei* Cockerell, 1925. County records: Benton<sup>1,2,3,9</sup>. Seasonality: May<sup>1,2,3</sup>, Jun<sup>9</sup> (1990<sup>1,2,3</sup>). Collections: AMNH

# Epeolini

# Genus Epeolus Latreille

- 212. † *Epeolus americanus* (Cresson, 1878). County records: Benton<sup>1,2</sup>, Walla Walla<sup>1,2</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: BBSL, iNaturalist
- **213.** *Epeolus compactus* Cresson, 1878. County records: King<sup>1,2</sup>, Klickitat<sup>1,2</sup>, Pierce<sup>1,2,4,73,74</sup>, Thurston<sup>1,2</sup>. Seasonality: Jun<sup>1,2,74</sup>, Jul<sup>1,2,4,73</sup> (2021<sup>1,2</sup>). Collections: BBSL, iNaturalist, PCYU. Host records: *Colletes kincaidii* Cockerell<sup>73</sup>
- **214.** *Epeolus emiliae* **Onuferko and Sheffield, 2022**. County records: Benton<sup>1,64</sup>. Seasonality: Sep<sup>1</sup>, Oct<sup>1,64</sup> (2023<sup>1</sup>). Collections: iNaturalist. Comments: iNaturalist record #98573666
- 215. *Epeolus minimus* (Robertson, 1902). County records: Benton<sup>1,2</sup>, Ferry<sup>1,2</sup>, Spokane<sup>1,2</sup>, Thurston<sup>3</sup>. Seasonality: May<sup>1,2</sup>, Jul<sup>1,2</sup>, Aug<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: AMNH, BBSL, SEMC
- **216.** † *Epeolus novomexicanus* Cockerell, 1912. County records: Benton<sup>1,2</sup>. Seasonality: Sep<sup>1,2</sup> (2021<sup>1,2</sup>). Collections: iNaturalist
- 217. *Epeolus olympiellus* Cockerell, 1904. County records: Benton<sup>1,2</sup>, Douglas<sup>1,2</sup>, Garfield<sup>1,2,4,73,74</sup>, San Juan<sup>22</sup>, Thurston<sup>1,2,3,52,73,74,118</sup>, Whitman<sup>1,2,73,74</sup>. Seasonality: May<sup>1,2,4,74</sup>, Jun<sup>1,2,74</sup>, Jul<sup>1,2,3,52,73,74,118</sup>, Aug<sup>1,2,73,74</sup> (2021<sup>1,2</sup>). Collections: AMNH, iNaturalist, NMNH, PCYU. Holotype. USA, Washington, Thurston County, Olympia; 2 July 1896; T Kincaid; USNM 534051. [= *Epeolus humillimus* Cockerell, 1918]. Holotype. USA, Washington, Whitman County, Pullman; 2 August 1908; WM Mann; Type No. 100017, USNM ENT 00534047

## Genus Triepeolus Robertson

- **218.** *Triepeolus argus* **Rightmyer, 2008**. County records: Benton<sup>3,75</sup>, Yakima<sup>3,75</sup>. Seasonality: Sep<sup>3,75</sup>, Oct<sup>3</sup> (1993<sup>3,75</sup>). Collections: Miliczky. Host records: *Melissodes pallidisignatus* Cockerell<sup>75</sup>. Floral records: ASTERACEAE: *Ericameria nauseosa* var. *nauseosa*<sup>3,75</sup>
- 219. Triepeolus argyreus (Cockerell, 1907). County records: Benton<sup>3</sup>, Klickitat<sup>3</sup>, Walla Walla<sup>3</sup>, Yakima<sup>3,75</sup>. Seasonality: Aug<sup>3,75</sup>, Sep<sup>3</sup> (1992<sup>3</sup>). Collections: Miliczky. Holotype. USA, Washington, Yakima County, North Yakima; 4 August 1903; USNM No. 100019. Host records: *Melissodes pallidisignatus* Cockerell<sup>3,75</sup>. Floral records: ASTERACEAE: Centromadia pungens ssp. pungens<sup>3</sup>, Dieteria canescens<sup>3</sup>, Ericameria nauseosa var. nauseosa<sup>3</sup>
- 220. † *Triepeolus concavus* (Cresson, 1878). County records: Adams<sup>3</sup>, Franklin<sup>1</sup>, Yakima<sup>3</sup>. Seasonality: Jul<sup>3</sup>, Aug<sup>3</sup> (2023<sup>1</sup>). Collections: NMNH, iNaturalist. Host records: *Epimelissodes obliquus* (Say)<sup>75</sup>
- **221.** † *Triepeolus grindeliae* Cockerell, 1907. County records: Benton<sup>1,2,3</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2,3</sup>, Sep<sup>1,2</sup> (1995<sup>1,2,3</sup>). Collections: BBSL. Floral records: ASTER-ACEAE: *Rhaponticum repens*<sup>3</sup>

- 222. † *Triepeolus helianthi* (Robertson, 1897). County records: Klickitat<sup>2,3</sup>, Whitman<sup>2,3</sup>. Seasonality: Aug<sup>2,3</sup>, Sep<sup>2,3</sup> (1982<sup>2,3</sup>). Collections: INHS. Host records: Nomia melanderi Cockerell<sup>75</sup>, Melissodes agilis Cresson<sup>75</sup>
- **223.** *Triepeolus paenepectoralis* Viereck, 1905. County records: Island<sup>3</sup>, Jefferson<sup>1,2</sup>, Kitsap<sup>2,3,75</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>59</sup>, Whitman<sup>1,2,3,51</sup>. Seasonality: Jul<sup>1,2</sup>, Aug<sup>1,2,3,51</sup>, Sep<sup>1,2,3,51</sup> (2022<sup>1,2</sup>). Collections: BBSL, iNaturalist, INHS. Host records: *Melissodes microstictus* Cockerell<sup>75</sup>
- 224. Triepeolus texanus (Cresson, 1878). County records: Walla Walla<sup>1,2</sup>, Whitman<sup>3</sup>, Yakima<sup>1,2,75</sup>. Seasonality: Jun<sup>1,2</sup>, Jul<sup>3</sup>, Aug<sup>1,2,75</sup> (2012<sup>1,2</sup>). Collection: BBSL, NMNH. [= Triepeolus eldredi Cockerell, 1907]. Holotype. USA, Washington, Yakima County, North Yakima; 7 August 1903; USNM No. 100029. Host records: Melissodes druriellus (Kirby)<sup>75</sup>, Nomia melanderi Cockerell<sup>75</sup>
- **225.** † *Triepeolus timberlakei* Cockerell, 1929. County records: Whitman<sup>1,2,3</sup>. Seasonality: Sep<sup>1,2,3</sup> (1982<sup>1,2,3</sup>). Collections: BBSL

#### Melectini

#### Genus Brachymelecta Linsley

226. † Brachymelecta californica (Cresson, 1878). County records: Benton<sup>7</sup>, Jefferson<sup>1,2</sup>, Whitman<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: Jun<sup>7</sup>, Aug<sup>1,2</sup>, Sep<sup>7</sup> (2022<sup>1,2</sup>). Collections: iNaturalist, WSUC. Conservation status: G5 – Secure globally (NatureServe 2024)

#### Genus Melecta Latreille

- 227. *Melecta (Melecta) pacifica* Cresson, 1878. County records: Benton<sup>1,2</sup>, Okanogan<sup>1,2,3,59</sup>, Spokane<sup>1,2</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2</sup>, Jun<sup>1,2,3</sup> (2015<sup>1,2</sup>). Collections: BBSL, SEMC
- 227a. *Melecta (Melecta) pacifica fulvida* Cresson, 1879. County records: Whitman<sup>35</sup>
- **228.** *Melecta (Melecta) separata* Cresson, 1879. County records: Chelan<sup>136</sup>, Pierce<sup>1,2</sup>, Spokane<sup>1,2</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3</sup> (2020<sup>1,2</sup>). Collections: BBSL, iNaturalist. Floral records: FABACEAE: *Astragalus speirocarpus*<sup>3</sup>
- **228a.** *Melecta* (*Melecta*) *separata callura* (Cockerell, 1926). County records: Walla Walla<sup>35</sup>. Comments: Linsley (1939) lists the Washington record as Whitman County (Walla Walla). Walla Walla is located in Walla Walla County.
- 228b. † *Melecta (Melecta) separata separata* Cresson, 1879. County records: Benton<sup>1,2</sup>, Chelan<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jul<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: BBSL, iNaturalist
- 229. † *Melecta (Melecta) thoracica* Cresson, 1875. County records: Douglas<sup>1,2</sup>, Spokane<sup>1,2</sup>, Whitman<sup>3</sup>. Seasonality: Apr<sup>1,2,3</sup>, May<sup>1,2,3</sup> (2015<sup>1,2</sup>). Collections: BBSL

### Genus Zacosmia Ashmead

**230.** ‡ *Zacosmia maculata maculata* (Cresson, 1879). County records: Walla Walla<sup>3,35</sup>. Seasonality: Jun<sup>3</sup> (1936<sup>3</sup>). Collections: BBSL. Comments: Linsley (1939) lists the Washington record as Whitman County (Walla Walla). Walla Walla is located in Walla Walla County.

## Nomadini

#### Genus Nomada Scopoli

- **231.** *Nomada aldrichi* **Cockerell, 1910**. County records: Spokane<sup>76</sup>. Seasonality: May<sup>76</sup>. [= *Nomada vicinalis aldrichi* Cockerell, 1910]
- **232.** ‡ *Nomada articulata* Smith, 1854. County records: Kitsap<sup>1,2,3</sup>, Whitman<sup>76</sup>. Seasonality: May<sup>1,2,3,76</sup> (1965<sup>1,2,3</sup>). Collections: BBSL, BugGuide
- 233. ‡ Nomada bella Cresson, 1863. County records: King<sup>120</sup>, Thurston<sup>120</sup>. Seasonality: Jun<sup>120</sup> (1897<sup>120</sup>)
- **234.** *Nomada civilis* Cresson, 1878. County records: Whitman<sup>76</sup>. Seasonality: May<sup>76</sup>. Comments: Discover Life has synonymized *N. civilis* with *N. opposita* without reference or explanation. We are not aware of any published work that that synonymizes these species and retain them as separate taxa in this checklist.
- **234a.** *Nomada civilis spokanensis* **Cockerell, 1910.** County records: Spokane<sup>1,2,3,76</sup>. Seasonality: May<sup>3,76</sup>. Collections: NMNH. **Holotype**. USA, Washington, Spokane County, Spokane; 30 May; WM Mann; Type No. 29476, USNM ENT 00533989. Comments: Discover Life has synonymized *N. civilis spokanensis* with *N. opposita* without reference or explanation. We are not aware of any published work that that synonymizes these species and retain them as separate taxa in this checklist.
- **235.** *Nomada citrina* Cresson, 1878. [= *Xanthidium citrinum* Cresson, 1878]. Comments: Viereck et al. (1905) notes *N. citrina* occurs in Washington, but do not provide a locality.
- **236.** †**‡** *Nomada collinsiana* **Cockerell, 1905**. County records: **Walla Walla**<sup>1,2,3</sup>. Seasonality: May<sup>1,2,3</sup>, Jun<sup>1,2</sup> (1939<sup>1,2</sup>). Collections: BBSL
- 237. Nomada coquilletti Cockerell, 1903. County records: Whitman<sup>76</sup>. Seasonality: Mar<sup>76</sup>, Apr<sup>76</sup>
- **238.** ‡ *Nomada cressonii trevoriana* Viereck, 1905. County records: Thurston<sup>1,2,76,118</sup>. Seasonality: Apr<sup>1,2,118</sup> (1894<sup>1,2,118</sup>). Collections: NMNH. Holotype. USA, Washington, Thurston County, Olympia; 22 April 1894
- **239.** † *Nomada crotchii* Cresson, 1878. County records: Benton<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>. Seasonality: Mar<sup>1,2</sup>, May<sup>1,2,3</sup> (2022<sup>1,2</sup>). Collections: BBSL, iNaturalist
- 240. Nomada cuneata (Robertson, 1903). County records: Whitman<sup>76</sup>. Seasonality: May<sup>76</sup>

- 241. *Nomada edwardsii* Cresson, 1878. County records: Benton<sup>1,2</sup>, Kittitas<sup>2,3</sup>, Spokane<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3,76</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>1,2,3</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,76</sup>, Jul<sup>1,2,3</sup> (2015<sup>1,2</sup>). Collections: BBSL, INHS. [= *Holonomada edwardsii* Cresson, 1878]
- **241a.** *Nomada edwardsii vinnula* Cresson, 1879. County records: Spokane<sup>76</sup>, Whitman<sup>76</sup>. Seasonality: May<sup>76</sup>
- 242. ‡ Nomada erythrochroa Cockerell, 1903. County records: Franklin<sup>1,2,3,50,76,118</sup>, Yakima<sup>50,76</sup>. Seasonality: May<sup>1,2,3,118</sup>, Jun<sup>50,76</sup> (1903<sup>50</sup>). Collections: NMNH. Holotype. USA, Washington, Franklin County, Pasco; 25 May 1896; Type No. 13185, USNM ENT 00533921
- 243. ‡ *Nomada flammigera* Cockerell, 1906. County records: Yakima<sup>2,50,76</sup>. Seasonality: May<sup>2,50</sup>, Jul<sup>76</sup> (1906<sup>76</sup>). Collections: LACM. Holotype. USA, Washington, Yakima County, North Yakima; 15 May 1903; E Jenne.
- **244.** *Nomada grayi eastonensis* **Cockerell, 1903**. County records: Kittitas<sup>1,2,3,76,118,120</sup>. Collections: NMNH. **Holotype**. USA, Washington, Kittitas County, Easton; Type No. 13163, USNM ENT 00533917. [= *Gnathias grayi eastonensis* Cockerell, 1903]
- 245. *Nomada hesperia hesperia* Cockerell, 1903. County records: Kittitas<sup>3</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>2,3,76,77</sup>. Seasonality: Apr<sup>3,77</sup>, May<sup>1,2,3,76,77</sup>, Jun<sup>77</sup> (1989<sup>3</sup>). Collections: BBSL, INHS. Floral records: ASTERACEAE: *Balsamorhiza*<sup>3</sup>
- **246.** *Nomada itamera* Cockerell, 1910. County records: Whitman<sup>2,76</sup>. Seasonality: May<sup>76</sup>. Collections: AMNH. Holotype. USA, Washington, Whitman County, Pullman; WM Mann; AMNH\_IZC 00323820
- 247. ‡ *Nomada jennei* Cockerell, 1906. County records: Yakima<sup>1,2,3,121</sup>. Seasonality: Sep<sup>1,2,3,121</sup> (1903<sup>1,2,3,121</sup>). Collections: NMNH. Holotype. USA, Washington, Yakima County, North Yakima; 26 September 1903; E Jenne; Type No. 29484; USNM ENT 00533939
- 248. Nomada kincaidiana Cockerell, 1903. Holotype. USA: Washington State
- 249. Nomada lehighensis Cockerell, 1903. County records: Asotin<sup>65</sup>. Seasonality: May<sup>65</sup> (2007<sup>65</sup>). Collection: PCYU
- **250.** ‡ *Nomada malonella* Cockerell, 1910. County records: Whitman<sup>1,2,76</sup>. Seasonality: May<sup>2,76</sup> (1909<sup>2,76</sup>). Collections: LACM, UCMC. Holotype. USA, Washington, Whitman County, Wawawai; 1 May 1909
- 251. ‡ Nomada malonina Cockerell, 1910. County records: Whitman<sup>1,2,3,76</sup>. Seasonality: May<sup>1,2,3,76</sup> (1909<sup>1,2,3,76</sup>). Collections: NMNH. Holotype. USA, Washington, Whitman County, Wawawai; 15 May 1909; WM Mann; Type No 29487, USNM ENT 00533947
- 252. Nomada mutans Cockerell, 1910. County records: Jefferson<sup>1,2</sup>, Pacific<sup>110</sup>, Whitman<sup>1,2,3,76,110,111</sup>, Yakima<sup>111</sup>. Seasonality: Jun<sup>1,2</sup>, Jul<sup>110</sup>, Aug<sup>1,2,3,76,110,111</sup> (2015<sup>1,2</sup>). Collections: BBSL, NMNH, UCMC. Holotype. USA, Washington, Whitman County, Pullman; 9 August 1908; WM Mann; USNM 13192. Paratype. USA, Washington, Whitman County, Pullman; 9 August 1908; WM Mann
- **253.** ‡ *Nomada orcusella* Cockerell, 1910. County records: San Juan<sup>2,76</sup>. Seasonality: Jul<sup>2,76</sup> (1909<sup>2,76</sup>). Collections: LACM

- **254.** ‡ *Nomada packardiella* Cockerell, 1906. County records: Ferry<sup>1,2</sup>, Whitman<sup>76</sup>. Seasonality: May<sup>76</sup>, Aug<sup>1,2</sup> (1931<sup>1,2</sup>). Collections: SEMC
- 255. Nomada pascoensis Cockerell, 1903. County records: Benton<sup>2,3</sup>, Franklin<sup>1,2,3,120</sup>, Klickitat<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>. Seasonality: Apr<sup>2,3</sup>, May<sup>1,2,3,120</sup>, Aug<sup>1,2</sup> (2011<sup>1,2</sup>). Collections: BBSL, NMNH, SEMC
- **256.** ‡ *Nomada perbella* (Viereck, 1905). County records: Grays Harbor<sup>76,118</sup>, King<sup>76</sup>, Thurston<sup>76,118</sup>, Whitman<sup>76</sup>. Seasonality: May<sup>76,118</sup>, Jun<sup>118</sup> (1904<sup>118</sup>). [= *Gnathias perbella* Viereck, 1905]
- **257.** ‡ *Nomada perplexans* Cockerell, 1910. County records: Whitman<sup>1,2,3,76</sup>. Seasonality: Jun<sup>1,2,3,76</sup> (1908<sup>1,2,3,76</sup>). Collections: NMNH. Holotype. USA, Washington, Whitman County, Pullman; 7 June 1908; WM Mann; Type No. 29493, USNM ENT 00533967
- **258.** *Nomada pulsatillae* Cockerell, 1906. County records: Spokane<sup>76</sup>, Whitman<sup>76</sup>. Seasonality: May<sup>76</sup>
- **259.** *Nomada rivalis* Cresson, 1878. [= *Xanthidium rivale* Cresson, 1878]. Comments: Viereck et al. (1905) note *N. rivalis* occurs in Washington, but do not provide a locality.
- **260.** † *Nomada scita* Cresson, 1878. County records: Adams<sup>1,2,3</sup>, Benton<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL, SEMC
- **261.** ‡ *Nomada semisuavis* **Cockerell, 1910**. County records: Whitman<sup>1,2,76</sup>. Seasonality: Jul<sup>1,2,76</sup> (1908<sup>1,2,76</sup>). Collections: LACM, UCMC. **Holotype**. USA, Washington, Whitman County, Wawawai; 4 July 1908; WM Mann
- 262. † *Nomada suavis* Cresson, 1878. County records: Clallam<sup>1,2,3</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>3</sup>. Seasonality: Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup> (2000<sup>1,2,3</sup>). Collections: AMNH, BBSL. Host record: *Nomia melanderi* Cockerell<sup>78</sup>
- 263. † *Nomada texana* Cresson, 1872. County records: Walla Walla<sup>1,2</sup>, Whitman<sup>1,2</sup>. Seasonality: Apr<sup>1,2</sup>, Jul<sup>1,2</sup> (2011<sup>1,2</sup>). Collections: BBSL, TTU. [= *Nomada heiligbrodtii* Cresson, 1878]
- **264.** *Nomada ultima* Cockerell, 1903. County records: Spokane<sup>76</sup>. Seasonality: May<sup>76</sup>. [= *Nomada modocorum* Cockerell, 1903]
- **265.** *Nomada washingtoni* **Cockerell, 1903**. Collections: NMNH. **Holotype**. USA, Washington State. [= *Gnathias washingtoni* Cockerell, 1903].

## Xylocopinae: Ceratinini

## Genus Ceratina Latreille

 266. Ceratina (Zadontomerus) acantha Provancher, 1895. County records: Chelan<sup>1,2,3</sup>, Clallam<sup>1,2,3</sup>, Cowlitz<sup>1,2,3</sup>, Jefferson<sup>1,2</sup>, King<sup>1,2,3,58,125</sup>, Kitsap<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Mason<sup>3</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>5,6</sup>, Spokane<sup>1,2</sup>, Thurston<sup>6,125,133</sup>, Walla Walla<sup>1,2,3,71</sup>, Whitman<sup>1,2,3,6,8</sup>. Seasonality: Apr<sup>1,2,5</sup>, May<sup>1,2,3,5,58</sup>, Jun<sup>1,2,3,133</sup>, Jul<sup>1,2,3,5,6</sup>, Aug<sup>1,2,3,6</sup>, Sep<sup>1,2,6</sup> (2020<sup>133</sup>). Collections: AMNH, BBSL, JRYA, SEMC, TAMU, WSDA, WSUC. Floral records: APIACEAE: Lomatium<sup>8</sup>; ASPARAGACEAE: Camassia quamash<sup>5</sup>; ASTERACEAE: Cirsium vulgare<sup>8</sup>, Eriophyllum lanatum<sup>8,133</sup>, Helianthus annuus<sup>8</sup>, Hypochaeris radicata<sup>5</sup>, Taraxacum officinale<sup>5</sup>; GERANIACE-AE: Geranium viscosissiumum<sup>8</sup>; HYPERICACEAE: Hypericum perforatum<sup>133</sup>; MALVACEAE: Iliamna longisepala<sup>3</sup>; PLANTAGINACEAE: Penstemon triphyllus<sup>8</sup>; ROSACEAE: Rosa<sup>8</sup>

- **267.** †**‡** *Ceratina* (*Zadontomerus*) *micheneri* Daly, 1973. County records: Whatcom<sup>7</sup>. Seasonality: Jun<sup>7</sup> (1945<sup>7</sup>). Collections: WSUC
- 268. Ceratina (Zadontomerus) nanula Cockerell, 1897. County records: Jefferson<sup>1,2</sup>, Klickitat<sup>1,2</sup>, San Juan<sup>1,2,5,124,136</sup>, Spokane<sup>1,2</sup>, Thurston<sup>133</sup>, Whitman<sup>1,2,3,6,61</sup>. Seasonality: Apr<sup>1,2,61</sup>, May<sup>1,2,6,133</sup>, Jun<sup>1,2,6,133</sup>, Jul<sup>1,2,5,6,133</sup>, Aug<sup>1,2,6</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2</sup> (2019<sup>133</sup>). Collections: BBSL, PWRC, WSDA. Floral records: ASPARAGACE-AE: Brodiaea coronaria<sup>133,136</sup>; ASTERACEAE: Cirsium arvense<sup>136</sup>, Crepis capillaris<sup>5,133,136</sup>, Eriophyllum lanatum<sup>133</sup>, Grindelia integrifolia<sup>5</sup>, Hypochaeris radicata<sup>5,136</sup>, Taraxacum officinale<sup>136</sup>; CARYOPHYLLACEAE: Cerastium arvense<sup>133</sup>; CON-VOLVULACEAE: Calystegia soldanella<sup>136</sup>; ONAGRACEAE: Clarkia amoena<sup>133</sup>; ROSACEAE: Rubus bifrons<sup>136</sup>
- **269.** *Ceratina* (*Zadontomerus*) *pacifica* H. S. Smith, 1907. County records: Chelan<sup>58</sup>, Grant<sup>1,2,4</sup>, Klickitat<sup>2,3</sup>, Okanogan<sup>58</sup>, Spokane<sup>1,2</sup>, Whitman<sup>1,2,58</sup>. Seasonality: Apr<sup>58</sup>, May<sup>1,2,58</sup>, Jun<sup>1,2,58</sup>, Jul<sup>1,2,58</sup>, Aug<sup>1,2,3,58</sup>, Sep<sup>1,2</sup> (2014<sup>1,2</sup>). Collections: BBSL, INHS, PCYU
- 270. ‡ Ceratina (Zadontomerus) sequoiae Michener, 1936. County records: Whitman<sup>58</sup>. Seasonality: Apr<sup>58</sup>, May<sup>58</sup> (1919<sup>58</sup>)

## **Xylocopini**

### Genus Xylocopa Latreille

271. †\* *Xylocopa (Xylocopoides) virginica* (Linnaeus, 1771). County records: Benton<sup>1</sup>, King<sup>1</sup>. Seasonality: Apr<sup>1</sup>, May<sup>1</sup> (2024<sup>1</sup>). Collections: iNaturalist

### Colletidae: Colletinae: Colletini

#### Genus Colletes Latreille

- **272.** *Colletes compactus hesperius* Swenk, 1906. County records: Walla Walla<sup>37,84</sup>, Whitman<sup>37,84,126</sup>, Yakima<sup>37,84</sup>. Collections: NMNH. Holotype. USA, Washington, Whitman County, Almota
- 273. Colletes consors Cresson, 1868. County records: Clallam<sup>3</sup>, Okanogan<sup>1,2,3,59</sup>, Yakima<sup>3</sup>. Seasonality: Jul<sup>1,2,3</sup> (2014<sup>3</sup>). Collections: BBSL, JRYA, SEMC. Floral records: HYDROPHYLLACEAE: *Phacelia leptosepala*<sup>3,59</sup>
- 273a. *Colletes consors pascoensis* Cockerell, 1898. County records: Franklin<sup>53,115</sup>, Okanogan<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>, Yakima<sup>1,2,3,37,84</sup>. Seasonality: May<sup>1,2,3</sup>, Jul<sup>1,2,3,37,84</sup>,

Aug<sup>1,2</sup> (2012<sup>1,2</sup>). Collections: NMNH. **Holotype**. USA, Washington, Franklin County, Pasco. Floral records: HYDROPHYLLACEAE: *Phacelia*<sup>84</sup>

- 274. ‡ *Colletes delodontus* Viereck, 1903. County records: Franklin<sup>115</sup>. Seasonality: May<sup>115</sup> (1896<sup>115</sup>)
- 275. *Colletes fulgidus* Swenk, 1904. County records: Asotin<sup>1,2,4</sup>, Benton<sup>1,2</sup>, Garfield<sup>46</sup>, Grant<sup>126</sup>, Jefferson<sup>1,2</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,4</sup>, San Juan<sup>22,136</sup>, Spokane<sup>1,2</sup>, Walla Walla<sup>1,2</sup>, Whitman<sup>6,126</sup>, Yakima<sup>126</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2,46</sup>, Jul<sup>1,2</sup>, Aug<sup>1,2,6</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2</sup> (2017<sup>136</sup>). Collections: BBSL, PCYU, WSDA. Floral records: ASTERACEAE: *Achillea millefolium*<sup>3,59</sup>, *Anaphalis margaritacea*<sup>59</sup>, *Crepis capillaris*<sup>136</sup>, *Erigeron speciosus*<sup>3,59</sup>; CAPRIFOLIACEAE: *Symphoricarpos albus*<sup>136</sup>; PLANTAGINACAE: *Penstemon washingtonensis*<sup>59</sup>
- 275a. *Colletes fulgidus fulgidus* Swenk, 1904. County records: Benton<sup>1,2,3</sup>, Clallam<sup>1,2,3</sup>, Cowlitz<sup>1,2,3</sup>, Ferry<sup>1,2,3</sup>, Garfield<sup>1,2,3</sup>, Grays Harbor<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>59</sup>, San Juan<sup>1,2</sup>, Spokane<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3</sup>. Seasonality: May<sup>1,2,3</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2</sup> (2012<sup>1,2</sup>). Collections: AMNH, BBSL, PWRC, SEMC. Floral records: FABACEAE: *Onobrychis viciifolia*<sup>3</sup>
- **276.** *Colletes gypsicolens* Cockerell, 1897. County records: Benton<sup>1,2,3</sup>, Franklin<sup>1,2,3</sup>, Yakima<sup>37,84</sup>. Seasonality: Sep<sup>1,2,3</sup>, Oct<sup>1,2</sup> (1994<sup>1,2,3</sup>). Collections: BBSL, SEMC
- 277. *Colletes hyalinus* Provancher, 1888. County records: Pacific<sup>1,2,3</sup>, Pend Oreille<sup>37,84</sup>, San Juan<sup>136</sup>. Seasonality: Jul<sup>1,2</sup>, Aug<sup>1,2,3</sup> (2017<sup>136</sup>). Collections: BBSL. Floral records: ROSACEAE: *Potentilla anserina* ssp. *pacifica*<sup>136</sup>
- **278.** ‡ *Colletes inaequalis* Say, 1837. County records: Chelan<sup>1,2,3,37,84</sup>, Douglas<sup>1,2</sup>. Seasonality: May<sup>1,2,3</sup> (1960<sup>1,2</sup>). Collections: SEMC
- 279. Colletes kincaidii Cockerell, 1898. County records: Asotin<sup>1,2,4</sup>, Jefferson<sup>1,2</sup>, San Juan<sup>136</sup>, Spokane<sup>1,2,53</sup>, Thurston<sup>1,2,3,53,84,115</sup>, Whitman<sup>1,2,3,53</sup>. Seasonality: May<sup>1,2,3,4</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2,3,53</sup> (2017<sup>136</sup>). Collections: BBSL, NMNH, PCYU, SEMC, UCRC. Holotype. USA, Washington, Thurston County, Olympia; 5 July 1946; *Potentilla haliastris*; Type No. 4270, USNM ENT 00534565. Floral records: ASTERACEAE: Cirsium arvense<sup>136</sup>; CAPRIFOLIACEAE: Symphoricarpos albus<sup>136</sup>; CAR-YOPHYLLACEAE: Spergularia macrotheca<sup>136</sup>; ROSACEAE: Potentilla
- 280. Colletes lutzi Timberlake, 1943. County records: Benton<sup>1,2</sup>, King<sup>54</sup>, Spo-kane<sup>1,2,3</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2,3</sup>, Jul<sup>54</sup> (2015<sup>1,2</sup>). Collections: BBSL
- **280a.** *Colletes lutzi interior* Timberlake, 1951. County records: Benton<sup>1,2,3</sup>, King<sup>37,84</sup>, Kittitas<sup>1,2,3,37</sup>, Whitman<sup>37,84</sup>. Seasonality: Jul<sup>1,2,3</sup>, Sep<sup>1,2,3</sup> (1995<sup>1,2,3</sup>). Collections: BBSL, SEMC
- **281.** *Colletes nigrifrons* **Titus, 1900**. County records: **Chelan**<sup>3</sup>, Okanogan<sup>1,2,3,59</sup>, **Skagit**<sup>3</sup>. Seasonality: Jul<sup>1,2</sup>, Aug<sup>1,2,3</sup> (2014<sup>3</sup>). Collections: BBSL, JRYA. Floral records: ASTERACEAE: *Achillea millefolium*<sup>59</sup>; CELASTRACEAE: *Parnassia fimbriata*<sup>3,59</sup>; CRASSULACEAE: *Sedum lanceolatum*<sup>59</sup>; PLANTAGINACEAE: *Penstemon washingtonensis*<sup>59</sup>; ROSACEAE: *Potentilla gracilis*<sup>3,59</sup>
- **282.** ‡ *Colletes paniscus sculleni* Timberlake, 1951. County records: Benton<sup>1,2,3</sup>, Pierce<sup>37,54,84</sup>, Yakima<sup>1,2,3,37,84</sup>. Seasonality: May<sup>1,2,3</sup>, Jul<sup>1,2,3,54</sup> (1949<sup>1,2,3</sup>). Collections: SEMC

- **283.** *Colletes phaceliae* Cockerell, 1906. County records: Ferry<sup>1,2</sup>, Franklin<sup>1,2,53</sup>, Thurston<sup>53</sup>, Walla Walla<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>53</sup>, Jun<sup>1,2,3,53</sup>, Jul<sup>53</sup>, Aug<sup>1,2</sup> (2012<sup>1,2</sup>). Collections: BBSL, PCYU, SEMC. Floral records: ONAGRACEAE: *Chamerion angustifolium* ssp. *angustifolium*<sup>53</sup>
- **284.** *Colletes simulans* Cresson, 1868. County records: Thurston<sup>115</sup>, Yakima<sup>126</sup>. Seasonality: Jul<sup>115</sup> (1896<sup>115</sup>). [= Colletes tegularis Swenk, 1905]
- **284a.** *Colletes simulans nevadensis* **Swenk, 1908**. County records: **Benton**<sup>1,2,3</sup>, Thurston<sup>133</sup>. Seasonality: Jul<sup>133</sup>, Sep<sup>1,2,3</sup> (2017<sup>133</sup>). Collections: BBSL. Floral records: APIACEAE: *Daucus carota*<sup>133</sup>; ASTERACEAE: *Senecio*<sup>3</sup>

285. Colletes slevini Cockerell, 1925. County records: Yakima<sup>37,84</sup>

#### Hylaeinae: Hylaeini

#### Genus Hylaeus Fabricius

- 286. Hylaeus (Cephalylaeus) basalis (Smith, 1853). County records: King<sup>1,2</sup>, Kitsap<sup>1,2</sup>, Okanogan<sup>1,2,3,59</sup>, San Juan<sup>5</sup>, Skagit<sup>1,2</sup>, Thurston<sup>1,2</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2,3,5</sup>, Jul<sup>1,2</sup>, Aug<sup>1</sup> (2014<sup>1</sup>). Collections: BBSL, UCMC. Floral records: ASTER-ACEAE: Arnica sororia<sup>59</sup>; BRASSICACEAE: Lepidium virginicum<sup>5</sup>; HYDRO-PHYLLACEAE: Phacelia leptosepala<sup>59</sup>; ROSACEAE: Rosa nutkana ssp. nutkana<sup>3,59</sup>
- 287. Hylaeus (Hylaeus) annulatus (Linnaeus, 1758). County records: Chelan<sup>3</sup>, Clallam<sup>3</sup>, King<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Skagit<sup>3</sup>. Seasonality: Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup> (2014<sup>3</sup>). Collections: AMNH, BBSL, JRYA. [= Hylaeus ellipticus (Kirby, 1837)]. Floral records: ASTERACEAE: Agoseris glauca var. dasycephala<sup>59</sup>, Anaphalis margaritacea<sup>59</sup>, Taraxacum officinale<sup>3,59</sup>; FABACEAE: Trifolium repens<sup>3,59</sup>; GERANIACE-AE: Geranium viscosissimum var. viscosissimum<sup>3,59</sup>; HYDROPHYLLACEAE: Phace-lia leptosepala<sup>59</sup>, ROSACEAE: Potentilla gracilis<sup>3,59</sup>, Rosa nutkana ssp. nutkana<sup>59</sup>
- 288. Hylaeus (Hylaeus) conspicuus (Metz, 1911). County records: Klickitat<sup>1,2</sup>, Spo-kane<sup>1,2</sup>, Whitman<sup>55</sup>. Seasonality: Aug<sup>1,2</sup> (2011<sup>1,2</sup>). Collections: BBSL, UCDC
- **289.** *Hylaeus* (*Hylaeus*) *granulatus* (Metz, 1911). County records: Whitman<sup>32</sup>. Seasonality: May<sup>32</sup>, Jun<sup>32</sup>, Jul<sup>32</sup> (2013<sup>32</sup>)
- 290. †\* Hylaeus (Hylaeus) leptocephalus (Morawitz, 1871). County records: Benton<sup>6</sup>, Douglas<sup>1,2,3</sup>, Walla Walla<sup>1,2</sup>, Yakima<sup>6</sup>. Seasonality: May<sup>6</sup>, Jun<sup>1,2</sup>, Jul<sup>6</sup>, Aug<sup>1,2,3</sup> (2023<sup>6</sup>). Collections: BBSL, iNaturalist, WSDA. [= Hylaeus bisinuatus Förster, 1871]
- 291. Hylaeus (Hylaeus) mesillae (Cockerell, 1896). County records: Benton<sup>1,2,6</sup>, Chelan<sup>6</sup>, Grant<sup>6</sup>, Okanogan<sup>6</sup>, Walla Walla<sup>6,71</sup>, Yakima<sup>6</sup>. Seasonality: May<sup>6</sup>, Jun<sup>1,2,6</sup>, Jul<sup>6</sup>, Aug<sup>6</sup>, Sep<sup>6</sup> (2023<sup>6</sup>). Collections: BBSL, WSDA
- **291a.** *Hylaeus* (*Hylaeus*) *mesillae cressoni* (Cockerell, 1907). County records: Benton<sup>1,2,3</sup>, Walla Walla<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2,3</sup>, Jun<sup>1,2</sup>, Sep<sup>1,2,3</sup> (1997<sup>1,2,3</sup>). Collections: BBSL
- 292. Hylaeus (Hylaeus) rudbeckiae (Cockerell and Casad, 1895). County records: Chelan<sup>6</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,6,59</sup>, Spokane<sup>1,2</sup>. Seasonality: Jun<sup>1,2</sup>, Jul<sup>1,2,6</sup>, Aug<sup>1,2,3,6</sup>, Sep<sup>1,2</sup> (2023<sup>6</sup>). Collections: BBSL, WSDA

- **293.** †‡ *Hylaeus* (*Hylaeus*) *verticalis* (Cresson, 1869). County records: Kittitas<sup>2,3</sup>. Seasonality: Jul<sup>2,3</sup> (1934<sup>2,3</sup>). Collections: BBSL
- **294.** †‡ *Hylaeus (Paraprosopis) calvus (Metz, 1911).* County records: Chelan<sup>1,2,3</sup>. Seasonality: Jul<sup>1,2,3</sup> (1949<sup>1,2,3</sup>). Collections: SEMC
- 295. Hylaeus (Paraprosopis) coloradensis (Cockerell, 1896). County records: Clallam<sup>3</sup>, Kittitas<sup>3</sup>, San Juan<sup>55</sup>, Whitman<sup>55</sup>. Seasonality: Aug<sup>3</sup> (2014<sup>3</sup>). Collections: CAS, JRYA, UCMC, UCRC
- **296.** *Hylaeus* (*Paraprosopis*) *nevadensis* (Cockerell, 1896). County records: Chelan<sup>3</sup>, King<sup>55</sup>. Seasonality: Aug<sup>3</sup> (2014<sup>3</sup>). Collections: JRYA
- **297.** † *Hylaeus* (*Paraprosopis*) *wootoni* (Cockerell, 1896). County records: Chelan<sup>1,2,3</sup>, Clallam<sup>3</sup>, Ferry<sup>1,2,3</sup>, Pierce<sup>3</sup>, Spokane<sup>1,2</sup>, Yakima<sup>6</sup>. Seasonality: Jun<sup>1,2</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3,6</sup> (2023<sup>6</sup>). Collections: BBSL, JRYA, SEMC, UCRC, WSDA
- **298.** ‡ *Hylaeus (Prosopis) affinis* (Smith, 1853). County records: Whitman<sup>83</sup>. Seasonality: Jul<sup>83</sup> (1957<sup>83</sup>). Collections: BBSL, SEMC, UCDC. Comments: Snelling (1966) indicates records from Pullman, WA in Garfield County; however, Pullman is located in Whitman County.
- **299.** *Hylaeus* (*Prosopis*) *episcopalis* (Cockerell, 1896). County records: Clallam<sup>3</sup>, King<sup>83</sup>, Klickitat<sup>1,2,3</sup>, Pacific<sup>1,2,3</sup>, Spokane<sup>1,2</sup>, Whitman<sup>3</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup> (2015<sup>1,2</sup>). Collections: BBSL, JRYA, UCMC, UCRC
- **300.** *Hylaeus* (*Prosopis*) *modestus citrinifrons* Say, 1837. County record: Chelan<sup>1,2,3</sup>, Clallam<sup>3</sup>, Cowlitz<sup>1,2,3</sup>, Grays Harbor<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Pacific<sup>1,2,3</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>136</sup> Skagit<sup>3</sup>, Whatcom<sup>1,2,3</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup> (2017<sup>136</sup>). Collections: BBSL, JRYA, SEMC, UCRC. Floral records: ASTER-ACEAE: *Anaphalis margaritacea<sup>3,59</sup>, Crepis capillaris*<sup>136</sup>, *Taraxacum officinale*<sup>3,59</sup>; PLANTAGINACEAE: *Penstemon confertus*<sup>3,59</sup>; ROSACEAE: *Potentilla anserina* ssp. *pacifica*<sup>136</sup>, *P. gracilis*<sup>59</sup>
- 301. †\* Hylaeus (Spatulariella) punctatus (Brullé, 1832). County records: Whitman<sup>7</sup>, Yakima<sup>6</sup>. Seasonality: Aug<sup>6,7</sup> (2023<sup>6</sup>). Collections: WSDA

### Halictidae: Halictinae: Halictini

#### Genus Agapostemon Guerin-Meneville

302. Agapostemon (Agapostemon) femoratus Crawford, 1901. County records: Adams<sup>1,2,7</sup>, Asotin<sup>7</sup>, Benton<sup>1,2,3,6,7,71</sup>, Chelan<sup>7</sup>, Douglas<sup>1,2</sup>, Ferry<sup>1,2,3</sup>, Franklin<sup>1,2,3,7</sup>, Garfield<sup>1,2,3,46</sup>, Grant<sup>1,2,7</sup>, Island<sup>7</sup>, Kittitas<sup>1,2,3</sup>, Mason<sup>7</sup>, Okanogan<sup>1,2,3,7,59</sup>, Pacific<sup>1,2,3</sup>, Spokane<sup>1,2,3,7</sup>, Walla Walla<sup>1,2,3,7,71</sup>, Whitman<sup>1,2,3,7</sup>, Yakima<sup>7</sup>. Seasonality: Apr<sup>1,2,3,7</sup>, May<sup>1,2,3,7</sup>, Jun<sup>1,2,3,46,7</sup>, Jul<sup>1,2,3,6,7</sup>, Aug<sup>1,2,3,7</sup>, Sep<sup>1,2,3,7</sup>, Oct<sup>1,2,7</sup>, Nov<sup>7</sup> (2022<sup>6</sup>). Collections: BBSL, EMEC, iNaturalist, INHS, OSUC, SEMC, TAMU, WSDA, WSUC. Holotype. USA, Washington Territory. Conservation status: G5 – Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Arnica cordifolia<sup>59</sup>, Erigeron speciosus<sup>59</sup>, Senecio integerrimus<sup>59</sup>, Rhaponticum repens<sup>3</sup>; FABACEAE: Astragalus<sup>3</sup>; PLANTAGINACEAE: Penstemon washingtonensis<sup>59</sup>

- 303. Agapostemon (Agapostemon) texanus Cresson, 1872. County records: Adams<sup>1,2,7</sup>, Benton<sup>1,2,3,7,71</sup>, Clallam<sup>1,2,3</sup>, Douglas<sup>7</sup>, Franklin<sup>1,2,7</sup>, Garfield<sup>1,2,3,10,46</sup>, Grant<sup>7</sup>, Island<sup>1,2,7</sup>, Jefferson<sup>1,2</sup>, King<sup>1,2,3,7</sup>, Kitsap<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,4,7,59</sup>, Pacific<sup>1,2,3</sup>, Pierce<sup>1,2,7</sup>, San Juan<sup>1,2,3,5,6,7,124</sup>, Skagit<sup>7,10</sup>, Spokane<sup>1,2,7</sup>, Thurston<sup>1,2,3,7</sup>, Walla Walla<sup>1,2,3,7,71</sup>, Whatcom<sup>1,2,3,7</sup>, Whitman<sup>2,3,7,8</sup>, Yakima<sup>1,2,3,7</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>1,2,3,7</sup>, May<sup>1,2,3,5,7</sup>, Jun<sup>1,2,3,5,7,46</sup>, Jul<sup>1,2,3,5,7</sup>, Aug<sup>1,2,3,4,6,7</sup>, Sep<sup>1,2,3,7</sup>, Oct<sup>1,2,3,7</sup> (2022<sup>1,2</sup>). Collections: AMNH, BBSL, BugGuide, EMEC, FMNH, iNaturalist, OSUC, PWRC, SEMC, UCMC, WSDA, WSUC. Conservation status: G5 – Secure globally (NatureServe 2024). Floral Records: ASTER-ACEAE: Anaphalis margaritacea<sup>5</sup>, Haplopappus<sup>8</sup>, Helianthus anuus<sup>8</sup>; CONVOL-VULACEAE: Convolvulus<sup>8</sup>; FABACEAE: Astragalus racemosus<sup>3</sup>, Medicago sativa<sup>8</sup>; ROSACEAE: Rosa nutkana<sup>5</sup>
- 303a. Agapostemon (Agapostemon) angelicus Cockerell, 1924/texanus Cresson, 1872. County records: Asotin<sup>1,2</sup>, Benton<sup>1,2,3</sup>, Chelan<sup>1,2,3</sup>, Columbia<sup>1,2</sup>, Franklin<sup>1,2</sup>, Garfield<sup>1,2,3</sup>, Jefferson<sup>1,2</sup>, King<sup>1,2</sup>, Kitsap<sup>1,2,3</sup>, Kittitas<sup>1,2</sup>, Klickitat<sup>1,2</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>6,136</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2</sup>, Thurston<sup>133</sup>, Walla Walla<sup>1,2,3</sup>, Whatcom<sup>1,2</sup>, Whitman<sup>2</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>1,2</sup>, May<sup>1,2,133</sup>, Jun<sup>1,2,3,6,133</sup>, Jul<sup>1,2,3,6,133</sup>, Aug<sup>1,2,6</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2</sup> (2020<sup>133</sup>). Collections: BBSL, SEMC, TAMU, WSDA. Floral records: ASPARAGACEAE: Camassia quamash133; ASTERACE-AE: Crepis capillaris<sup>133</sup>, Balsamorhiza deltoidea<sup>133</sup>, Erigeron speciosus<sup>133</sup>, Hypochaeris radicata<sup>133,136</sup>, Leucanthemum vulgare<sup>133</sup>, Microseris laciniata<sup>133</sup>, Solidago missouriensis<sup>133</sup>; BRASSICACEAE: Cakile maritima<sup>136</sup>; CAPRIFOLIACEAE: Plectritis congesta<sup>133</sup>; CONVOLVULACEAE: Calystegia soldanella<sup>136</sup>; FABACEAE: Onobrychis arenaria<sup>3</sup>, Vicia satvia<sup>133</sup>; HYPERICACEAE: Hypericum perforatum<sup>133</sup>; MALVACEAE: Iliamna longisepala3; OROBANCHACEAE: Parentucellia viscosa<sup>133</sup>; ONAGRACEAE: Clarkia amoena<sup>133</sup>; PLUMBAGINACEAE: Armeria maritima<sup>133</sup>; ROSACEAE: Potentilla gracilis<sup>133</sup>. Comments: Females of A. angelicus and A. texanus cannot be separated morphologically (Roberts 1973), so these uncertain records are combined here. No male A. angelicus have been recorded in Washington, suggesting these are most likely records of *A. texanus*.
- 304. Agapostemon (Agapostemon) virescens (Fabricius, 1775). County records: Benton<sup>1,2,3,7</sup>, Chelan<sup>1,2</sup>, Douglas<sup>3</sup>, Garfield<sup>7</sup>, Jefferson<sup>1,2</sup>, King<sup>1,2</sup>, Klickitat<sup>1,2</sup>, Lewis<sup>1,2</sup>, Okanogan<sup>1,2,3,7,59</sup>, Skagit<sup>1,2</sup>, Snohomish<sup>1,2</sup>, Spokane<sup>1,2,3,7</sup>, Stevens<sup>1,2</sup>, Thurston<sup>1,2,133</sup>, Walla Walla<sup>1,2,3,7,71</sup>, Whitman<sup>1,2,3,6,7,8</sup>, Yakima<sup>1,2,7</sup>. Seasonality: Apr<sup>1,2,7</sup>, May<sup>1,2,7,133</sup>, Jul<sup>1,2,3,7,133</sup>, Jul<sup>1,2,3,6,7,133</sup>, Aug<sup>1,2,3,6,7</sup>, Sep<sup>1,2,3,7</sup>, Oct<sup>1,2,7</sup>, Nov<sup>7</sup> (2022<sup>1,2</sup>). Collections: BBSL, BugGuide, iNaturalist, INHS, SEMC, WSDA, WSUC. Conservation status: G5 – Secure globally (NatureServe 2024). Floral records: ASPARAGACEAE: Camassia quamash<sup>133</sup>; ASTERACEAE: Balsamorhiza deltoidea<sup>133</sup>, Cirsium vulgare<sup>8</sup>, Erigeron speciosus<sup>133</sup>, Eriophyllum lanatum<sup>133</sup>, Gaillardia aristata<sup>8,133</sup>, Helianthus anuus<sup>8</sup>, Hypochaeris radicata<sup>133</sup>, Microseris laciniata<sup>133</sup>, Solidago simplex<sup>133</sup>, Taraxacum officinale<sup>133</sup>; BRASSICACEAE: Lepidium campestre<sup>133</sup>, Sisymbrium altissimum<sup>3,59</sup>; FABACEAE: Vicia<sup>8</sup>, V. hirsuta<sup>133</sup>; GEN-TIANACEAE: Gentiana calycosa<sup>8</sup>; GERANIACEAE: Geranium dissectum<sup>133</sup>;

HYPERICACEAE: Hypericum perforatum<sup>133</sup>; IRIDACEAE: Sisyrinchium idahoense<sup>133</sup>; ONAGRACEAE: Chamerion angustifolium<sup>133</sup>, C. angustifolium ssp. angustifolium<sup>8</sup>, Clarkia amoena<sup>133</sup>; PLUMBAGINACEAE: Armeria maritima<sup>133</sup>; ROSACEAE: Rosa<sup>8</sup>

## Genus Halictus Latreille

- 305. Halictus (Nealictus) farinosus Smith, 1853. County records: Benton<sup>1,2,3,71</sup>, Chelan<sup>1,2,3</sup>, Douglas<sup>3</sup>, Grant<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,59</sup>, Pierce<sup>1,2,3</sup>, Spokane<sup>1,2,3,6</sup>, Stevens<sup>1,2</sup>, Walla Walla<sup>1,2,3,71</sup>, Whitman<sup>1,2,3,6,8,119</sup>, Yakima<sup>1,2,3,6,119</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3,6</sup>, Aug<sup>1,2,3,6</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: BBSL, BugGuide, EMEC, iNaturalist, OSUC, SEMC, WSDA, WSUC. Floral records: APIACEAE: Lomatium<sup>8</sup>; ASTERACEAE: Achillea millefolium<sup>59</sup>, Agoseris glauca var. dasycephala<sup>3,59</sup>, Anaphalis margaritacea<sup>59</sup>, Arnica cordifolia<sup>3,59</sup>, Erigeron speciosus<sup>59</sup>, Helianthus annuus<sup>8</sup>, Senecio triangularis<sup>59</sup>, Solidago<sup>8</sup>; BRASSI-CACEAE: Brassica rapa<sup>8</sup>, Sisymbrium altissimum<sup>8</sup>; ROSACEAE: Malus domestica<sup>8</sup>
- 306. Halictus (Odontalictus) ligatus Say, 1837. County records: Adams<sup>1,2</sup>, Benton<sup>1,2,3,71</sup>, Chelan<sup>1,2,3</sup>, Douglas<sup>1,2</sup>, Grant<sup>1,2,3</sup>, King<sup>1,2,3</sup>, Klickitat<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Spokane<sup>1,2,3,6</sup>, Thurston<sup>1,2</sup>, Walla Walla<sup>1,2,3,71</sup>, Whitman<sup>1,2,6,8</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3,6</sup>, Jul<sup>1,2,3,6</sup>, Aug<sup>1,2,3,6</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: BBSL, BugGuide, FMNH, iNaturalist, WSDA, WSUC. Floral records: ASTERACEAE: Anaphalis margaritacea<sup>3,59</sup>, Cirsium arvense<sup>8</sup>, Haplopappus<sup>8</sup>, Helianthus annuus<sup>8</sup>, Solidago<sup>8</sup>
- **307.** Halictus (Protohalictus) rubicundus (Christ, 1791). [= Halictus lerouxii var. ruborum Cockerell, 1898]. County records: Benton<sup>1,2</sup>, Chelan<sup>1,2,3</sup>, Clallam<sup>1,2,3</sup>, Clark<sup>1,2,3</sup>, Cowlitz<sup>1,2,3</sup>, Douglas<sup>1,2</sup>, Garfield<sup>46</sup>, Jefferson<sup>1,2,3</sup>, King<sup>1,2,3,119</sup>, Kitsap<sup>1,2,3</sup>, Kittitas<sup>2,3</sup>, Klickitat<sup>1,2</sup>, Mason<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Pacific<sup>1,2,3</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>1,2,3,6,22,124,136</sup>, Skagit<sup>1,2,3,10,124</sup>, Snohomish<sup>1,2,3</sup>, Spokane<sup>1,2,3,6</sup>, Stevens<sup>1,2,3</sup>, Thurston<sup>1,2,3,6,133</sup>, **Walla Walla**<sup>1,2,3</sup>, **Whatcom**<sup>1,2,3,6</sup>, Whitman<sup>1,2,6,8</sup>. Seasonality: Feb<sup>1,2</sup>, Mar<sup>1,2,3</sup>, Apr<sup>1,2,133</sup>, May<sup>1,2,133</sup>, Jun<sup>1,2,3,6,133</sup>, Jul<sup>1,2,3,6</sup>, Aug<sup>1,2,3,6</sup>, Sep<sup>1,2,3</sup>, Oct<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: AMNH, BBSL, BugGuide, FMNH, iNaturalist, JRYA, PWRC, TAMU, WSDA, WSUC. Floral records: APIACEAE: Lomatium<sup>8</sup>; AS-PARAGACEAE: Camassia quamash<sup>133</sup>; ASTERACEAE: Achillea millefolium<sup>59</sup>, Cirsium arvense<sup>8</sup>, Erigeron speciosus<sup>59</sup>, Hypochaeris radicata<sup>136</sup>, Senecio triangularis<sup>3,59</sup>, Taraxacum officinale<sup>8,133</sup>; BRASSICACEAE: Sisymbrium altissimum<sup>3,59</sup>; CAMPANULACAEAE: Campanula rotundifolia<sup>59</sup>; CONVOLVULACEAE: Calystegia soldanella<sup>136</sup>; CRASSULACEAE: Sedum lanceolatum<sup>59</sup>; FABACEAE: Lupinus sericeus<sup>59</sup>, Trifolium pratense<sup>3</sup>, T. repens<sup>8,59</sup>; OROBANCHACEAE: Parentucellia viscosa<sup>133</sup>; RANUNCULACEAE: Ranunculus<sup>8</sup>; ROSACEAE: Fragaria virginiana<sup>133</sup>, Rubus bifrons<sup>136</sup>
- 308. Halictus (Seladonia) confusus Smith, 1853. County records: Chelan<sup>3</sup>, Clallam<sup>3</sup>, Jefferson<sup>1,2</sup>, King<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Pacific<sup>1,2</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>5,6</sup>, Spokane<sup>1,2</sup>, Thurston<sup>1,2,3,133</sup>, Whatcom<sup>1,2,3</sup>, Whitman<sup>6</sup>. Seasonality: Apr<sup>133</sup>,

May<sup>1,2,5,133</sup>, Jun<sup>1,2,3,6,133</sup>, Jul<sup>1,2,3,6,133</sup>, Aug<sup>1,2,3,6</sup> (2020<sup>133</sup>). Collections: AMNH, BBSL, BugGuide, EMEC, iNaturalist, JRYA, OSUC, PCYU, SEMC, WSDA. Floral records: ASPARAGACEAE: *Brodiaea coronaria*<sup>133</sup>, *Camassia quamash*<sup>133</sup>; ASTER-ACEAE: *Crepis capillaris*<sup>133</sup>, *Hypochaeris radicata*<sup>133</sup>, *Leucanthemum vulgare*<sup>133</sup>; BRASSICACEAE: *Lepidium campestre*<sup>133</sup>, *Teesdalia nudicaulis*<sup>133</sup>; CARYOPHYL-LACEAE: *Cerastium arvense*<sup>133</sup>; CAPRIFOLIACEAE: *Plectritis congesta*<sup>133</sup>; FA-BACEAE: *Lupinus bicolor*<sup>133</sup>, *Trifolium repens*<sup>133</sup>; IRIDACEAE: *Sisyrinchium idahoense*<sup>133</sup>; LAMIACEAE: *Prunella vulgari*<sup>133</sup>; PLANTAGINACEAE: *Collinsia grandiflora*<sup>133</sup>; POLEMONIACEAE: *Gilia capitata*<sup>133</sup>; ROSACEAE: *Fragaria virginiana*<sup>133</sup>; *Potentilla gracilis*<sup>133</sup>

- 309. Halictus (Seladonia) tripartitus Cockerell, 1895. County records: Benton<sup>1,2,3,71</sup>, Clallam<sup>1,2</sup>, Douglas<sup>1,2</sup>, Jefferson<sup>1,2</sup>, Kittitas<sup>2,3</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,59</sup>, San Juan<sup>1,2,3,5,6,124</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2</sup>, Thurston<sup>133</sup>, Walla Walla<sup>1,2,3,71</sup>, Whitman<sup>1,2,3,6,8</sup>, Yakima<sup>1,2</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>1,2</sup>, May<sup>1,2,3,133</sup>, Jun<sup>1,2,3,133</sup>, Jul<sup>1,2,3,5,6</sup>, Aug<sup>1,2,3,6</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: AMNH, BBSL, BugGuide, iNaturalist, INHS, TAMU, UMNH, WSDA, WSUC. Floral records: APIACEAE: *Lomatium*<sup>8</sup>; ASPARAGACEAE: *Triteleia hyacinthina*<sup>133</sup>; ASTERACEAE: *Cirsium arvense*<sup>8</sup>, *Erigeron speciosus*<sup>133</sup>, *Eriophyllum lanatum*<sup>133</sup>, *Leucanthemum vulgare*<sup>133</sup>, *Microseris laciniata*<sup>133</sup>, *Solidago*<sup>8</sup>, *Taraxacum officinale*<sup>8</sup>; CAMPANULACEAE: *Campanula rotundifolia*<sup>133</sup>; FABACEAE: *Trifolium repens*<sup>8</sup>; OROBANCHACE-AE: *Parentucellia viscosa*<sup>133</sup>; PLANTAGINACEAE: *Collinsia parviflora*<sup>8</sup>; PLUM-BAGINACEAE: *Armeria maritima*<sup>133</sup>, *Potentilla gracilis*<sup>3,59,133</sup>, *Rosa*<sup>8</sup>, *Rubus ulmifolius*<sup>5</sup>
- 310. † *Halictus (Seladonia) virgatellus* Cockerell, 1901. County records: Chelan<sup>3</sup>, Clallam<sup>3</sup>, Pierce<sup>1,2,3</sup>, Stevens<sup>1,2</sup>, Whatcom<sup>3</sup>. Seasonality: May<sup>1,2,3</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2</sup>, Aug<sup>3</sup> (2014<sup>1,2,3</sup>). Collections: BBSL, EMEC, JRYA

## Genus Lasioglossum Curtis

- 311. † Lasioglossum (Dialictus) albipenne (Robertson, 1890). County records: San Juan<sup>1,2,3</sup>, Whitman<sup>7</sup>. Seasonality: May<sup>7</sup>, Jun<sup>7</sup>, Jul<sup>1,2,7</sup>, Aug<sup>7</sup>, Sep<sup>7</sup> (2011<sup>1,2</sup>). Collections: PWRC, WSUC
- 312. Lasioglossum (Dialictus) albohirtum (Crawford, 1907). County records: Adams<sup>7</sup>, Benton<sup>1,2,3,6,7,71</sup>, Columbia<sup>1,2,4,38</sup>, Grant<sup>7</sup>, Okanogan<sup>7</sup>, Pierce<sup>7</sup>, Walla Walla<sup>1,2,3,7,71</sup>, Whitman<sup>7</sup>, Yakima<sup>7,38</sup>. Seasonality: Apr<sup>7</sup>, May<sup>1,2,4,6,7,38</sup>, Jun<sup>7</sup>, Jul<sup>1,2,7</sup>, Aug<sup>1,2,3,7</sup>, Sep<sup>1,2,3,7</sup>, Oct<sup>1,2,7</sup> (2022<sup>6</sup>). Collections: BBSL, PCYU, WSDA, WSUC. Floral records: FABACEAE: *Melilotus officinalis*<sup>38</sup>; *Ericameria nauseosa*<sup>38</sup>, *Eriogonum*<sup>38</sup>
- 313. † Lasioglossum (Dialictus) brunneiventre (Crawford, 1907). County records: Benton<sup>7</sup>, Walla Walla<sup>7</sup>, Whitman<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: May<sup>7</sup>, Jun<sup>7</sup>, Jul<sup>7</sup>, Aug<sup>7</sup>, Sep<sup>7</sup>, Oct<sup>7</sup> (2014<sup>7</sup>). Collections: WSUC
- **314.** † *Lasioglossum (Dialictus) cressonii* (Robertson, 1890). County records: King<sup>1,2,3</sup>, Skagit<sup>7</sup>, Snohomish<sup>7</sup>, Stevens<sup>7</sup>, Whatcom<sup>6,7</sup>, Whitman<sup>7</sup>. Seasonality:

Apr<sup>7</sup>, Jun<sup>7</sup>, Jul<sup>1,2,3,6</sup>, Aug<sup>6</sup>, Sep<sup>7</sup>, Oct<sup>7</sup> (2011<sup>1,2,3</sup>). Collections: AMNH, WSDA, WSUC

- 315. Lasioglossum (Dialictus) dashwoodi Gibbs, 2010. County records: Garfield<sup>38</sup>, Klickitat<sup>7</sup>, Okanogan<sup>38</sup>, Spokane<sup>7</sup>, Whitman<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: May<sup>7,38</sup>, Jun<sup>7</sup>, Jul<sup>7</sup>, Aug<sup>38</sup> (2022<sup>7</sup>). Collections: BBSL, PCYU, WSUC. Allotype. USA, Washington, Okanogan County, 1 mi E Muckamuck Hill, 48.601661°N, -119.765108°W; 9 August 2004; J Wilson. Paratype. USA, Washington, Okanogan County, 25 km W Clarkston, Hwy 12, 805 m; 29 May 2007; Gibbs and Sheffield
- **316.** † *Lasioglossum (Dialictus) diversopunctatum* (Ellis, 1914). County records: Benton<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: Jun<sup>7</sup>, Jul<sup>7</sup>, Aug<sup>7</sup> (2014<sup>7</sup>). Collections: WSUC
- 317. Lasioglossum (Dialictus) helianthi (Cockerell, 1916). County records: Adams<sup>7</sup>, Benton<sup>7</sup>, Grant<sup>7</sup>, Grays Harbor<sup>6</sup>, Okanogan<sup>7</sup>, Pierce<sup>122</sup>, Walla Walla<sup>7</sup>, Whitman<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: Apr<sup>7,122</sup>, May<sup>7</sup>, Jun<sup>7</sup>, Jul<sup>7</sup>, Aug<sup>6,7</sup> (2020<sup>6</sup>). Collections: PCYU, WSDA, WSUC. [= Lasioglossum (Dialictus) imbrex Gibbs, 2010].
- **318.** † *Lasioglossum (Dialictus) byalinum* (Crawford, 1907). County records: Adams<sup>7</sup>, Benton<sup>7</sup>, Chelan<sup>7</sup>, Grant<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: Mar<sup>7</sup>, Apr<sup>7</sup>, May<sup>7</sup>, Jun<sup>7</sup>, Jul<sup>6</sup>, Aug<sup>7</sup>, Oct<sup>7</sup> (2022<sup>6</sup>). Collections: WSDA, WSUC
- 319. Lasioglossum (Dialictus) incompletum (Crawford, 1907). County records: Asotin<sup>7</sup>, Benton<sup>1,2,3,7,71</sup>, Chelan<sup>7</sup>, Garfield<sup>1,2,3,4</sup>, Grant<sup>7</sup>, Island<sup>7</sup>, Kittitas<sup>7</sup>, Klickitat<sup>7</sup>, San Juan<sup>1,2,3,124</sup>, Spokane<sup>7</sup>, Walla Walla<sup>1,2,3,6,7,71</sup>, Whitman<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: Mar<sup>7</sup>, Apr<sup>7</sup>, May<sup>1,2,3,4,7</sup>, Jun<sup>1,2,7</sup>, Jul<sup>1,2,6,7</sup>, Aug<sup>1,2,3,7</sup>, Sep<sup>1,2,7</sup>, Oct<sup>1,2,7</sup> (2022<sup>6</sup>). Collections: BBSL, PCYU, PWRC, WSDA, WSUC
- 320. Lasioglossum (Dialictus) knereri Gibbs, 2010. County records: Asotin<sup>7</sup>, Clark<sup>7</sup>, Island<sup>7</sup>, King<sup>1,2,3</sup>, Klickitat<sup>7</sup>, Okanogan<sup>1,2,3,38</sup>, San Juan<sup>1,2,3,7,124</sup>, Skagit<sup>7</sup>, Spokane<sup>7</sup>, Whitman<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: Apr<sup>7</sup>, May<sup>1,2,7</sup>, Jun<sup>1,2,3,7</sup>, Jul<sup>1,2,3,7</sup>, Aug<sup>1,2,3,7</sup> (2011<sup>1,2,124</sup>). Collections: BBSL, PWRC, WSUC. Floral records: BRASSICACE-AE: Smelowskia calycina<sup>3</sup>, CAMPANULACEAE: Campanula rotundifolia<sup>38</sup>
- 321. Lasioglossum (Dialictus) laevissimum (Smith, 1853). County records: Benton<sup>7</sup>, Clark<sup>7</sup>, Grant<sup>7</sup>, Grays Harbor<sup>6</sup>, Island<sup>7</sup>, King<sup>7</sup>, Okanogan<sup>7</sup>, Pacific<sup>7</sup>, Pierce<sup>6,7</sup>, San Juan<sup>6</sup>, Skagit<sup>10</sup>, Snohomish<sup>7</sup>, Stevens<sup>7</sup>, Whatcom<sup>6</sup>, Whitman<sup>7</sup>. Seasonality: Apr<sup>7</sup>, May<sup>7</sup>, Jun<sup>6,7</sup>, Jul<sup>6,7</sup>, Aug<sup>6,7</sup>, Sep<sup>6,7</sup>, Oct<sup>7</sup> (2021<sup>6</sup>). Collections: WSDA, WWUC, WSUC
- **322.** † *Lasioglossum (Dialictus) longicorne* (Crawford, 1907). County records: San Juan<sup>1,2</sup>. Seasonality: May<sup>1,2</sup> (2011<sup>1,2</sup>). Collections: PWRC. Comments: This species plausibly occurs in Washington, but the specimens were not seen by the authors and its taxonomy is known to be uncertain (the taxon is part of the difficult *Lasioglossum viridatum* species complex.)
- 323. Lasioglossum (Dialictus) macroprosopum Gibbs, 2010. County records: Benton<sup>7</sup>, Kittitas<sup>7</sup>, Skagit<sup>10</sup>, Spokane<sup>7</sup>, Walla Walla<sup>7</sup>, Whitman<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: Mar<sup>7</sup>, Apr<sup>7</sup>, May<sup>7</sup>, Jun<sup>7</sup>, Jul<sup>7</sup>, Aug<sup>7</sup>, Oct<sup>7</sup> (2014<sup>7</sup>). Collections: WSUC, WWUC

- **324.** *Lasioglossum (Dialictus) marinense* (Michener, 1936). County records: Asotin<sup>7</sup>, Okanogan<sup>1,2,3,38,59</sup>, San Juan<sup>1,2,3</sup>, Stevens<sup>7</sup>. Seasonality: Jun<sup>1,2,3,7,38</sup>, Jul<sup>1,2,7</sup>, Aug<sup>1,2,3,38</sup> (2011<sup>1,2</sup>). Collections: BBSL, PCYU, PWRC, WSUC. Floral records: ASTERACEAE: *Taraxacum officinale*<sup>59</sup>; ROSACEAE: *Rosa nutkana* ssp. *nutkana*<sup>3</sup>
- 325. Lasioglossum (Dialictus) nevadense (Crawford, 1907). County records: Asotin<sup>7</sup>, Benton<sup>7</sup>, Chelan<sup>7</sup>, Clark<sup>7</sup>, Cowlitz<sup>7</sup>, Okanogan<sup>1,2,3,7,38,59</sup>, San Juan<sup>1,2,3,124</sup>, Spokane<sup>7</sup>, Walla Walla<sup>7</sup>, Whitman<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: Apr<sup>7</sup>, May<sup>1,2,7</sup>, Jun<sup>1,2,7,38</sup>, Jul<sup>1,2,3,7,38</sup>, Aug<sup>1,2,3,7</sup> (2014<sup>7</sup>). Collections: BBSL, PCYU, PWRC, WSUC. Floral records: ASTERACEAE: Cirsium vulgare<sup>3</sup>
- 326. † Lasioglossum (Dialictus) nigroviride (Graenicher, 1911). County records: Chelan<sup>3</sup>, Pend Oreille<sup>7</sup>. Seasonality: Jun<sup>7</sup>, Aug<sup>3</sup> (2014<sup>3</sup>). Collections: JRYA, WSUC
- 327. † Lasioglossum (Dialictus) novascotiae (Mitchell, 1960). County records: Benton<sup>7</sup>, Okanogan<sup>7</sup>, Spokane<sup>7</sup>, Stevens<sup>7</sup>, Walla Walla<sup>7</sup>, Whatcom<sup>7</sup>, Whitman<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: Apr<sup>7</sup>, May<sup>7</sup>, Jun<sup>7</sup>, Jul<sup>7</sup>, Aug<sup>7</sup>, Sep<sup>7</sup> (2013<sup>7</sup>). Collections: WSUC. Floral records: ASTERACEAE: Taraxacum officinale<sup>7</sup>; FABACE-AE: Medicago sativa<sup>7</sup>
- **328.** *Lasioglossum (Dialictus) pacatum* (Sandhouse, 1924). County records: Okanogan<sup>1,2,3,59</sup>, San Juan<sup>1,2,3,124</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup> (2011<sup>1,2,124</sup>). Collections: BBSL, PWRC. Floral records: ASTERACEAE: *Taraxacum officinale*<sup>3</sup>
- **329.** † *Lasioglossum (Dialictus) pallidellum* (Ellis, 1914). County records: Benton<sup>7</sup>, Grant<sup>7</sup>. Seasonality: May<sup>7</sup>, Jul<sup>7</sup>, Oct<sup>7</sup> (1995<sup>7</sup>). Collections: WSUC. Floral records: SARCOBATACEAE: *Sarcobatus vermiculatus*<sup>7</sup>
- **330.** *Lasioglossum (Dialictus) perdifficile* (Cockerell, 1895). County records: Benton<sup>1,2,3,71</sup>, Walla Walla<sup>1,2,3,71</sup>. Seasonality: Aug<sup>1,2</sup>, Sep<sup>1,2,3</sup> (1997<sup>1,2,3</sup>). Collections: BBSL. Comments: *Lasioglossum perdifficile* belongs to a difficult complex that includes multiple undescribed species. Washington records of this species (originally described from New Mexico) are likely misidentifications or based on overinclusive species concepts. Several Washington specimens have been examined and they are believed to comprise two species, one of which may be a morphological variant within *L. yukonae* Gibbs, 2010, and the other of which is probably undescribed. Further taxonomic work is needed to resolve this complex.
- 331. †‡ Lasioglossum (Dialictus) platyparius (Robertson, 1895). County records: Whitman<sup>7</sup>. Seasonality: May<sup>7</sup> (1917<sup>7</sup>). Collections: WSUC. Comments: This social parasite is primarily distributed east of the Rocky Mountains. The Washington record, based on a single specimen collected at Wawawai in 1917, represents a significant and unexpected range extension both for the species and for socially parasitic *Dialictus* in general. But considering that Whitman County is one of the most well-collected regions in Washington and *L. platyparius* has not been re-collected in over 100 years, it is possible that the species is not permanently established in Washington, or it has been extirpated.
- 332. Lasioglossum (Dialictus) prasinogaster Gibbs, 2010. County records: Adams<sup>7</sup>, Benton<sup>7</sup>, Garfield<sup>38</sup>, Franklin<sup>7</sup>, Grant<sup>7</sup>, Klickitat<sup>7</sup>, Okanogan<sup>1,2,3,59</sup>, Spokane<sup>7</sup>,

**Walla Walla**<sup>7</sup>, **Whitman**<sup>7</sup>, **Yakima**<sup>7</sup>. Seasonality: Apr<sup>7</sup>, May<sup>7,38</sup>, Jun<sup>7</sup>, Jul<sup>1,2,3,7</sup>, Aug<sup>7</sup>, Sep<sup>7</sup> (2013<sup>7</sup>). Collections: BBSL, PCYU, WSUC. Floral records: ASTER-ACEAE: *Chrysothamnus*<sup>7</sup>, *Taraxacum*<sup>38</sup>

- 333. Lasioglossum (Dialictus) pruinosum (Robertson, 1892). County records: Benton<sup>1,2,3,7,71</sup>, Douglas<sup>7</sup>, Garfield<sup>7</sup>, Okanogan<sup>7</sup>, Walla Walla<sup>1,2,3,7,71</sup>, Whitman<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: Apr<sup>7</sup>, May<sup>1,2,7</sup>, Jun<sup>1,2,7</sup>, Jul<sup>1,2,3,7</sup>, Aug<sup>1,2,3,7</sup>, Sep<sup>1,2,7</sup>, Oct<sup>1,2</sup> (2014<sup>7</sup>). Collections: BBSL, WSUC
- 334. Lasioglossum (Dialictus) punctatoventre (Crawford, 1907). County records: Benton<sup>7</sup>, Okanogan<sup>1,2,3,59</sup>, Spokane<sup>7</sup>, Whitman<sup>7</sup>. Seasonality: May<sup>7</sup>, Jun<sup>7</sup>, Jul<sup>1,2,3,7</sup>, Aug<sup>1,2,7</sup> (2011<sup>1,2</sup>). Collections: BBSL, PWRC, WSUC. Floral records: ROSACEAE: Potentilla gracilis<sup>59</sup>
- **335.** † *Lasioglossum (Dialictus) reasbeckae* Gibbs, 2010. County records: Thurston<sup>1,2,4</sup>. Seasonality: May<sup>7</sup>, Jun<sup>1,2,4</sup> (2009<sup>1,2,4</sup>). Collections: PCYU, WSUC. Comments: A specimen in WSUC labeled "Rock Creek" was probably collected in Spokane County, based on other specimens from the collector (Robin D. Gray). However, there are at least 33 Rock Creeks in Washington, so the exact location is unknown.
- 336. Lasioglossum (Dialictus) ruidosense (Cockerell, 1897). County records: Asotin<sup>7</sup>, Benton<sup>7</sup>, Clallam<sup>3</sup>, Clark<sup>7</sup>, Grant<sup>7</sup>, Okanogan<sup>1,2,3,59</sup>, Skagit<sup>7</sup>, Spokane<sup>7</sup>, Stevens<sup>7</sup>, Thurston<sup>1,2,4,7</sup>, Whitman<sup>7</sup>. Seasonality: May<sup>7</sup>, Jun<sup>1,2,3,4,7</sup>, Jul<sup>7</sup>, Aug<sup>1,2,3,7</sup> (2014<sup>3</sup>). Collections: BBSL, JRYA, PCYU, WSUC. Floral records: ASTERACE-AE: Achillea millefolium<sup>3</sup>, Taraxacum officinale<sup>59</sup>
- **337.** *Lasioglossum (Dialictus) sandhousiellum* Gibbs, 2010. County records: Okanogan<sup>3,59</sup>. Seasonality: Jul<sup>3</sup> (2004<sup>3,59</sup>). Floral records: ASTERACEAE: *Achillea millefolium<sup>59</sup>, Taraxacum officinale<sup>59</sup>*; POLEMONIACEAE: *Ipomopsis aggregata* ssp. *aggregata<sup>59</sup>*
- 338. Lasioglossum (Dialictus) sedi (Sandhouse, 1924). County records: Asotin<sup>7</sup>, Chelan<sup>7</sup>, King<sup>1,2,3</sup>, Klickitat<sup>1,2,3</sup>, Okanogan<sup>1,2,3,38,59</sup>, Whitman<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: Apr<sup>1,2,3,7</sup>, May<sup>7</sup>, Jun<sup>1,2,3,7,38</sup>, Jul<sup>1,2,3,7,38</sup>, Aug<sup>1,2</sup> (2004<sup>1,2,38,59</sup>). Collections: AMNH, BBSL, PCYU, WSUC. Floral records: ASTERACEAE: Erigeron speciosus<sup>3,59</sup>; CAMPANULACEAE: Campanula rotundifolia<sup>3,38,59</sup>; CELASTRACEAE: Parnassia fimbriata<sup>59</sup>; CRASSULACEAE: Sedum lanceolatum<sup>59</sup>, S. stenopetalum<sup>38</sup>; HYDROPHYLLACEAE: Phacelia leptosepala<sup>38</sup>; PLANTAGINACEAE: Penstemon davidsonii var. davidsonii<sup>59</sup>; ROSACEAE: Rosa nutkana ssp. nutkana<sup>3,59</sup>
- 339. Lasioglossum (Dialictus) tegulariforme (Crawford, 1907). County records: Benton<sup>1,2,3,71</sup>, Grant<sup>7</sup>, Stevens<sup>122</sup>, Walla Walla<sup>1,2,3,71</sup>, Whitman<sup>1,2</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2</sup>, Jul<sup>7</sup>, Aug<sup>1,2,3,122</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2</sup> (2011<sup>122</sup>). Collections: BBSL, EMEC, FWSE, WSUC. Comments: Prior to 2010, *L. helianthi* was considered a synonym of *L. tegulariforme* (Gibbs 2010 [as *L. imbrex*]; Gardner and Gibbs 2022). As the specimen from Whitman County was collected prior to 2010 and has not been examined, it is possible that this specimen could be *L. helianthi*.
- **340.** *Lasioglossum (Dialictus) tenax* (Sandhouse, 1924). County records: Okanogan<sup>1,2,3,59</sup>, Pierce<sup>1,2,4</sup>, Thurston<sup>1,2,4</sup>. Seasonality: May<sup>1,2,4</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,4</sup>

(2009<sup>1,2,4</sup>). Collections: BBSL, PCYU. Floral records: ASTERACEAE: Achillea millefolium<sup>59</sup>, Cirsium vulgare<sup>59</sup>; CAMPANULACEAE: Campanula rotundifolia<sup>3</sup>. Comments: All Washington specimens of *L. tenax* that have been examined so far have turned out to be an undescribed species closely related to *L. tenax*. This species is distinguished from the true *L. tenax* by the smooth, shiny, sparsely punctate mesepisternum (contrasted with the dull, rugulose mesepisternum of *L. tenax*). It seems likely that the true *L. tenax* does not occur in Washington, and all published records actually correspond to this undescribed species. The undescribed species will be described in a forthcoming publication.

- 341. Lasioglossum (Dialictus) zephyrus (Smith, 1853). County records: Benton<sup>7</sup>, Clark<sup>1,2,79</sup>, Spokane<sup>7</sup>, Walla Walla<sup>7</sup>, Whitman<sup>1,2,7,79</sup>, Yakima<sup>7</sup>. Seasonality: Apr<sup>7</sup>, May<sup>1,2,7,79</sup>, Jun<sup>7</sup>, Jul<sup>1,2,7,79</sup>, Aug<sup>7</sup>, Sep<sup>7</sup>, Oct<sup>7</sup> (2014<sup>7</sup>). Collections: CAS, UCDC, WSUC
- 342. † *Lasioglossum (Evylaeus) argemonis* (Cockerell, 1897). County records: Asotin<sup>7</sup>, Chelan<sup>7</sup>, Columbia<sup>7</sup>, Whitman<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: Apr<sup>7</sup>, May<sup>7</sup>, Jul<sup>7</sup> (1980<sup>7</sup>). Collections: WSUC
- 343. † *Lasioglossum (Evylaeus) robustum* (Crawford, 1907). County records: Clark<sup>7</sup>. Seasonality: Jul<sup>7</sup> (1970<sup>7</sup>). Collections: WSUC
- 344. † *Lasioglossum (Hemihalictus) aspilurus* (Cockerell, 1925). County records: Benton<sup>7</sup>, Walla Walla<sup>7</sup>, Whitman<sup>7</sup>. Seasonality: Apr<sup>7</sup>, May<sup>7</sup> (1973<sup>7</sup>). Collections: WSUC
- 345. †\* *Lasioglossum (Hemihalictus) buccale* (Pérez, 1903). County records: Spokane<sup>7</sup>. Seasonality: Jul<sup>7</sup>, Aug<sup>7</sup> (1970<sup>7</sup>). Collections: WSUC
- 346. † Lasioglossum (Hemihalictus) glabriventre (Crawford, 1907). County records: Benton<sup>7</sup>, Cowlitz<sup>7</sup>, Garfield<sup>7</sup>, Klickitat<sup>1,2</sup>, Spokane<sup>1,2,7</sup>, Walla Walla<sup>7</sup>, Whitman<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: May<sup>1,2,7</sup>, Jun<sup>1,2,7</sup>, Jul<sup>1,2,7</sup>, Aug<sup>1,2,7</sup>, Sep<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL, WSUC
- 347. Lasioglossum (Hemihalictus) inconditum (Cockerell, 1916). County records: Asotin<sup>7</sup>, Clallam<sup>7</sup>, Cowlitz<sup>7</sup>, Island<sup>7,80</sup>, King<sup>80</sup>, Klickitat<sup>7</sup>, Lewis<sup>7</sup>, San Juan<sup>7</sup>, Skagit<sup>7</sup>, Spokane<sup>7</sup>, Stevens<sup>7</sup>, Thurston<sup>80</sup>, Whitman<sup>80</sup>, Yakima<sup>7</sup>. Seasonality: Apr<sup>7</sup>, May<sup>7</sup>, Jun<sup>7</sup>, Jul<sup>7</sup>, Aug<sup>7</sup>, Sep<sup>7</sup> (1985<sup>7</sup>). Collections: WSUC
- 348. Lasioglossum (Hemihalictus) kincaidii (Cockerell, 1898). County records: Benton<sup>7</sup>, Clark<sup>7</sup>, Grant<sup>7</sup>, Jefferson<sup>7</sup>, King<sup>7</sup>, Klickitat<sup>1,2</sup>, Pacific<sup>7</sup>, Pierce<sup>1,2,4</sup>, Spokane<sup>1,2</sup>, Thurston<sup>119</sup>, Walla Walla<sup>1,2,7</sup>, Whitman<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,7</sup>, Jun<sup>1,2,7</sup>, Jul<sup>1,2,4,7</sup>, Aug<sup>7</sup> (2015<sup>1,2</sup>). Collections: BBSL, PCYU, WSUC. [= Halictus kincaidii Cockerell, 1898]
- **349.** *Lasioglossum* (*Hemihalictus*) *ovaliceps* (Cockerell, 1898). County records: Asotin<sup>7</sup>, Chelan<sup>7</sup>, Clark<sup>7</sup>, King<sup>1,2,3</sup>, Lewis<sup>7</sup>, Okanogan<sup>7</sup>, San Juan<sup>22</sup>, Snohomish<sup>1,2,3</sup>, Thurston<sup>1,2,7</sup>, Whitman<sup>7</sup>, Yakima<sup>1,2,4,7</sup>. Seasonality: Apr<sup>1,2,7</sup>, May<sup>1,2,3,4,7</sup>, Jun<sup>1,2,7</sup>, Jul<sup>1,2,7</sup>, Aug<sup>1,2,3,7</sup>, Sep<sup>7</sup>, Oct<sup>1,2</sup>, Nov<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: iNaturalist, PCYU, WSUC. Floral records: ASTERACEAE: *Hypochaeris radicata*<sup>3</sup>
- **350.** † *Lasioglossum (Hemihalictus) sequoiae* (Michener, 1936). County records: San Juan<sup>1,2,3</sup>. Seasonality: May<sup>1,2</sup>, Jul<sup>1,2</sup> (2011<sup>1,2</sup>). Collections: PWRC

- **351.** †\* *Lasioglossum (Hemihalictus) villosulum* (Kirby, 1802). County records: King<sup>7</sup>, Snohomish<sup>7</sup>. Seasonality: May<sup>7</sup>, Jun<sup>7</sup>, Jul<sup>7</sup> (2019<sup>7</sup>). Collections: WSUC
- **352.** *Lasioglossum* (*Lasioglossum*) *anhypops* McGinley, 1986. County record: Asotin<sup>81</sup>, Chelan<sup>3,7</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,59</sup>, Pierce<sup>1,2,3,81</sup>, Stevens<sup>1,2</sup>, Whitman<sup>81</sup>. Seasonality: May<sup>1,2,7</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup> (2014<sup>1,2,3</sup>). Collections: BBSL, JRYA, OSUC, WSUC. Floral records: ASTERACEAE: *Achillea millefolium*<sup>59</sup>, *Anaphalis margaritacea*<sup>3,59</sup>; FABACEAE: *Lupinus sericeus*<sup>3,59</sup>
- **353.** *Lasioglossum* (*Lasioglossum*) *athabascense* (Sandhouse, 1933). County records: Asotin<sup>7</sup>, Island<sup>81</sup>, King<sup>81</sup>, Okanogan<sup>1,2,3,59</sup>, Pend Oreille<sup>7,81</sup>, San Juan<sup>1,2,3,124</sup>, Stevens<sup>7,81</sup>, Whitman<sup>7</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2,3,7</sup>, Jul<sup>1,2,7</sup>, Sep<sup>7</sup> (2011<sup>1,2,124</sup>). Collections: BBSL, PWRC, WSUC. Floral records: ROSACEAE: *Potentilla gracilis*<sup>3,59</sup>
- **354.** *Lasioglossum* (*Lasioglossum*) *colatum* (Vachal, 1904). County records: Asotin<sup>81</sup>, King<sup>81</sup>, **Skagit**<sup>1,2,3</sup>, Stevens<sup>81</sup>, Thurston<sup>81</sup>, Walla Walla<sup>7,81</sup>, Whitman<sup>7,81</sup>. Seasonality: May<sup>7</sup>, Jun<sup>7</sup>, Jul<sup>7</sup>, Aug<sup>1,2,7</sup> (2013<sup>7</sup>). Collections: PWRC, WSUC
- 355. Lasioglossum (Lasioglossum) egregium (Vachal, 1904). County records: Chelan<sup>7</sup>, Columbia<sup>7</sup>, Cowlitz<sup>7</sup>, Grant<sup>7</sup>, Island<sup>7</sup>, Klickitat<sup>1,2</sup>, Lincoln<sup>7</sup>, Mason<sup>7,81</sup>, Okanogan<sup>1,2,3,7,59,81</sup>, Pend Oreille<sup>7,81</sup>, San Juan<sup>1,2,3,124</sup>, Spokane<sup>1,2,7,81</sup>, Thurston<sup>133</sup>, Walla Walla<sup>1,2,7</sup>, Whatcom<sup>3</sup>, Whitman<sup>1,2,3,4,6,7,81</sup>, Yakima<sup>7</sup>. Seasonality: Apr<sup>7</sup>, May<sup>1,2,7,133</sup>, Jun<sup>1,2,6,7,133</sup>, Jul<sup>1,2,3,4,6,7</sup>, Aug<sup>3,6,7</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2</sup>, Nov<sup>7</sup> (2018<sup>133</sup>). Collections: BBSL, JRYA, PWRC, WSDA, WSUC. Floral records: ASTERACE-AE: Leucanthemum vulgare<sup>133</sup>; PLUMBAGINACEAE: Armeria maritima<sup>133</sup>
- **356.** *Lasioglossum* (*Lasioglossum*) *heterorhinus* (Cockerell, 1930). County records: Thurston<sup>133</sup>. Seasonality: May<sup>133</sup>, Jul<sup>133</sup> (2019<sup>133</sup>). Floral records: ASPARAGACE-AE: *Camassia quamash*<sup>133</sup>; ASTERACEAE: *Erigeron speciosus*<sup>133</sup>
- 357. Lasioglossum (Lasioglossum) mellipes (Crawford, 1907). County records: Douglas<sup>7</sup>, Island<sup>7,81</sup>, King<sup>81</sup>, Kittitas<sup>2,3,81</sup>, Klickitat<sup>1,2</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>1,2,124,136</sup>, Stevens<sup>1,2</sup>, Walla Walla<sup>1,2</sup>. Seasonality: Apr<sup>1,2,7</sup>, May<sup>1,2,7</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2,3</sup> (2017<sup>136</sup>). Collections: BBSL, PWRC, WSUC
- 358. Lasioglossum (Lasioglossum) olympiae (Cockerell, 1898). County records: Asotin<sup>7,81</sup>, Island<sup>7,81</sup>, Klickitat<sup>1,2</sup>, Pierce<sup>81</sup>, San Juan<sup>1,2,3,5,6,7,81,124,136</sup>, Spokane<sup>1,2,81</sup>, Thurston<sup>81,119,130,133</sup>, Walla Walla<sup>81</sup>, Whitman<sup>2,6</sup>, Yakima<sup>7</sup>. Seasonality: May<sup>1,2,5,133</sup>, Jun<sup>1,2,6,7,133</sup>, Jul<sup>1,2</sup>, Aug<sup>6,7</sup>, Sep<sup>1,2</sup> (2020<sup>133</sup>). Collections: BBSL, NMNH, PWRC, WSDA, WSUC. [= Halictus olympiae Cockerell, 1898]. Holotype. USA, Washington, Thurston County, Olympia; 26 June 1896; USNM Type No. 29420. [= Halictus olympiae var. subangustatus Crawford, 1906]. Floral records: APIACEAE: Heracleum sphondylium ssp. montanum<sup>5</sup>, Lomatium pugetensis<sup>133</sup>; ASTERACEAE: Microseris laciniata<sup>133</sup>; GROSSULARIACEAE: Ribes divaricatum<sup>136</sup>; PLUM-BAGINACEAE: Armeria maritima<sup>133</sup>; POLEMONIACEAE: Gilia capitata<sup>133</sup>; ROSACEAE: Potentilla gracilis<sup>133</sup>
- 359. Lasioglossum (Lasioglossum) pacificum (Cockerell, 1898). County records: Clark<sup>7,81</sup>, Island<sup>7,81</sup>, Jefferson<sup>1,2</sup>, King<sup>7,81,119</sup>, Kitsap<sup>81</sup>, Pacific<sup>1,2,3,81</sup>, Pierce<sup>1,2,4,81</sup>, San Juan<sup>1,2,3,5,7,124</sup>, Skagit<sup>10</sup>, Thurston<sup>81,119,133</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Apr<sup>7</sup>, May<sup>1,2,5,7,133</sup>, Jun<sup>1,2,133</sup>, Jul<sup>1,2,3,5</sup>, Aug<sup>1,2,3,4</sup>, Sep<sup>7</sup> (2020<sup>133</sup>). Collections: BBSL,

EMEC, PCYU, PWRC, SEMC, WSUC. [= *Halictus pacificus* Cockerell, 1898]. **Lectotype**. USA, Washington, Thurston County, Olympia; 24 June 1895. Floral records: APIACEAE: *Heracleum sphondylium* ssp. *Montanum*<sup>5</sup>; ASPARAGACE-AE: *Camassia quamash*<sup>133</sup>; ASTERACEAE: *Crepis capillaris*<sup>5</sup>, *Microseris laciniata*<sup>133</sup>; BRASSICACEAE: *Lepidium campestre*<sup>133</sup>; CAPRIFOLIACEAE: *Plectritis congesta*<sup>133</sup>; FABACEAEA: *Lupinus albicaulis*<sup>133</sup>, *L. lepidus*<sup>133</sup>; LAMIACEAE: *Prunella vulgaris*<sup>133</sup>; PLUMBAGINACEAE: *Armeria maritima*<sup>133</sup>; RANUNCU-LACEAE: *Ranunculus californicus*<sup>5</sup>; ROSACEAE: *Potentilla gracilis*<sup>133</sup>; VIOL-ACEAE: *Viola adunca*<sup>133</sup>

- **360.** *Lasioglossum* (*Lasioglossum*) *pavonotus* (Cockerell, 1925). County records: Grays Harbor<sup>1,2,3,81</sup>, Pacific<sup>1,2,3,7,81</sup>. Seasonality: Jun<sup>7</sup>, Jul<sup>1,2,3,7</sup>, Aug<sup>7</sup> (1976<sup>7</sup>). Collections: BBSL, SEMC, WSUC
- 361. Lasioglossum (Lasioglossum) sisymbrii (Cockerell, 1895). County records: Asotin<sup>7</sup>, Benton<sup>1,2,7</sup>, Chelan<sup>7,81</sup>, Clark<sup>7,81</sup>, Columbia<sup>7</sup>, Garfield<sup>7,81</sup>, Grant<sup>1,2</sup>, Island<sup>7</sup>, King<sup>1,2,81</sup>, Kittitas<sup>2</sup>, Klickitat<sup>1,2,81</sup>, Okanogan<sup>1,2,3,59,81</sup>, San Juan<sup>1,2,3,81,124</sup>, Skagit<sup>1,2,3,81,124</sup>, Spokane<sup>1,2,3,7,81</sup>, Stevens<sup>81</sup>, Thurston<sup>81,119,133</sup>, Walla Walla<sup>1,2,3,7,81</sup>, Whitman<sup>1,2,3,6,7,81</sup>, Yakima<sup>7,81</sup>. Seasonality: Apr<sup>1,2,7</sup>, May<sup>1,2,3,7,133</sup>, Jun<sup>1,2,3,7,133</sup>, Jul<sup>1,2,3,7</sup>, Aug<sup>1,2,6,7</sup>, Sep<sup>1,2,7</sup>, Oct<sup>7</sup> (2022<sup>1,2</sup>). Collections: BBSL, BugGuide, iNaturalist, PWRC, TAMU, WSDA, WSUC. [= Halictus sisymbrii Cockerell, 1895]. Floral records: ASPARAGACEAE: Camassia quamash<sup>133</sup>, Triteleia hyacinthina<sup>133</sup>; ASTERACEAE: Balsamorhiza deltoidea<sup>133</sup>, Crepis capillaris<sup>133</sup>, Eriophyllum lanatum<sup>133</sup>, Leucanthemum vulgare<sup>133</sup>, Microseris laciniata<sup>133</sup>; BRASSICACEAE: Sisymbrium altissimum<sup>3,59</sup>; CAMPANULACEAE: Campanula rotundifolia<sup>133</sup>; CAPRIFOLIACEAE: Plectritis congesta<sup>133</sup>, Symphoricarpos albus<sup>133</sup>; FABACEAE: Lupinus albicaulis<sup>133</sup>; HYPERICACEAE: Hypericum perforatum<sup>133</sup>; LAMIACE-AE: Prunella vulgaris<sup>133</sup>; ONAGRACEAE: Chamerion angustifolium<sup>133</sup>; PLUM-BAGINACEAE: Armeria maritima<sup>133</sup>; ROSACEAE: Potentilla gracilis<sup>133</sup>
- **362.** *Lasioglossum* (*Lasioglossum*) *titusi* (Crawford, 1902). County records: Benton<sup>1,2</sup>, Chelan<sup>7</sup>, Grays Harbor<sup>7,81</sup>, Island<sup>7,81</sup>, Klickitat<sup>1,2,81</sup>, Pierce<sup>1,2,3,81</sup>, **Spokane**<sup>1,2</sup>, Thurston<sup>7,81,133</sup>, Walla Walla<sup>1,2,3,81</sup>, Whitman<sup>2,7,81</sup>, **Yakima**<sup>7</sup>. Seasonality: Apr<sup>1,2,133</sup>, May<sup>1,2,3,7,133</sup>, Jul<sup>1,2,7,133</sup>, Jul<sup>1,2,7,133</sup>, Aug<sup>1,2</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2</sup> (2020<sup>133</sup>). Collections: BBSL, SEMC, WSUC. Floral records: ASPARAGACEAE: *Camassia quamash*<sup>133</sup>, *Triteleia hyacinthina*<sup>133</sup>, ASTERACEAE: *Achillea millefolium*<sup>133</sup>, *Balsamorhiza deltoidea*<sup>133</sup>, *Crepis capillaris*<sup>133</sup>, *Erigeron speciosus*<sup>133</sup>, *Eriophyllum lanatum*<sup>133</sup>, *Hypochaeris radicata*<sup>133</sup>, *Leucanthemum vulgare*<sup>133</sup>, *Microseris laciniata*<sup>133</sup>, *Solidago simplex*<sup>133</sup>, *Taraxacum officinale*<sup>133</sup>; BRASSICACEAE: *Teesdalia nudicaulis*<sup>133</sup>; CAPRIFOLIACEAE: *Plectritis congesta*<sup>133</sup>; CARYOPHYLLACEAE: *Cerastium arvense*<sup>133</sup>; PLUMBAGI-NACEAE: *Armeria maritima*<sup>133</sup>; RANUNCULACEAE: *Ranunculus occidentalis*<sup>133</sup>
- 363. Lasioglossum (Lasioglossum) trizonatum (Cresson, 1874). County records: Adams<sup>81</sup>, Benton<sup>1,2,7</sup>, San Juan<sup>1,2,3,124</sup>, Stevens<sup>1,2</sup>, Thurston<sup>119</sup>, Walla Walla<sup>7</sup>, Whatcom<sup>3</sup>, Whitman<sup>2,3,7,81</sup>, Yakima<sup>7,81</sup>. Seasonality: Apr<sup>1,2,7</sup>, May<sup>1,2,7</sup>, Jun<sup>1,2,7</sup>, Jul<sup>7</sup>, Aug<sup>1,2,3,7</sup> (2015<sup>1,2</sup>). Collections: BBSL, JRYA, PWRC, WSUC. [= Halictus trizonatus Cresson, 1874]

- **364.** \* *Lasioglossum (Leuchalictus) leucozonium* (Schrank, 1781). County records: Thurston<sup>119</sup>. [= *Halictus similis* Smith, 1853].
- 365. \* *Lasioglossum (Leuchalictus) zonulus* (Smith, 1848). County records: Clallam<sup>3</sup>, Jefferson<sup>1,2,3</sup>, King<sup>3,81</sup>, Kitsap<sup>7,134</sup>, Klickitat<sup>1,2</sup>, Pierce<sup>1,2,3,81</sup>, San Juan<sup>1,2,3,6,124</sup>, Skagit<sup>7,10,81</sup>, Spokane<sup>1,2</sup>, Thurston<sup>133</sup>, Walla Walla<sup>1,2,7</sup>, Whatcom<sup>6,81</sup>. Seasonality: May<sup>1,2,6,133</sup>, Jun<sup>1,2,7,133</sup>, Jul<sup>1,2,6,7</sup>, Aug<sup>1,2,3,6</sup> (2020<sup>133</sup>). Collections: BBSL, CUIC, JRYA, PWRC, WSDA, WSUC. Floral records: ASTEACEAE: *Gaillardia aristata*<sup>133</sup>, *Microseris laciniata*<sup>133</sup>; BRASSICACEAE: *Lepidium campestre*<sup>133</sup>; LILI-ACEAE: *Fritillaria affinis*<sup>133</sup>; ONAGRACEAE: *Epilobium cilatum*<sup>3</sup>; OROBAN-CHACEAE: *Parentucellia viscosa*<sup>133</sup>; ROSACEAE: *Potentilla gracilis*<sup>133</sup>
- **366.** *Lasioglossum* (*Sphecodogastra*) *aberrans* (Crawford, 1903). County records: Adams<sup>57</sup>, **Spokane**<sup>1,2</sup>. Seasonality: Jun<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL
- **367.** † *Lasioglossum* (*Sphecodogastra*) *allonotus* (Cockerell, 1936). County records: Chelan<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: Apr<sup>7</sup>, May<sup>7</sup>, Jun<sup>7</sup>, Sep<sup>7</sup> (2008<sup>7</sup>). Collections: WSUC
- **368.** Lasioglossum (Sphecodogastra) comagenense (Knerer and Atwood, 1964). County records: Pierce<sup>1,2,4,80</sup>, Thurston<sup>1,2,4,80</sup>, Yakima<sup>1,2</sup>. Seasonality: Apr<sup>1,2,4</sup>, Jun<sup>1,2,4</sup>, Jul<sup>1,2</sup> (2009<sup>1,2,4</sup>). Collections: INHS, PCYU
- **369.** *Lasioglossum* (*Sphecodogastra*) *cooleyi* (Crawford, 1906). County records: Jefferson<sup>1,2</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,59</sup>, San Juan<sup>1,2,124</sup>, Skagit<sup>3</sup>, Spokane<sup>1,2</sup>, Stevens<sup>1,2</sup>, Walla Walla<sup>1,2</sup>, Whitman<sup>61</sup>. Seasonality: Apr<sup>1,2,61</sup>, May<sup>1,2</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL, PWRC, UCMS. Floral records: ROSACEAE: *Potentilla gracilis*<sup>3</sup>
- **370.** † *Lasioglossum* (*Sphecodogastra*) *cordleyi* (Crawford, 1906). County records: Clark<sup>7</sup>. Seasonality: Jul<sup>7</sup>, Aug<sup>7</sup> (1970<sup>7</sup>). Collections: WSUC
- 371. Lasioglossum (Sphecodogastra) lusorium (Cresson, 1872). County records: Benton<sup>57,80</sup>, Grant<sup>7</sup>, Walla Walla<sup>1,2</sup>, Yakima<sup>57</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2,7</sup>, Jul<sup>1,2</sup>, Aug<sup>1,2</sup> (2012<sup>1,2</sup>). Collections: BBSL, WSUC. Comments: McGinley (2003) records this species on the Yakima River at Morgan's Ferry and places the location in Kittitas County; however, a review of historical maps indicates Morgan's Ferry is located in Yakima County.
- **372.** † *Lasioglossum (Sphecodogastra) occultum* (Vachal, 1904). [= *Halictus occultus* Vachal, 1904]. County records: **Skagit**<sup>1,2</sup>, **Thurston**<sup>1,2,4</sup>. Seasonality: Jun<sup>1,2,4</sup>, Aug<sup>1,2</sup> (2011<sup>1,2</sup>). Collections: PWRC
- 373. † Lasioglossum (Sphecodogastra) orthocarpi (Cockerell, 1936). County records: Island<sup>7</sup>, San Juan<sup>1,2,124</sup>. Seasonality: May<sup>1,2</sup>, Jul<sup>1,2</sup>, Aug<sup>1,2,7</sup> (2011<sup>1,2,124</sup>). Collections: PWRC, WSUC

## Genus Sphecodes Latreille

- **374.** *Sphecodes arvensiformis* **Cockerell, 1904**. County records: **Cowlitz**<sup>1,2,3</sup>, Thurston<sup>117</sup>, **Walla Walla**<sup>1,2,3</sup>. Seasonality: Jun<sup>1,2,3,117</sup>, Jul<sup>1,2,3</sup> (1979<sup>1,2,3</sup>). Collections: BBSL
- 375. ‡ *Sphecodes columbiae* Cockerell, 1906. County records: Grant<sup>1,2,3,121</sup>. Seasonality: Jul<sup>1,2,3,121</sup> (1902<sup>1,2,3,121</sup>). Collections: NMNH. Holotype. USA, Washington,

Grant County, Grand Coulee; 12 July 1902; Type No. 29398, USNM ENT 00535232

- **376.** ‡ *Sphecodes hesperellus* Cockerell, 1904. County records: Thurston<sup>117</sup>. Season-ality: Jun<sup>117</sup> (1895<sup>117</sup>)
- **377.** ‡ *Sphecodes kincaidii* Cockerell, 1898. County records: Thurston<sup>1,2,3,117</sup>. Seasonality: Jun<sup>1,2,3,117</sup> (1895<sup>1,2,3</sup>). Collections: NMNH. Holotype. USA, Washington, Thurston County, Olympia; 19 June 1895; Type No. 18975, USNM ENT 00535248
- 378. ‡ Sphecodes manni Cockerell, 1913. County records: Whitman<sup>1,2,3,127</sup>. Seasonality: Sep<sup>1,2,3,127</sup> (1908<sup>1,2,3,127</sup>). Collections: NMNH. Holotype. USA, Washington, Whitman County, Wawawai; 6 September 1908; WM Mann; Type No. 23322, USNM ENT 535259.
- **379.** ‡ *Sphecodes minor* Robertson, 1898. County records: Thurston<sup>117</sup>. Seasonality: Jun<sup>117</sup> (1896<sup>117</sup>)
- **380.** ‡ *Sphecodes olympicus* Cockerell, 1904. County records: Pacific<sup>1,2</sup>, Thurston<sup>117</sup>. Seasonality: May<sup>117</sup>, Aug<sup>1,2</sup> (1952<sup>1,2</sup>). Collections: EMEC. Comments: Discover Life has synonymized *S. olympicus* with *S. confertus* without reference or explanation. We are not aware of any published work that that synonymizes these species and retain them as separate taxa in this checklist.
- **381.** ‡ *Sphecodes washingtoni* Cockerell, 1904. County records: Thurston<sup>117</sup>. Seasonality: Jun<sup>117</sup> (1895<sup>117</sup>)

### Nomiinae: Nominiini

### Genus Nomia Latreille

382. Nomia (Acunomia) melanderi Cockerell, 1906. County records: Benton<sup>1,2</sup>, Walla Walla<sup>1,2,3,78</sup>, Whitman<sup>1,2,3</sup>, Yakima<sup>121</sup>. Seasonality: Jun<sup>1,2</sup>, Jul<sup>1,2,121</sup>, Nov<sup>1</sup> (2022<sup>1,2</sup>). Collections: AMNH, iNaturalist, NMNH, SEMC. Conservation status: G5 – Secure globally (NatureServe 2024)

## Rophitinae

## Genus Dufourea Lepeletier

- **383.** †‡ *Dufourea calochorti* (Cockerell, 1924). County records: Yakima<sup>1,2,3</sup>. Seasonality: Jul<sup>1,2,3</sup> (1925<sup>1,2,3</sup>). Collections: BBSL
- **384.** *Dufourea campanulae* (Cockerell, 1897). County records: Clallam<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2,3</sup>, Pierce<sup>1,2,3</sup>, Thurston<sup>1,2,118,133</sup>. Seasonality: Jun<sup>1,2,118,133</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup> (2018<sup>133</sup>). Collections: BBSL, EMEC, JRYA, SEMC. [= *Halictoides campanulae* Cockerell, 1897]. Floral records: CAMPANULACEAE: *Campanula rotundifolia*<sup>133</sup>, *C. scouleri*<sup>118</sup>
- **385.** † *Dufourea holocyanea* (Cockerell, 1925). County records: Asotin<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>2,3</sup>, Stevens<sup>2,3</sup>, Yakima<sup>1,2,3</sup>. Seasonality: May<sup>1,2,3</sup>, Jun<sup>2,3</sup>, Jul<sup>1,2,3</sup> (2000<sup>1,2,3</sup>). Collections: BBSL, SEMC

- **386.** *Dufourea maura* (Cresson, 1878). County records: Clallam<sup>3</sup>, Okanogan<sup>1,2,3,4,59</sup>, Spokane<sup>1,2</sup>. Seasonality: Jun<sup>1,2,3,4</sup>, Jul<sup>1,2</sup>, Aug<sup>3</sup> (2015<sup>1,2</sup>). Collections: BBSL, JRYA. Floral records: ASTERACEAE: *Achillea millefolium*<sup>3,59</sup>
- **387.** *Dufourea trochantera* **Bohart, 1948.** County records: Clallam<sup>1,2,3,82</sup>, Okanogan<sup>1,2,3,59</sup>, Yakima<sup>1,2,3</sup>. Seasonality: May<sup>1,2</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3,82</sup> (2007<sup>1,2</sup>). Collections: BBSL, SEMC. Floral records: HYDROPHYLLACEAE: *Phacelia*<sup>82</sup>, *P. leptosepala*<sup>3,59</sup>

Megachilidae: Megachilinae: Anthidiini

## Genus Anthidiellum Cockerell

- **388.** † *Anthidiellum (Loyolanthidium) notatum* (Latreille, 1809). County records: Lincoln<sup>2</sup>, Spokane<sup>2</sup>. Seasonality: Jun<sup>2</sup>, Aug<sup>2</sup> (2015<sup>2</sup>). Collections: BugGuide
- 389. † Anthidiellum (Loyolanthidium) robertsoni (Cockerell, 1904). County records: Benton<sup>1,2</sup>, Chelan<sup>1,2,3</sup>, Klickitat<sup>1,2,3</sup>. Seasonality: Jul<sup>1,2,3</sup>, Aug<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: BBSL. [= Anthidiellum notatum robertsoni (Cockerell, 1904)]

## Genus Anthidium Fabricius

- **390.** † *Anthidium* (*Anthidium*) *atrifrons* Cresson, 1868. County records: Asotin<sup>3</sup>, Columbia<sup>135</sup>, Whitman<sup>3</sup>, Yakima<sup>3</sup>. Seasonality: May<sup>3</sup>, Jun<sup>135</sup>, Jul<sup>3</sup> (2021<sup>135</sup>). Collections: AMNH, BBSL, NMDG, SEMC. Conservation status: G5 Secure Globally (NatureServe 2024)
- **391.** †§ *Anthidium* (*Anthidium*) *banningense* Cockerell, 1904. County records: Benton<sup>7</sup>, Garfield<sup>135</sup>. Seasonality: May<sup>7,135</sup> (2023<sup>135</sup>). Collections: NMDG, WSUC. Conservation status: G3 – Vulnerable globally (NatureServe 2024). Floral records: HYDROPHYLLACEAE: *Phacelia heterophylla*<sup>135</sup>
- **392.** † *Anthidium* (*Anthidium*) *clypeodentatum* Swenk, 1914. County records: Benton<sup>1,2</sup>, Spokane<sup>1,2</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL. Conservation status: G4 – Apparently Secure Globally (NatureServe 2024)
- **393.** *§ Anthidium (Anthidium) edwardsii* Cresson, 1878. County records: Grant<sup>41,91</sup>. Collections: NMNH. [= Anthidium depressum H. F. Schwarz, 1927]. Holotype. USA, Washington, Grant County, Coulee City; USNM 40164. Conservation status: G3 Vulnerable globally (NatureServe 2024)
- 394. Anthidium (Anthidium) emarginatum (Say, 1824). County records: Adams<sup>1,2,3</sup>, Benton<sup>1,2</sup>, Jefferson<sup>1,2</sup>, Lincoln<sup>3</sup>, Whitman<sup>8</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2</sup>, Jun<sup>1,2,3</sup>, Aug<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL, FMNH, UCRC, WSUC. Conservation status: G5 Secure globally (NatureServe 2024). Floral records: HYDROPHYL-LACEAE: *Phacelia heterophylla*<sup>8</sup>
- 395. †‡ Anthidium (Anthidium) formosum Cresson, 1878. County records: Spokane<sup>1,3</sup>. Seasonality: Jul<sup>1,3</sup> (1882<sup>1,3</sup>). Collections: INHS. Conservation status: G4

   Apparently Secure Globally (NatureServe 2024)
- 396. †\* Anthidium (Anthidium) manicatum (Linnaeus, 1758). County records: Benton<sup>1,2</sup>, Chelan<sup>1,2,3</sup>, Clallam<sup>1,2,3</sup>, Clark<sup>1,2,3</sup>, Douglas<sup>1,2,3</sup>, Grant<sup>1,2,3</sup>, Jefferson<sup>1,2,3</sup>,

King<sup>1,2,3</sup>, Kittitas<sup>1,2</sup>, Lewis<sup>1,2,3</sup>, San Juan<sup>1,2,5,6</sup>, Skamania<sup>1,2</sup>, Snohomish<sup>1,2,6</sup>, Spokane<sup>1,2,3</sup>, Thurston<sup>1,2,3,6</sup>, Walla Walla<sup>1,2</sup>, Whatcom<sup>1,2,3</sup>, Yakima<sup>1,2,3</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3,5,6</sup>, Aug<sup>1,2,3,6</sup>, Sep<sup>1,2,3</sup> (2022<sup>1,2</sup>). Collections: AMNH, Bug-Guide, iNaturalist, WSDA. Conservation status: G5 – Secure globally (Nature-Serve 2024)

- **397.** *Anthidium* (*Anthidium*) *mormonum* Cresson, 1878. County records: Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,59</sup>, Spokane<sup>1,2</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL, INHS, SEMC. Conservation status: G5 – Secure globally (NatureServe 2024). Floral records: ASTERACEAE: *Erigeron nivalis*<sup>59</sup>; HYDROPHYLLACEAE: *Phacelia leptosepala*<sup>59</sup>
- **398.** Anthidium (Anthidium) tenuiflorae Cockerell, 1907. County records: Kittitas<sup>1,2,3</sup>, Okanogan<sup>1,2,4,59</sup>, San Juan<sup>1,2,3,5,6,124</sup>, Skagit<sup>3</sup>. Seasonality: Jun<sup>5</sup>, Jul<sup>1,2,5,6</sup>, Aug<sup>1,2,3,4</sup> (2017<sup>6</sup>). Collections: BBSL, JRYA, PWRC, SEMC, WSDA. Conservation status: G5 – Secure globally (NatureServe 2024). Floral records: CRASSU-LACEAE: Sedum lanceolatum<sup>59</sup>; HYDROPHYLLACEAE: Phacelia leptosepala<sup>59</sup>; LAMIACEAE: Micromeria douglasii<sup>5</sup>; ROSACEAE: Rubus ulmifolius<sup>5</sup>
- 399. Anthidium (Anthidium) utahense Swenk, 1914. County records: Grant<sup>1,3</sup>, Klickitat<sup>1,2</sup>, Spokane<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>8,41,91,98</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Jun<sup>1,2</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: AMNH, BBSL, INHS, NMNH, SEMC, WSUC. [= Anthidium sagittipictum Swenk, 1914]. Holotype. USA, Washington, Whitman County, Pullman. Conservation status: G5 Secure globally (NatureServe 2024). Floral Records: FABACEAE: Vicia villosa<sup>8</sup>
- **400.** †\* *Anthidium (Proanthidium) oblongatum* (Illiger, 1806). County records: Clark<sup>1,2</sup>, King<sup>1,2,3</sup>, Pierce<sup>1,2</sup>, Snohomish<sup>1,2</sup>, Spokane<sup>1,2</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2</sup>, Sep<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: BugGuide, iNaturalist. Conservation status: G5 Secure globally (NatureServe 2024)

## Genus Dianthidium Cockerell

- **401.** *Dianthidium* (*Dianthidium*) *curvatum* (Smith, 1854). County records: Garfield<sup>1,2,3.</sup> Seasonality: Jul<sup>1,2</sup> (1998<sup>1,2</sup>). Collections: BBSL. Floral records: ASTER-ACEAE: *Carthamus tinctorius*<sup>3</sup>
- **401a.** † *Dianthidium* (*Dianthidium*) *curvatum sayi* Cockerell, 1907. County records: Benton<sup>1,2,3</sup>, Garfield<sup>1,2,3</sup>, Whitman<sup>1,2,3</sup>. Seasonality: Jul<sup>1,2,3</sup>, Aug<sup>1,2</sup>, Sep<sup>2,3</sup> (2021<sup>1,2</sup>). Collections: BBSL, iNaturalist, INHS
- **402.** *Dianthidium* (*Dianthidium*) *heterulkei* Schwarz, 1940. County records: Okanogan<sup>1,2,3,59</sup>. Seasonality: Aug<sup>1,2,3</sup> (2004<sup>1,2,3,59</sup>). Collections: BBSL. Floral records: ASTERACEAE: *Erigeron speciosus*<sup>3,59</sup>
- **403.** Dianthidium (Dianthidium) parvum (Cresson, 1878). County records: Thurston<sup>133</sup>. Seasonality: Jul<sup>133</sup> (2018<sup>133</sup>). Floral records: ASTERACEAE: Crepis capillaris<sup>133</sup>, Erigeron speciosus<sup>133</sup>, Hieracium scouleri<sup>133</sup>, Solidago missouriensis<sup>133</sup>
- **404.** † *Dianthidium (Dianthidium) plenum* Timberlake, 1943. County records: Klickitat<sup>1,2,3</sup>. Seasonality: Jul<sup>1,2,3</sup> (2010<sup>1,2,3</sup>). Collections: BBSL

- **405.** *Dianthidium* (*Dianthidium*) *pudicum* (Cresson, 1879). County records: Benton<sup>1,2,3,71</sup>, Spokane<sup>7</sup>, Walla Walla<sup>1,2</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2</sup>, Aug<sup>1,2,3,7</sup>, Sep<sup>1,2</sup> (2023<sup>7</sup>). Collections: BBSL
- 406. *Dianthidium* (*Dianthidium*) *subparvum* Swenk, 1914. County records: Chelan<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Spokane<sup>1,2</sup>, Thurston<sup>133</sup>, Walla Walla<sup>1,2,3,71</sup>, Whitman<sup>91</sup>. Seasonality: Jul<sup>1,2,3,133</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2,3</sup> (2019<sup>133</sup>). Collections: BBSL. Holotype. USA, Washington, Whitman County, Pullman. Floral records: ASTER-ACEAE: *Crepis capillaris*<sup>133</sup>, *Erigeron speciosus*<sup>133</sup>
- 407. *Dianthidium* (*Dianthidium*) *ulkei* (Cresson, 1878). County records: Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,59</sup>, Pierce<sup>91</sup>, Spokane<sup>1,2</sup>. Seasonality: Jul<sup>1,2</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2</sup> (2014<sup>1,2</sup>). Collections: BBSL, CAS. [= *Dianthidium ulkei reductum* Timberlake, 1943]. Holotype. USA, Washington, Pierce County, Longmire, Mt. Rainier National Park.

#### Genus Stelis Panzer

- **408.** † *Stelis* (*Dolichostelis*) *laticincta* Cresson, 1878. County records: Benton<sup>1,2</sup>, Clark<sup>1,2</sup>, Douglas<sup>1,2</sup>, Klickitat<sup>1,2</sup>. Seasonality: Jul<sup>1,2</sup>, Aug<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: BugGuide, iNaturalist
- **409.** † *Stelis* (*Stelis*) *calliphorina* (Cockerell, 1911). County records: Spokane<sup>1,2</sup>, Whitman<sup>2,3</sup>. Seasonality: May<sup>2,3</sup>, Jul<sup>1,2</sup> (2014<sup>1,2</sup>). Collections: BBSL
- **410.** † *Stelis* (*Stelis*) *callura* Cockerell, 1925. County records: Adams<sup>1,2,3</sup>, Benton<sup>1,2,3</sup>, Spokane<sup>1,2</sup>, Whitman<sup>2,3</sup>. Seasonality: May<sup>1,2,3</sup>, Jun<sup>2,3</sup> (2016<sup>1,2</sup>). Collections: BBSL
- **411.** †**‡** *Stelis* (*Stelis*) *foederalis* Smith, 1854. County records: Spokane<sup>1,2,3</sup>. Seasonality: Jul<sup>1,2,3</sup> (1963<sup>1,2,3</sup>). Collections: BBSL
- **412.** † *Stelis* (*Stelis*) *holocyanea* (Cockerell, 1925). County records: Spokane<sup>1,2</sup>. Seasonality: May<sup>1,2</sup>, Jul<sup>1,2,3</sup> (2015<sup>1,2</sup>). Collections: BBSL
- **413.** † *Stelis* (*Stelis*) *lateralis* Cresson, 1864. County records: Spokane<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>. Seasonality: May<sup>1,2,3</sup>, Jun<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL
- **414.** *Stelis (Stelis) montana* Cresson, 1864. County records: Benton<sup>1,2,3</sup>, Chelan<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Stevens<sup>3</sup>, Thurston<sup>1,2,3</sup>, Walla Walla<sup>3</sup>, Yakima<sup>1,2,3</sup>. Seasonality: May<sup>1,2,3</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup> (2004<sup>1,2,3,59</sup>). Collections: BBSL, SEMC. Floral records: ASTERACEAE: *Erigeron speciosus*<sup>3,59</sup>; FABACEAE: *Lupinus sericeus*<sup>3,59</sup>
- **415.** † *Stelis* (*Stelis*) *monticola* Cresson, 1878. County records: King<sup>1,2,3</sup>, San Juan<sup>1,2,3</sup>, Spokane<sup>1,2</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jul<sup>3</sup> (2015<sup>1,2</sup>). Collections: AMNH, BBSL
- **416.** †‡ *Stelis (Stelis) nitida* Cresson, 1878. County records: King<sup>1,2,3</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2,3</sup> (1928<sup>1,2,3</sup>). Collections: BBSL. Floral records: ASTERACEAE: *Hypochaeris*<sup>3</sup>
- 417. †‡ Stelis (Stelis) occidentalis Parker and Griswold, 2013. County records: Spokane<sup>1,2,3</sup>. Seasonality: Jun<sup>1,2,3</sup> (1969<sup>1,2,3</sup>). Collections: BBSL
- **418.** † *Stelis* (*Stelis*) *pavonina* (Cockerell, 1908). County records: Lincoln<sup>2,3</sup>, Spokane<sup>1,2</sup>. Seasonality: May<sup>1,2,3</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL

- **419.** ‡ *Stelis* (*Stelis*) *rubi* Cockerell, 1898. County records: King<sup>1,2,98</sup>, Thurston<sup>98</sup>. Seasonality: May<sup>1,2,98</sup>, Jun<sup>98</sup> (1897<sup>1,2</sup>). Collections: NMNH. Holotype. USA, Washington, King County, Seattle; 11 May 1897; 18979 USNM, USNM ENT 00537080. Floral records: ROSACEAE: *Rubus ursinus*<sup>98</sup>. Comments: Discover Life has synonymized *S. rubi* with *S. monticola* without reference or explanation. We are not aware of any published work that that synonymizes these species and retain them as separate taxa in this checklist.
- **420.** *Stelis* (*Stelis*) *subcaerulea* Cresson, 1878. County records: Okanogan<sup>1,2,3,59</sup>, Whitman<sup>8</sup>. Seasonality: Aug<sup>1,2,3</sup> (2004<sup>1,2,3,59</sup>). Collections: BBSL, WSUC. Floral records: ASTERACEAE: *Achillea millefolium<sup>8</sup>*, *Eriophyllum lanatum<sup>8</sup>*; CRASSU-LACEAE: *Sedum lanceolatum<sup>3,59</sup>*
- **421.** *Stelis* (*Stelis*) *subemarginata* Cresson, 1878. County records: Benton<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Spokane<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3</sup>. Seasonality: May<sup>1,2,3</sup>, Jun<sup>1,2,3</sup>, Aug<sup>1,2,3</sup> (2015<sup>1,2</sup>). Collections: BBSL. Floral records: ASTERACEAE: *Anaphalis margaritacea*<sup>3,59</sup>, *Erigeron corymbosus*<sup>3,59</sup>
- **422.** † *Stelis subglauca* (Cockerell, 1925). County records: Spokane<sup>1,2</sup>. Seasonality: Jul<sup>1,2</sup> (2011<sup>1,2</sup>). Collections: BBSL. Comments: Discover Life has synonymized *S. subglauca* with *S. foederalis* without reference or explanation. We are not aware of any published work that that synonymizes these species and retain them as separate taxa in this checklist.

# Dioxyini

### Genus Dioxys Lepeletier and Serville

- **423.** † *Dioxys aurifuscus* (Titus, 1901). County records: Grant<sup>1</sup>. Seasonality: Jun<sup>1</sup> (2022<sup>1</sup>). Collections: iNaturalist
- **424.** † *Dioxys pacificus* Cockerell, 1916. County records: Benton<sup>1,2</sup>. Seasonality: May<sup>1,2</sup> (2014<sup>1,2</sup>). Collections: BBSL
- **425.** † *Dioxys pomonae* Cockerell, 1910. County records: Pierce<sup>3</sup>, Spokane<sup>1,2</sup>. Seasonality: Jun<sup>1,2,3</sup> (2014<sup>1,2</sup>). Collections: BBSL
- **426.** † *Dioxys productus* (Cresson, 1879). County records: Spokane<sup>1,2</sup>. Seasonality: Jul<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL

## Megachilini

## Genus Coelioxys Latreille

- **427.** *Coelioxys* (*Boreocoelioxys*) *moestus* Cresson, 1864. County records: Okanogan<sup>1,2,59</sup>, Thurston<sup>1,2</sup>. Seasonality: Jun<sup>1,2</sup>, Aug<sup>1,2</sup> (2004<sup>1,2,59</sup>). Collections: BBSL, UCMC. Floral records: ASTERACEAE: *Erigeron speciosus*<sup>59</sup>
- **428.** *Coelioxys* (*Boreocoelioxys*) *octodentatus* Say, 1824. County records: Kittitas<sup>1,2</sup>, Walla Walla<sup>1,2,71</sup>, Yakima<sup>1,2</sup>. Seasonality: Jun<sup>1,2</sup>, Jul<sup>1,2</sup>, Sep<sup>1,2</sup> (2012<sup>1,2</sup>). Collections: AMNH, BBSL, MCZ, SEMC

- 429. Coelioxys (Boreocoelioxys) rufitarsis Smith, 1854. County records: Benton<sup>1,2,3,71</sup>, Chelan<sup>3</sup>, Clallam<sup>3</sup>, Ferry<sup>1,2</sup>, Franklin<sup>3</sup>, Jefferson<sup>1,2</sup>, King<sup>1,2</sup>, Kittitas<sup>2,3</sup>, Lewis<sup>1,2,4</sup>, Okanogan<sup>1,2</sup>, San Juan<sup>1,2,3,5,22,124,136</sup>, Thurston<sup>133</sup>, Walla Walla<sup>1,2,3,71</sup>, Whitman<sup>1,2,3</sup>, Yakima<sup>1,2,3</sup>. Seasonality: May<sup>1,2,3</sup>, Jun<sup>1,2,3,133</sup>, Jul<sup>1,2,3,5,133</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2,3</sup> (2021<sup>1,2</sup>). Collections: AMNH, BBSL, CUIC, FMNH, iNaturalist, JRYA, PCYU, PWRC, RUAC, SEMC. Host records: Megachile perihirta Cockerell<sup>134</sup>. Floral records: APOCYNACEAE: Apocynum androsaemifolium<sup>133</sup>; ASTERACEAE: Crepis capillaris<sup>133,136</sup>, Hypochaeris radicata<sup>5</sup>, Leucanthemum vulgare<sup>133</sup>, Microseris laciniata<sup>133</sup>; ONAGRACEAE: Clarkia amoena<sup>133</sup>
- **430.** *Coelioxys* (*Coelioxys*) *sodalis* Cresson, 1878. County records: Clallam<sup>3</sup>, Okanogan<sup>1,2,3,59</sup>, Thurston<sup>52,133</sup>. Seasonality: Jun<sup>52,133</sup>, Aug<sup>1,2,3</sup> (2018<sup>133</sup>). Collections: AMNH, BBSL, JRYA. Holotype. USA, Washington, Thurston County, Olympia; 9–24 June 1895, 26 June 1896; T Kincaid. Floral records: ASTERACEAE: *Agoseris glauca* var. *dasycephala*<sup>3,59</sup>, *Eriophyllum lanatum*<sup>133</sup>, *Leucanthemum vulgare*<sup>133</sup>
- **431.** † *Coelioxys (Xerocoelioxys) edita* Cresson, 1872. County records: Asotin<sup>1,2,4</sup>. Seasonality: May<sup>1,2,4</sup> (2007<sup>1,2,4</sup>). Collections: PCYU
- **432.** *Coelioxys (Xerocoelioxys) grindeliae* Cockerell, 1900. County records: Benton<sup>1,2,3,71</sup>. Seasonality: Aug<sup>1,2,3</sup> (1997<sup>1,2,3</sup>). Collections: BBSL
- **433.** † *Coelioxys (Xerocoelioxys) mesae* Cockerell, 1921. County records: Grant<sup>1,2,4</sup>. Collections: PCYU
- **434.** *Coelioxys (Xerocoelioxys) serricaudatus* J. R. Baker, 1975. County records: Spokane<sup>7</sup>, Whitman<sup>58,90</sup>. Seasonality: May<sup>7</sup>, Jun<sup>58,90</sup> (2024<sup>7</sup>). Paratype. USA, Washington, Whitman County, Palouse; 26 June 1961; RW Dawson.

# Genus Megachile Latreille

- **435.** *Megachile* (*Argyropile*) *parallela* Smith, 1853. County records: Asotin<sup>1,2</sup>, Benton<sup>1,2,3</sup>, Walla Walla<sup>1,2,3,25</sup>, Whitman<sup>2,3,8,25,71</sup>, Yakima<sup>25</sup>. Seasonality: Jun<sup>1,2,3,25</sup>, Jul<sup>2,3</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2,3</sup> (2015<sup>1,2</sup>). Collections: BBSL, iNaturalist, INHS, TAMU, WSUC. Conservation status: G5 – Secure globally (NatureServe 2024). Floral records: ASTERACEAE: *Helianthus annuus*<sup>8</sup>
- **436.** *Megachile* (*Chelostomoides*) *angelarum* Cockerell, 1902. County records: Benton<sup>1,2,3</sup>, Chelan<sup>1,2</sup>, King<sup>1,2</sup>, Thurston<sup>6</sup>, Walla Walla<sup>1,2,3,26</sup>, Whitman<sup>1,2</sup>. Seasonality: Jun<sup>1,2,3,26</sup>, Jul<sup>1,2</sup>, Aug<sup>1,2,6</sup> (2020<sup>1,2</sup>). Collections: BBSL, iNaturalist, TAMU, WSDA. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: ASTERACEAE: *Rhaponticum repens*<sup>3</sup>
- **437.** \* *Megachile (Eutricharaea) apicalis* Spinola, 1808. County records: Benton<sup>1,2,3</sup>, Columbia<sup>1,2,4</sup>, Kittitas<sup>1,2</sup>, Spokane<sup>1,2,3</sup>, Walla Walla<sup>1,2,3,71</sup>, Whitman<sup>2,3</sup>. Seasonality: Jun<sup>1,2,3</sup>, Jul<sup>1,2</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2</sup> (2021<sup>1,2</sup>). Collections: BBSL, iNaturalist, PCYU. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: ASTERACEAE: *Rhaponticum repens*<sup>3</sup>
- **438.** †\*‡ *Megachile (Eutricharaea) concinna* Smith, 1879. County records: Yakima<sup>1,2,3</sup>. Seasonality: Feb<sup>1,2,3</sup> (1969<sup>1,2,3</sup>). Collections: BBSL

- 439. \* *Megachile (Eutricharaea) rotundata* (Fabricius, 1787). County records: Benton<sup>1,2,3,128</sup>, Chelan<sup>1,2,3</sup>, King<sup>1,2</sup>, Spokane<sup>1,2,3</sup>, Walla Walla<sup>1,2,3</sup>, Yakima<sup>2,128</sup>. Seasonality: Feb<sup>2</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup> (2020<sup>1,2</sup>). Collections: BBSL, BugGuide, iNaturalist, TAMU. Conservation status: G5 Secure globally (NatureServe 2024)
- **440.** *Megachile* (*Litomegachile*) *brevis* Say, 1837. County records: Benton<sup>71</sup>, Garfield<sup>46</sup>, Skamania<sup>1,2</sup>, Spokane<sup>1,2,3</sup>, Thurston<sup>133</sup>, Walla Walla<sup>71</sup>, Whitman<sup>8</sup>, Yakima<sup>1,2,27</sup>. Seasonality: Jun<sup>1,2,46,133</sup>, Jul<sup>1,2,3,133</sup> (2020<sup>133</sup>). Collections: BBSL, Bug-Guide, MSU, MCZ, UCRC, WSUC. Conservation status: G5 – Secure globally (NatureServe 2024). Floral records: APOCYNACEAE: *Apocynum androsaemifolium*<sup>133</sup>; ASTERACEAE: *Gaillardia aristata*<sup>133</sup>, *Helianthus annuus*<sup>8</sup>, *Solidago missouriensis*<sup>133</sup>; HYPERICACEAE: *Hypericum perforatum*<sup>133</sup>; ONAGRACEAE: *Clarkia amoena*<sup>133</sup>
- **441.** *Megachile* (*Litomegachile*) *cleomis* Cockerell, 1900. County records: Grant<sup>7</sup>, Whitman<sup>7</sup>, Yakima<sup>7</sup>. Seasonality: May<sup>7</sup>, Jul<sup>7</sup>, Sep<sup>7</sup> (1900<sup>7</sup>). Collections: WSUC. Conservation status: G5 Secure globally (NatureServe 2024). Comments: Records from Grant and Yakima counties during May and September were males identified by Mitchell. *Megachile cleomis* was raised to full species from a subspecies of *M. texana* based on DNA barcodes with no morphological diagnosis (Sheffield and Genaro 2013). Mitchell (1935b) indicates that males of *M. cleomis* and *M. lippiae* are indistinguishable. As there is no way to confirm the identification of these males, it is possible they may represent records of *M. lippiae*.
- 441a. Megachile (Litomegachile) cleomis Cockerell, 1900/lippiae Cockerell, 1900. County records: Chelan<sup>1,2</sup>, Garfield<sup>46</sup>, Walla Walla<sup>1,2,3</sup>, Whatcom<sup>1,2,3</sup>, Whitman<sup>1,2,3</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2,3</sup> (1995<sup>1,2</sup>). Collections: BBSL, SEMC, TAMU. Floral records: FABACEAE: Lupinus sericeus<sup>3</sup>. Comments: These records were originally identified as *M. texana*. Sheffield et al. (2011) and Sheffield and Genaro (2013) raised *M. lippiae* and *M. cleomis*, respectively, to full species from subspecies of *M. texana*, which has a distinctly eastern distribution compared to *M. cleomis*. While Sheffield and Genaro (2013) don't describe where the east/west dividing line is located, it is highly likely that Washington is far enough west for these records to not be *M. texana*. Since these specimens have not been physically examined, it is unclear whether these records are actually *M. lippiae* or *M. cleomis*.
- **442.** *Megachile* (*Litomegachile*) *coquilletti* Cockerell, 1915. County records: Benton<sup>1,2,3</sup>, Chelan<sup>1,2,3</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>27</sup>, Yakima<sup>27</sup>. Seasonality: Jul<sup>1,2,3</sup> (1998<sup>1,2</sup>). Collections: BBSL, SEMC. Conservation status: G4 Apparently Secure globally (NatureServe 2024)
- **443.** *Megachile* (*Litomegachile*) *mendica* Cresson, 1878. County records: Kittitas<sup>1,3</sup>, Whitman<sup>2,3</sup>. Seasonality: Jun<sup>1,2,3</sup> (2003<sup>2,3</sup>). Collections: AMNH, BBSL. Conservation status: G5 – Secure globally (NatureServe 2024)
- 444. *Megachile (Litomegachile) onobrychidis* Cockerell, 1908. County records: Benton<sup>1,2,3</sup>, Clark<sup>1,2</sup>, Ferry<sup>1,2,3</sup>, Garfield<sup>1,2,3,46</sup>, Grant<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Spokane<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,3,6,27</sup>, Yakima<sup>1,2,3</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3,6</sup>, Sep<sup>1,2</sup>, Oct<sup>1,2</sup> (2014<sup>1,2</sup>). Collections: AMNH, BBSL, SEMC, WSDA. [= *Megachile*

*brevis onobrychidis* Cockerell, 1908]. Conservation status: G5 – Secure globally (NatureServe 2024). Floral records: ASTERACEAE: *Rhaponticum repens*<sup>3</sup>

- **445.** § *Megachile* (*Litomegachile*) *snowi* Mitchell, 1927. County records: Whitman<sup>32</sup>. Seasonality: Jul<sup>32</sup> (2013<sup>32</sup>). Conservation status: G3 – Vulnerable globally (NatureServe 2024)
- **446.** *Megachile (Megachile) centuncularis* (Linnaeus, 1758). County records: Okanogan<sup>1,2,3,59</sup>, Pierce<sup>24</sup>, Whitman<sup>24</sup>. Seasonality: Jul<sup>24</sup>, Aug<sup>1,2,3</sup> (2012<sup>1,2</sup>). Collections: BBSL. Conservation status: G5 Secure globally (NatureServe 2024). Floral records: ASTERACEAE: *Erigeron speciosus*<sup>3,59</sup>
- 447. ‡ *Megachile (Megachile) lapponica* Thomson, 1872. County Records: Pend Oreille<sup>94</sup>. Seasonality: Jul<sup>94</sup> (1931<sup>94</sup>). [= *Megachile nivalis* Friese, 1903]. Conservation status: G5 Secure globally (NatureServe 2024)
- 448. Megachile (Megachile) montivaga Cresson, 1878. County records: Benton<sup>1,2,3,71</sup>, Grant<sup>1,2</sup>, Kittitas<sup>1,2</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,59</sup>, Pierce<sup>1,2,3,24</sup>, Spokane<sup>1,2</sup>, Thurston<sup>24</sup>, Wahkiakum<sup>1,2</sup>, Walla Walla<sup>1,2,3,71</sup>, Whitman<sup>2,3,24</sup>, Yakima<sup>24</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2,3,24</sup>, Jul<sup>1,2,3,24</sup>, Aug<sup>1,2,3</sup> (2020<sup>1,2</sup>). Collections: BBSL, iNaturalist, INHS, SEMC, TAMU. Conservation status: G5 Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Cirsium vulgare<sup>3,59</sup>
- 449. Megachile (Megachile) relativa Cresson, 1878. County records: Chelan<sup>3</sup>, Clallam<sup>1,2,3</sup>, Clark<sup>1,2,3</sup>, Jefferson<sup>2,3</sup>, King<sup>24</sup>, Mason<sup>3</sup>, Okanogan<sup>1,2,3,59</sup>, Pierce<sup>1,2,3,24</sup>, Thurston<sup>24</sup>, Whitman<sup>1,2,3,24</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Jun<sup>1,2,3,24</sup>, Jul<sup>1,2,3,24</sup>, Aug<sup>1,2,3</sup> (2014<sup>3</sup>). Collections: AMNH, BBSL, INHS, JRYA, SEMC, UCRC. Conservation status: G5 Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Achillea millefolium<sup>59</sup>, Erigeron speciosus<sup>3,59</sup>, Taraxacum officinale<sup>3,59</sup>; BRASSICACEAE: Smelowskia calycina<sup>59</sup>; ONAGRACEAE: Chamerion angustifolium ssp. angustifolium<sup>3,59</sup>
- **450.** § *Megachile (Megachiloides) anograe* Cockerell, 1908. County records: Asotin<sup>131</sup>, Benton<sup>1,2</sup>, Grant<sup>1,2,4</sup>. Seasonality: May<sup>1,2,131</sup> (2015<sup>1,2</sup>). Collections: BBSL, PCYU. [= *Megachile laurita* Mitchell, 1927]. Conservation status: G3 Vulnerable globally (NatureServe 2024)
- **451.** *Megachile* (*Megachiloides*) *gravita* Mitchell, 1933. County records: Klickitat<sup>1,2</sup>, Thurston<sup>99</sup>. Seasonality: Jul<sup>1,2</sup>, Aug<sup>99</sup> (2011<sup>1,2</sup>). Collections: BBSL. [= *Meg-achile astata* Mitchell, 1933]. Paratype. USA, Washington, Thurston County, Olympia; 20 August 1893; T Kincaid. Conservation status: G4 – Apparently Secure globally (NatureServe 2024)
- 452. §‡ Megachile (Megachiloides) legalis Cresson, 1879. County records: Grant<sup>131,132</sup>. Seasonality: Jun<sup>131,132</sup> (1902<sup>131,132</sup>). Collections: WSUC. [= Megachile (Xeromegachile) couleeana Mitchell, 1938]. Holotype. USA, Washington, Grant County, Grand Coulee, Wash Soap Lake; 29 June 1902; WSU No. 425. Conservation status: G3 – Vulnerable globally (NatureServe 2024)
- **453.** § *Megachile* (*Megachiloides*) *nevadensis* Cresson, 1879. County records: Benton<sup>1,2,3</sup>, Yakima<sup>131</sup>. Seasonality: Aug<sup>1,2,3</sup>, Sep<sup>1,2,3</sup> (1995<sup>1,2,3</sup>). Collections: BBSL. Conservation status: G3 Vulnerable globally (NatureServe 2024). Floral records: ASTERACEAE: *Senecio*<sup>3</sup>

- **454.** *Megachile (Megachiloides) pascoensis* Mitchell, **1934**. County records: Franklin<sup>1,2,3,99</sup>, **Spokane**<sup>1,2</sup>, Thurston<sup>133</sup>, Whitman<sup>99</sup>. Seasonality: May<sup>1,2,3,99</sup>, Jun<sup>133</sup>, Jul<sup>99,133</sup> (2020<sup>133</sup>). Collections: BBSL, NMNH. Holotype. USA, Washington, Franklin County, Pasco; 25 May 1896; USNM No. 39982. Paratype. USA, Washington, Whitman County Pullman; July. Conservation status: G5 – Secure globally (NatureServe 2024). Floral records: ONAGRACEAE: *Clarkia amoe-na*<sup>133</sup>; POLEMONIACEAE: *Gilia capitata*<sup>133</sup>
- **455.** *Megachile* (*Megachiloides*) *subnigra* Cresson, 1879. County records: Adams<sup>30,131</sup>, Benton<sup>1,2</sup>, Grant<sup>1,2,4,131</sup>, Whitman<sup>131</sup>, Yakima<sup>1,2,3,30,92</sup>. Seasonality: May<sup>1,2,4,131</sup>, Jun<sup>131</sup>, Jul<sup>1,2,3,92</sup> (2015<sup>1,2</sup>). Collections: BBSL, RSKM, SEMC. Conservation status: G4 – Apparently Secure globally (NatureServe 2024)
- 456. § Megachile (Megachiloides) umatillensis (Mitchell, 1927). County records: Benton<sup>1,2,3,6,29,95</sup>, Spokane<sup>29,95</sup>, Walla Walla<sup>1,2</sup>. Seasonality: May<sup>1,2,6</sup>, Jun<sup>1,2,29,95</sup>, Jul<sup>1,2,3,29,95</sup>, Aug<sup>1,2</sup> (2022<sup>6</sup>). Collections: BBSL, WSDA. Paratype. USA, Washington Territory, Little Spokane; 26 July 1882; S Henshaw. [= Megachiloides umatillensis Mitchell, 1927]. Holotype. USA, Washington Territory, Camp Umatilla; 26 June 1882; MCZ Type No 15714. Conservation status: G3 – Vulnerable globally (NatureServe 2024)
- **457.** ‡ *Megachile (Megachiloides) wheeleri* Mitchell, 1927. County records: Benton<sup>95</sup>, Spokane<sup>1,2,93,95</sup>, Yakima<sup>131</sup>. Seasonality: Jun<sup>95</sup>, Jul<sup>1,2,131</sup> (1936<sup>131</sup>). Collections: MCZ. [= *Megachile spokanensis* Mitchell, 1927]. Holotype. USA, Washington Territory, Little Spokane. **Paratype**. USA, Washington Territory, Camp Umatilla; 26 June 1882. Conservation status: G4 Apparently Secure globally (NatureServe 2024)
- **458.** *Megachile* (*Sayapis*) *fidelis* Cresson, 1878. County records: Benton<sup>1,2,3</sup>, Chelan<sup>1,2,3</sup>, Ferry<sup>1,2,3</sup>, King<sup>1,2</sup>, Kitsap<sup>1,2</sup>, Kittias<sup>1,2</sup>, Okanogan<sup>1,2,3,59</sup>, Thurston<sup>1,2,3</sup>. Seasonality: Jun<sup>1,2,3</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: BBSL, iNaturalist, SEMC. Conservation status: G5 Secure globally (NatureServe 2024). Floral records: BRASSICACEAE: *Sisymbrium altissimum*<sup>3,59</sup>
- **459.** *Megachile (Sayapis) mellitarsis* Cresson, 1878. County records: Grant<sup>1,2</sup>, Yakima<sup>28</sup>. Seasonality: May<sup>1,2</sup>, Jul<sup>28</sup> (2007<sup>1,2</sup>). Collections: PCYU. Conservation status: G4 – Apparently Secure globally (NatureServe 2024)
- 460. Megachile (Sayapis) pugnata Say, 1837. County records: Chelan<sup>1,2,3</sup>, Ferry<sup>2</sup>, King<sup>3</sup>, Kitsap<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, San Juan<sup>3,28</sup>, Spokane<sup>2</sup>, Thurston<sup>2</sup>, Walla Walla<sup>1,2,3,71</sup>, Whitman<sup>2,8</sup>, Yakima<sup>28</sup>. Seasonality: Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2,3</sup> (2021<sup>1,2</sup>). Collections: AMNH, BBSL, BugGuide, iNaturalist, UCRC, WSUC. Conservation status: G5 Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Achillea millefolium<sup>3</sup>, Erigeron speciosus<sup>3,8</sup>, Taraxacum officinale<sup>3</sup>
- **461.** § *Megachile (Xanthosarus) dentitarsus* Sladen, 1919. County records: San Juan<sup>1,2,3,124</sup>, Yakima<sup>1,2,29</sup>. Seasonality: Jul<sup>1,2,29</sup> (2011<sup>1,2,124</sup>). Collections: MCZ, PWRC. Conservation status: G3 Vulnerable globally (NatureServe 2024)
- 462. † *Megachile (Xanthosarus) frigida* Smith, 1853. County records: Grays Harbor<sup>1,2,3</sup>, King<sup>3</sup>, Lewis<sup>2,3</sup>, Okanogan<sup>1,2,3</sup>, Thurston<sup>2,3</sup>, Walla Walla<sup>1,2,3</sup>, Yakima<sup>1,2,3</sup>.

Seasonality: Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>3</sup> (2017<sup>2</sup>). Collections: BBSL, BugGuide, SEMC, UCRC. Conservation status: G5 – Secure globally (NatureServe 2024)

- **463.** *Megachile* (*Xanthosarus*) *gemula* Cresson, 1878. County records: Okanogan<sup>1,2,3,59</sup>, San Juan<sup>2</sup>, Thurston<sup>3,24,133</sup>. Seasonality: May<sup>133</sup>, Jun<sup>1,2,3,24,133</sup>, Jul<sup>1,2,3,24</sup> (2020<sup>133</sup>). Collections: BBSL, SEMC, UCRC, WSUC. Conservation status: G5 Secure globally (NatureServe 2024). Floral records: ASPARAGACEAE: *Triteleia hyacinthina*<sup>133</sup>; CAMPANULACEAE: *Campanula rotundifolia*<sup>3,59</sup>; CAPRI-FOLIACEAE: *Plectritis congesta*<sup>133</sup>; FABACEAE: *Lupinus*<sup>3,59</sup>; HYDROPHYL-LACEAE: *Phacelia leptosepala*<sup>3,59</sup>; ROSACEAE: *Physocarpus malvaceus*<sup>8</sup>
- **463a.** *Megachile (Xanthosarus) gemula cressonii* Dalla Torre, 1896. County records: Thurston<sup>24</sup>. Seasonality: Jul<sup>24</sup> (1896<sup>24</sup>)
- **463b.** *Megachile (Xanthosarus) gemula gemula* Cresson, 1878. County records: Garfield<sup>46</sup>. Seasonality: (1989<sup>46</sup>)
- 464. Megachile (Xanthosarus) melanophaea Smith, 1853. County records: **Chelan**<sup>3</sup>, **Clallam**<sup>1,2,3</sup>, **Jefferson**<sup>1,2,3</sup>, **King**<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Pierce<sup>1,2,3,24</sup>, San Juan<sup>1,2,3,5,24,124,136</sup>, Skamania<sup>1,2,3</sup>, Thurston<sup>2,24,133</sup>, Wahkiakum<sup>1,2</sup>, Yakima<sup>1,2,3</sup>. Seasonality: May<sup>1,2,133</sup>, Jun<sup>1,2,3,5,24,133</sup>, Jul<sup>1,2,3,5,24,32</sup>, Aug<sup>1,2,3,24</sup> (2021<sup>1,2</sup>). Collections: AMNH, BBSL, BugGuide, iNaturalist, JRYA, PWRC, SEMC, UCRC. [= Megachile gemula fulvogemula Mitchell, 1935]. Paratype. USA, Washington, Thurston County, Olympia; 2 June 1894. Conservation status: G5 – Secure globally (NatureServe 2024). Floral records: APOCYNACEAE: Apocynum androsaemifolium<sup>133</sup>; ASTERACEAE: Eriophyllum lanatum<sup>133</sup>, Hypochaeris radicata<sup>133</sup>, Microseris laciniata<sup>133</sup>; CAMPANULACEAE: Campanula rotundifolia<sup>3,59,133</sup>; CAPRIFOLIACEAE: Plectritis congesta<sup>133</sup>; CONVOLVULACEAE: Calystegia soldanella<sup>136</sup>; FABACEAE: Lupinus albicaulis<sup>133</sup>, L. littoralis<sup>136</sup>, Trifolium repens<sup>3,59</sup>, Vicia sativa<sup>5,133</sup>; LAMIACEAE: Micromeria douglasii<sup>5</sup>; ONAGRACEAE: *Chamerion angustifolium*<sup>133</sup>; PLANTAGINACEAE: *Penstemon washingtonensis*<sup>59</sup>; PLUMBAGINACEAE: Armeria maritima<sup>133</sup>; ROSACEAE: Potentilla gracilis<sup>133</sup>, Rubus ulmifolius<sup>5</sup>
- **464a.** *Megachile (Xanthosarus) melanophaea calogaster* **Cockerell, 1898**. County records: King<sup>24</sup>, Thurston<sup>24</sup>. Seasonality: Jun<sup>24</sup> (1895<sup>24</sup>). Collections: NMNH, WSUC. **Holotype**. USA, Washington, Thurston County, Olympia; 21 June 1895; USNM No. 4268
- 465. *Megachile (Xanthosarus) perihirta* Cockerell, 1898. County records: Benton<sup>1,2,3</sup>, Chelan<sup>1,2,3</sup>, Clallam<sup>1,2,3</sup>, Douglas<sup>1,2</sup>, Ferry<sup>1,2,3</sup>, Garfield<sup>46</sup>, Grant<sup>1,2,3,29</sup>, Island<sup>1,2</sup>, Jefferson<sup>1,2,3</sup>, King<sup>1,2,3,29</sup>, Kitsap<sup>1,2,3,134</sup>, Kittitas<sup>1,2,3,29</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,59</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>1,2,3,56,29,124,136</sup>, Skamania<sup>1,2</sup>, Snohomish<sup>1,2,3</sup>, Spokane<sup>1,2</sup>, Stevens<sup>3</sup>, Thurston<sup>1,2,3,29,133</sup>, Wahkiakum<sup>1,2</sup>, Walla Walla<sup>1,2,3,71</sup>, Whatcom<sup>1,2,3,6</sup>, Whitman<sup>1,2,3,8,29</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Jan<sup>1,2</sup>, May<sup>1,2</sup>, Jun<sup>1,2,3,133</sup>, Jul<sup>1,2,3,5,133</sup>, Aug<sup>1,2,3,6</sup>, Sep<sup>1,2,3,29</sup>, Oct<sup>1,2</sup> (2021<sup>1,2</sup>). Collections: AMNH, BBSL, BugGuide, FMNH, iNaturalist, INHS, JRYA, PWRC, SEMC, TAMU, UCRC, WSDA, WSUC. Conservation status: G5 Secure globally (NatureServe 2024). Floral records: APOCYNACEAE: *Apocynum androsaemifolium*<sup>133</sup>; ASTERACEAE: *Achillea*

millefolium<sup>59</sup>, Cirsium arvense<sup>8,133</sup>, C. vulgare<sup>8</sup>, Crepis capillaris<sup>133,136</sup>, Erigeron speciosus<sup>3,59,133</sup>, Gaillardia aristata<sup>8,133</sup>, Grindelia integrifolia<sup>5</sup>, Helianthus<sup>3</sup>, Hieracium scouleri<sup>133</sup>, Hypochaeris radicata<sup>133</sup>, Leucanthemum vulgare<sup>133</sup>, Senecio jacobaea<sup>133</sup>, S. serra<sup>8</sup>, S. triangularis<sup>59</sup>, Solidago<sup>8</sup>, S. canadensis<sup>133</sup>, S. missouriensis<sup>133</sup>, Taraxacum officinale<sup>59</sup>, Xanthium<sup>8</sup>; BRASSICACEAE: Cakile maritima<sup>136</sup>; CONVOL-VULACEAE: Calystegia soldanella<sup>136</sup>; FABACEAE: Lupinus<sup>59</sup>, L. sericeus<sup>3</sup>, Vicia villosa<sup>8</sup>; HYPERICACEAE: Hypericum perforatum<sup>133</sup>; ONAGRACEAE: Chamerion angustifolium<sup>133</sup>, Clarkia amoena<sup>133</sup>; ROSACEAE: Rubus ulmifolius<sup>5</sup>

## Osmiini

### Genus Ashmeadiella Cockerell

- **466.** ‡ *Ashmeadiella* (*Arogochila*) *foxiella* Michener, 1939. County records: Yakima<sup>44</sup>. Seasonality: May<sup>44</sup> (1903<sup>44</sup>)
- **467.** *Ashmeadiella* (*Arogochila*) *timberlakei timberlakei* Michener, 1936. Comments: Michener (1939) notes an observation of a single specimen from Washington but does not provide a locality within the state.
- **468.** *Ashmeadiella* (*Ashmeadiella*) *aridula* Cockerell, 1910. County records: Spokane<sup>1,2</sup>, Whitman<sup>44</sup>, Yakima<sup>2,3</sup>. Seasonality: Jul<sup>1,2,3,44</sup> (2015<sup>1,2</sup>). Collections: BBSL, SEMC
- **469.** ‡ *Ashmeadiella* (*Ashmeadiella*) *bucconis denticulata* (Cresson, 1878). County records: Chelan<sup>44</sup>, Yakima<sup>44</sup>. Seasonality: Jul<sup>44</sup> (1918<sup>44</sup>)
- **470.** *Ashmeadiella* (*Ashmeadiella*) *cactorum* (Cockerell, 1897). County records: King<sup>44</sup>, Okanogan<sup>1,2,3,59</sup>, Thurston<sup>97</sup>. Seasonality: Jul<sup>44,97</sup>, Aug<sup>1,2,3</sup> (2004<sup>1,2,3,59</sup>). Collections: BBSL. [= *Ashmeadiella curriei curriei* Titus, 1904]. Floral records: ASTER-ACEAE: *Taraxacum officinale*<sup>3,59</sup>; HYDROPHYLLACEAE: *Phacelia leptosepala*<sup>3,59</sup>
- **471.** ‡ *Ashmeadiella* (*Ashmeadiella*) *californica californica* (Ashmead, 1897). County records: Grant<sup>44</sup>, Whitman<sup>1,2,3,44</sup>. Seasonality: Jul<sup>1,2,3,44</sup> (1925<sup>1,2,3,44</sup>). Collections: SEMC
- **472.** *Ashmeadiella* (*Ashmeadiella*) *cubiceps* (Cresson, 1879). County records: Okanogan<sup>1,2,3,59</sup>. Seasonality: Aug<sup>1,2,3</sup> (2004<sup>1,2,3,59</sup>). Collections: BBSL. Floral records: ASTERACEAE: *Erigeron speciosus*<sup>3,59</sup>, *Hieracium scouleri*<sup>3,59</sup>
- **473.** † *Ashmeadiella* (*Ashmeadiella*) *meliloti* (Cockerell, 1897). County records: Spokane<sup>1,2</sup>. Seasonality: Jul<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL

### Genus Atoposmia Cockerell

- **474.** *Atoposmia* (*Atoposmia*) *elongata* (Michener, 1936). County records: Okanogan<sup>1,2,3,4,59</sup>, Pierce<sup>96</sup>. Seasonality: Jul<sup>1,2,3,4</sup> (2004<sup>1,2,3,4,59</sup>). Collections: BBSL
- **475.** *Atoposmia* (*Hexosmia*) *copelandica* (Cockerell, 1908). County records: Okanogan<sup>1,2,3,59</sup>, Stevens<sup>1,2</sup>. Seasonality: Jul<sup>1,2</sup>, Aug<sup>1,2,3</sup> (2014<sup>1,2</sup>). Collections: BBSL. Floral records: HYDROPHYLLACEAE: *Phacelia leptosepala*<sup>3,59</sup>

## Genus Chelostoma Latreille

- **476.** *Chelostoma* (*Neochelostoma*) *minutum* Crawford, 1916. County records: Okanogan<sup>1,2,3,59</sup>, Spokane<sup>43,96</sup>. Seasonality: Jun<sup>1,2,3</sup>, Jul<sup>43</sup>, Aug<sup>1,2,3</sup> (2004<sup>1,2,3,59</sup>). Collections: BBSL. Floral records: CRASSULACEAE: *Sedum lanceolatum*<sup>3,59</sup>
- **477.** *Chelostoma* (*Neochelostoma*) *phaceliae* Michener, **1938**. County records: Asotin<sup>96</sup>, Benton<sup>1,2,3</sup>, Walla Walla<sup>43,96</sup>. Seasonality: May<sup>43</sup>, Jun<sup>1,2,3</sup> (1994<sup>1,2,3</sup>). Collections: BBSL

## Genus Heriades Spinola

- 478. † Heriades (Neotrypetes) carinata Cresson, 1864. County records: Cowlitz<sup>1,2</sup>, King<sup>1,2,3</sup>, Thurston<sup>3</sup>, Yakima<sup>1,2</sup>. Seasonality: Jul<sup>1,2</sup>, Aug<sup>1,2,3</sup> (1983<sup>1,2,3</sup>). Collections: BBSL, SEMC, UCRC
- **479.** *Heriades* (*Neotrypetes*) *cressoni* Michener, **1938**. County records: Chelan<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>. Seasonality: Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup> (2004<sup>1,2,3,59</sup>). Collections: BBSL. Floral records: ASTERACEAE: *Erigeron speciosus*<sup>3,59</sup>; MALVACEAE: *Iliamna longisepala*<sup>3</sup>
- **480.** †**‡** *Heriades* (*Neotrypetes*) *occidentalis* Michener, 1938. County records: Yakima<sup>3</sup>. Seasonality: Jul<sup>3</sup> (1920<sup>3</sup>). Collections: UCRC
- **481.** *Heriades (Neotrypetes) variolosa* (Cresson, 1872). County records: Stevens<sup>1,2</sup>, Yakima<sup>1,2,3,42</sup>. Seasonality: Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup> (2011<sup>1,2</sup>). Collections: BBSL, SEMC

## Genus Hoplitis Klug

- 482. Hoplitis (Alcidamea) albifrons (Kirby, 1837). County records: Chelan<sup>3</sup>, Clallam<sup>1,2,3</sup>, Columbia<sup>1,2,3</sup>, Kittitas<sup>1,2</sup>, Klickitat<sup>1,2,3</sup>, Okanogan<sup>1,2,3,4,59</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>3</sup>, Spokane<sup>1,2</sup>, Stevens<sup>1,2</sup>, Thurston<sup>2,133</sup>, Yakima<sup>1,2,3,96</sup>. Seasonality: Apr<sup>2</sup>, Jun<sup>1,2,3,4,133</sup>, Jul<sup>1,2,3,4</sup>, Aug<sup>1,2,4</sup> (2018<sup>2,133</sup>). Collections: AMNH, BBSL, BugGuide, SEMC, UCRC, WSUC. Floral records: ASTERACEAE: Arnica sororia<sup>59</sup>, Erigeron speciosus<sup>59</sup>, Senecio triangularis<sup>59</sup>, Taraxacum officinale<sup>3,59</sup>; FABACEAE: Lupinus<sup>3,59</sup>, L. polyphyllus<sup>8</sup>, Trifolium pratense<sup>59</sup>, T. repens<sup>3,59</sup>; HYDROPHYL-LACEAE: Phacelia leptosepala<sup>8,59</sup>; MALVACEAE: Sidalcea oregana<sup>3</sup>; PLANTAGI-NACEAE: Penstemon confertus<sup>59</sup>; ROSACEAE: Potentilla gracilis<sup>3,59,133</sup>, Rosa nutkana ssp. nutkana<sup>59</sup>
- 483. Hoplitis (Alcidamea) fulgida (Cresson, 1864). County records: Clallam<sup>3</sup>, Columbia<sup>135</sup>, Ferry<sup>2</sup>, Grant<sup>104</sup>, Kittitas<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Pierce<sup>3</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2</sup>, Yakima<sup>1,2,3</sup>. Seasonality: May<sup>1,2,104</sup>, Jun<sup>1,2,3,135</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup> (2021<sup>135</sup>). Collections: BBSL, BugGuide, NMDG, INHS, JRYA, SEMC, UCRC, WSUC. Floral records: ASTERACEAE: Achillea millefolium<sup>3,59</sup>, Crepis atrabarba<sup>59</sup>, Taraxacum officinale<sup>3,59</sup>; BORANGINACEAE: Myosotis laxa<sup>3,59</sup>; HYDROPHYL-LACEAE: Phacelia leptsepala<sup>3,59</sup>, P. heterophylla<sup>8</sup>; POLEMONIACEAE: Polemonium pulcherrimum<sup>59</sup>; RANUNCULACEAE: Delphinium nuttallianum<sup>8</sup>, Ranunculus<sup>8</sup>; ROSACEAE: Physocarpus malvaceus<sup>8</sup>, Potentilla gracilis<sup>3,59</sup>

- **484.** *Hoplitis* (*Alcidamea*) *grinnelli* (Cockerell, 1910). County records: Benton<sup>1,2,3</sup>, Garfield<sup>1,2,3,46,104</sup>, Grant<sup>1,2,4</sup>, Klickitat<sup>1,2</sup>, Lewis<sup>1,2,4,104</sup>, Okanogan<sup>1,2,3,59</sup>, Spokane<sup>1,2</sup>, Thurston<sup>133</sup>, Whitman<sup>1,2,3,103</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3,4,104</sup>, Jun<sup>1,2,103,133</sup>, Jul<sup>103</sup>, Aug<sup>1,2,3</sup> (2018<sup>133</sup>). Collections: BBSL, PCYU, SEMC. Floral records: FABACE-AE: *Astragalus*<sup>3</sup>, *Lupinus lepidus*<sup>133</sup>; ROSACEAE: *Potentilla gracilis*<sup>133</sup>
- **485.** *Hoplitis* (*Alcidamea*) *hypocrita* (Cockerell, 1906). County records: Benton<sup>1,2,3</sup>, Garfield<sup>1,2,3,46</sup>, **Spokane**<sup>1,2,3</sup>, Whitman<sup>1,2,3,8</sup>, **Yakima**<sup>1,2,4</sup>. Seasonality: May<sup>1,2,3,4</sup>, Jun<sup>1,2,3,46</sup>, Jul<sup>1,2,3</sup> (2012<sup>1,2</sup>). Collections: BBSL, WSUC. Floral records: APIACE-AE: *Lomatium*<sup>8</sup>; ASTERACEAE: *Balsamorhiza sagitta*<sup>8</sup>; FABACEAE: *Astragalus*<sup>3</sup>, *A. bungeanus*<sup>3</sup>, *A. falcatus*<sup>3</sup>; PLANTAGINACEAE: *Penstemon attenuatus*<sup>8</sup>
- **486.** *Hoplitis* (*Alcidamea*) *louisae* (Cockerell, 1934). County records: Benton<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Thurston<sup>103</sup>, Yakima<sup>103</sup>. Seasonality: Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup> (1994<sup>1,2,3</sup>). Collections: BBSL, SEMC
- 487. Hoplitis (Alcidamea) producta (Cresson, 1864). County records: Benton<sup>1,2</sup>, Klickitat<sup>1,2,104</sup>, Okanogan<sup>59</sup>, Skamania<sup>1,2</sup>, Spokane<sup>1,2</sup>, Thurston<sup>133</sup>, Wahkia-kum<sup>1,2</sup>, Whitman<sup>6,104</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>104</sup>, Jun<sup>1,2,133</sup>, Jul<sup>1,2,6,104</sup>, Aug<sup>1,2</sup> (2019<sup>133</sup>). Collections: BBSL. Floral records: ASTERACEAE: Achillea millefo-lium<sup>59</sup>; FABACEAE: Lupinus lepidus<sup>133</sup>; ROSACEAE: Potentilla gracilis<sup>133</sup>
- **487a.** § *Hoplitis (Alcidamea) producta subgracilis* Michener, 1947. County records: Okanogan<sup>1,2,3</sup>, Pierce<sup>103</sup>, Skagit<sup>1,2,3</sup>, Whitman<sup>103</sup>. Seasonality: Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup> (2004<sup>1,2,3</sup>). Collections: BBSL. Conservation status: Vulnerable (National Research Council 2005, Shepherd 2005d). Floral records: ASTERACEAE: Achillea millefolium<sup>3</sup>
- 488. Hoplitis (Alcidamea) sambuci Titus, 1904. County records: Garfield<sup>1,2,3,46</sup>, Klickitat<sup>1,2</sup>, Spokane<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3,96,103</sup>. Seasonality: May<sup>1,2,3</sup>, Jun<sup>1,2,3,46</sup>, Jul<sup>1,2</sup>, Aug<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL, NMNH. Holotype. USA, Washington, Whitman County, Pullman; CV Piper; Type No. 66860, USNM ENT 00536520. Floral records: Sambucus glacua<sup>96</sup>
- **489.** †**‡** *Hoplitis* (*Alcidamea*) *spoliata* (Provancher, 1888). County records: Whitman<sup>1,3</sup>. Seasonality: Jul<sup>1,3</sup> (1908<sup>1,3</sup>). Collections: INHS
- **490.** † *Hoplitis* (*Alcidamea*) *uvulalis* (Cockerell, 1902). County records: Okanogan<sup>1,2</sup>. Seasonality: Aug<sup>1,2</sup> (2012<sup>1,2</sup>). Collections: BBSL
- **491.** *Hoplitis* (*Alcidamea*) *viridimicans* (Cockerell, 1897). County records: Thurston<sup>96,103</sup>. Collections: NMNH. Holotype. USA, Washington, Thurston County, Olympia
- **492.** *Hoplitis* (*Formicapis*) *robusta* (Nylander, 1848). County records: Chelan<sup>1,2,3</sup>, Garfield<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>. Seasonality: Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup> (2010<sup>1,2,3</sup>). Collections: BBSL
- 493. § Hoplitis (Proteriades) orthognatha (Griswold, 1983). County records: Asotin<sup>102,112</sup>. Seasonality: Jun<sup>102</sup> (1973<sup>102</sup>). Collections: WSUC. [= Proteriades orthognathus Griswold, 1983]. Holotype. USA, Washington, Asotin County, Fields Spring, 6.4 km S Anatone; 7 June 1973; M Jackson; WSUC No. 370. Conservation status: Vulnerable (Shepherd 2005e; National Research Council 2007)

## Genus Osmia Panzer

- 494. Osmia (Cephalosmia) californica Cresson, 1864. County records: Benton<sup>1,2,3</sup>, Chelan<sup>136</sup>, Franklin<sup>121,129</sup>, Grant<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Lincoln<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Spokane<sup>1,2</sup>, Stevens<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3,8</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2,3</sup>, May<sup>1,2,3,129</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup> (2015<sup>1,2</sup>). Collections: AMNH, BBSL, INHS, SEMC, WSUC. [= Osmia pascoensis Cockerell, 1897]. Paratype. USA, Washington, Franklin County, Pasco; May; Kincaid; Type No. 6868. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: APIACEAE: Lomatium<sup>8</sup>; ASTERACEAE: Arnica sororia<sup>3,59</sup>, Balsamorhiza sagittata<sup>8</sup>, Gaillardia aristata<sup>8</sup>, Senecio hydrophiloides<sup>3,59</sup>; FABACEAE: Lupinus sericeus<sup>59</sup>; GROSSULARIACEAE: Ribes aureum<sup>8</sup>
- **495.** † *Osmia* (*Cephalosmia*) *grinnelli* Cockerell, 1910. County records: Yakima<sup>7</sup>. Seasonality: May<sup>7</sup>, Aug<sup>7</sup> (2012<sup>7</sup>). Collections: WSUC
- **496.** *Osmia* (*Cephalosmia*) *marginipennis* Cresson, 1878. County records: Chelan<sup>3</sup>, Okanogan<sup>1,2,3,59</sup>, Stevens<sup>1,2</sup>, Whitman<sup>97</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jul<sup>1,2,3</sup> (2012<sup>1,2</sup>). Collections: BBSL, UCRC. Floral records: ROSACEAE: *Potentilla gracilis*<sup>3,59</sup>
- **497.** Osmia (Cephalosmia) montana Cresson, 1864. County records: Douglas<sup>7</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,4,59</sup>, Spokane<sup>1,2</sup>, Stevens<sup>1,2</sup>, Whitman<sup>8</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3,7</sup>, Aug<sup>1,2</sup> (2016<sup>1,2</sup>). Collections: BBSL, BugGuide, EMEC, SEMC, WSUC. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Arnica sororia<sup>59</sup>, Crepis atrabarba<sup>59</sup>, Erigeron speciosus<sup>3,59</sup>, Gaillardia aristata<sup>8</sup>, Senecio hydrophiloides<sup>59</sup>, S. triangularis<sup>59</sup>, Taraxacum officinale<sup>3,59</sup>; POLEMONIACEAE: Polemonium pulcherrimum<sup>3,59</sup>; ROSACEAE: Potentilla gracilis<sup>3,59</sup>, Rosa<sup>8</sup>
- **498.** Osmia (Cephalosmia) subaustralis Cockerell, 1900. County records: Clallam<sup>3</sup>, Okanogan<sup>1,2,3,4,59</sup>, Spokane<sup>1,2</sup>, Stevens<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>8</sup>. Seasonality: Apr<sup>1,2</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3,4</sup>, Aug<sup>1,2,3,4</sup> (2014<sup>1,2,3</sup>). Collections: BBSL, JRYA, WSUC. Conservation status: G5 Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Arnica cordifolia<sup>59</sup>, Erigeron speciosus<sup>3,59</sup>, Gaillardia aristata<sup>8</sup>, Packera cana<sup>3</sup>, Senecio<sup>59</sup>, S. triangularis<sup>59</sup>, Taraxacum officinale<sup>59</sup>; ROSACEAE: Fragaria virginiana ssp. platypetala<sup>59</sup>
- **499.** †§ *Osmia (Hapsidosmia) iridis* Cockerell and Titus, 1902. County records: Garfield<sup>7</sup>, Spokane<sup>1,2</sup>. Seasonality: May<sup>1,2</sup>, Jul<sup>7</sup> (2014<sup>1,2</sup>). Collections: BBSL, WSUC. Conservation status: G3 Vulnerable globally (NatureServe 2024)
- 500. †\* Osmia (Helicosmia) caerulescens (Linnaeus, 1758). County records: Clallam<sup>2</sup>, King<sup>1,2,3</sup>, Skamania<sup>1,2</sup>, Spokane<sup>2</sup>, Thurston<sup>1,2,3</sup>, Wahkiakum<sup>1,2</sup>, Yakima<sup>2</sup>. Seasonality: May<sup>1,2,3</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2</sup> (2019<sup>1,2</sup>). Collections: BBSL, BugGuide, iNaturalist. [= Osmia coerulescens (Linnaeus, 1758)]. Conservation status: G5 Secure globally (NatureServe 2024)
- 501. Osmia (Helicosmia) coloradensis Cresson, 1878. County records: Chelan<sup>1,2,3</sup>, Clallam<sup>3</sup>, Island<sup>1,2,3</sup>, King<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2,3</sup>, Lewis<sup>1,2,4</sup>,

Okanogan<sup>1,2,3,4,59</sup>, **Pierce**<sup>1,2,3</sup>, **Spokane**<sup>1,2,3</sup>, **Stevens**<sup>1,2</sup>, **Thurston**<sup>1,2,3</sup>, **Walla Walla**<sup>1,2,3</sup>, **Whatcom**<sup>1,2,3</sup>, Whitman<sup>1,2,3</sup>, **Yakima**<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3,4</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3,4</sup>, Aug<sup>1,2,3,4</sup> (2016<sup>1,2</sup>). Collections: BBSL, JRYA, PCYU, SEMC, WSUC. Conservation status: G4 – Apparently Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Achillea millefolium<sup>3,59</sup>, Agoseris glauca var. dasycephala<sup>59</sup>, Arnica cordifolia<sup>8</sup>, A. sororia<sup>59</sup>, Cirsium vulgare<sup>59</sup>, Erigeron speciosus<sup>3,59</sup>, Senecio<sup>3</sup>, S. hydrophiloides<sup>59</sup>, S. triangularis<sup>59</sup>, Taraxacum officinale<sup>3,59</sup>; FA-BACEAE: Trifolium repens<sup>8</sup>; POLEMONIACEAE: Polemonium pulcherrimum<sup>59</sup>

- **502.** † *Osmia* (*Helicosmia*) *texana* Cresson, 1872. County records: Asotin<sup>2,3</sup>, Clark<sup>1,2</sup>, Klickitat<sup>1,2</sup>, Pierce<sup>1,2,3,4</sup>, Wahkiakum<sup>1,2</sup>, Whitman<sup>1,4</sup>, Yakima<sup>7</sup>. Seasonality: May<sup>1,4</sup>, Jun<sup>1,3,4</sup>, Jul<sup>1</sup>, Aug<sup>7</sup> (2016<sup>1</sup>). Collections: BBSL, PCYU, WSUC. Conservation status: G5 Secure globally (NatureServe 2024)
- 503. Osmia (Melanosmia) aglaia Sandhouse, 1939. County records: Whitman<sup>32</sup>. Seasonality: May<sup>32</sup> (2012<sup>32</sup>). Conservation status: G5 Secure globally (Nature-Serve 2024)
- 504. Osmia (Melanosmia) albolateralis Cockerell, 1906. County records: Benton<sup>1,2,3</sup>, Chelan<sup>136</sup>, Garfield<sup>1,2,3,46</sup>, Kittitas<sup>2,3</sup>, Klickitat<sup>1,2</sup>, Lincoln<sup>2,3</sup>, Okanogan<sup>1,2,3,4,59</sup>, Skagit<sup>7</sup>, Skamania<sup>1,2</sup>, Spokane<sup>1,2</sup>, Stevens<sup>1,2</sup>, Wahkiakum<sup>1,2</sup>, Whitman<sup>1,2,3,6</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3,6,7</sup>, Jul<sup>1,2,3,7</sup>, Aug<sup>1,2,3,4</sup> (2016<sup>1,2</sup>). Collections: BBSL, SEMC, WSDA, WSUC. Conservation status: G5 Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Taraxacum officinale<sup>3,59</sup>; BORAGINACEAE: Myosotis laxa<sup>59</sup>; FABACEAE: Astragalus miser var. miser<sup>3,59</sup>; LAMIACEAE: Salvia dorrit<sup>3</sup>, PLANTAGINACEAE: Penstemon confertus<sup>3,59</sup>; POLEMONIACEAE: Polemonium pulcherrimum<sup>59</sup>
- 505. † Osmia (Melanosmia) atriventris Cresson, 1864. County records: Whitman<sup>2,3</sup>. Seasonality: (2003<sup>2,3</sup>). Collections: BBSL. Conservation status: G5 – Secure globally (NatureServe 2024)
- 506. Osmia (Melanosmia) atrocyanea Cockerell, 1897. County records: Chelan<sup>1,2,3</sup>, Clark<sup>1,2</sup>, Garfield<sup>1,2,3,46</sup>, Klickitat<sup>1,2,3</sup>, Lincoln<sup>2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2</sup>, Thurston<sup>1,2,129</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3,129</sup> (2015<sup>1,2</sup>). Collections: BBSL, NMNH, SEMC, WSUC. Holotype. USA, Washington, Thurston County, Olympia; 4 July 1896; Type No. 28209, USNM ENT 00536700. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Balsamorhiza sagittata<sup>8</sup>; FA-BACEAE: Astragalus bungeanus<sup>3</sup>, Lupinus polyphyllus<sup>8</sup>, Trifolium repens<sup>3,59</sup>, Vicia villosa<sup>8</sup>; PLANTAGINACEAE: Penstemon confertus<sup>3,59</sup>; ROSACEAE: Malus domestica<sup>8</sup>
- **507.** †§ *Osmia (Melanosmia) austromaritima* Michener, 1936. County records: Benton<sup>1,2</sup>, Spokane<sup>1,2</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2</sup>, Jun<sup>1,2</sup> (2014<sup>1,2</sup>). Collections: BBSL. [= *Osmia hurdi* White, 1952]. Conservation status: G3 Vulnerable globally (NatureServe 2024)
- **508.** † *Osmia (Melanosmia) bella* Cresson, 1878. County records: Grant<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2,3</sup>, Okanogan<sup>1,2,3</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>1,2,3</sup>. Seasonality: Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup> (2004<sup>1,2,3</sup>). Collections: BBSL
- **509.** Osmia (Melanosmia) brevis Cresson, 1864. County records: Kittitas<sup>2,3</sup>, Klickitat<sup>1,2,3</sup>, Okanogan<sup>1,2,3,4,59</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2</sup>, Whitman<sup>1,2,3,4,8</sup>, Yakima<sup>1,2,3</sup>. Seasonality: May<sup>1,2,3,4</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3,4</sup>, Aug<sup>1,2,3,4</sup> (2015<sup>1,2</sup>). Collections: BBSL, INHS, PCYU WSUC. Conservation status: G5 – Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Agoseris glauca var. dasycephala<sup>3,59</sup>, Erigeron speciosus<sup>59</sup>; FABACEAE: Trifolium repens<sup>8</sup>, Vicia villosa<sup>8</sup>; HYDROPHYL-LACEAE: Phacelia heterophylla<sup>8</sup>; PLANTAGINACEAE: Penstemon confertus<sup>3,59</sup>, P. serrulatus<sup>3</sup>, P. washingtonensis<sup>59</sup>
- 510. Osmia (Melanosmia) bruneri Cockerell, 1897. County records: Benton<sup>1,2,3</sup>, Chelan<sup>136</sup>, Columbia<sup>1,2,3</sup>, Garfield<sup>1,2,3,46</sup>, Grant<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Spokane<sup>1,2</sup>, Stevens<sup>1,2</sup>, Walla Walla<sup>3</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2,3</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup> (2015<sup>1,2</sup>). Collections: BBSL. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral record: FABACEAE: Astragalus<sup>3</sup>, Trifolium<sup>3</sup>; LAMIACEAE: Salvia dorrii<sup>3</sup>
- 511. Osmia (Melanosmia) bucephala Cresson, 1864. County records: Clark<sup>1,2</sup>, Gar-field<sup>1,2,3,46</sup>, Jefferson<sup>1,2</sup>, King<sup>1,2,3</sup>, Kitsap<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, San Juan<sup>1,2,3,136</sup>, Skamania<sup>1,2</sup>, Stevens<sup>1,2</sup>, Thurston<sup>40,129</sup>, Wahkiakum<sup>1,2</sup>, Whatcom<sup>7</sup>, Whitman<sup>1,2,3,40</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3,40</sup>, Jun<sup>1,2,3,7,40,129</sup>, Jul<sup>1,2,3</sup> (2017<sup>136</sup>). Collections: BBSL, CUIC, NMNH, SEMC, UCRC, WSUC. [= Osmia subornata Cockerell, 1897]. Paratype. USA, Washington, Thurston County, Olympia; 1 June 1894; Type No. 6879, USNM ENT 00536996. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: FABACEAE: Astragalus miser var. serotinus<sup>3</sup>, Lathyrus japonicus<sup>7,136</sup>; OLEACEAE: Syringa<sup>3</sup>
- **512.** †‡ *Osmia (Melanosmia) cahuilla* Cooper, 1993. County records: Pierce<sup>1,2,3</sup>. Seasonality: Jul<sup>1,2,3</sup> (1920<sup>1,2,3</sup>). Collections: BBSL. Conservation status: G4 Apparently Secure globally (NatureServe 2024)
- 513. Osmia (Melanosmia) calla Cockerell, 1897. County records: Benton<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Spokane<sup>1,2</sup>, Thurston<sup>129</sup>, Whitman<sup>1,2,3,6,8</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2,6</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2</sup> (2015<sup>1,2</sup>). Collections: BBSL, NMNH, WSDA, WSUC. Paratype. USA, Washington, Thurston County, Olympia; Kincaid; Type No. 6866. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: FABACEAE: Astragalus<sup>3</sup>, Vicia villosa<sup>8</sup>; HYDROPHYLLACEAE: Phacelia hastata<sup>3</sup>
- **514.** †‡ *Osmia (Melanosmia) cara* Cockerell, 1910. County records: Kittitas<sup>1,2,3</sup>. Seasonality: Jul<sup>1,2,3</sup> (1935<sup>1,2,3</sup>). Collections: BBSL
- 515. † Osmia (Melanosmia) cobaltina Cresson, 1878. County records: Chelan<sup>1,2,3</sup>, Franklin<sup>1,2,3</sup>, Grant<sup>1,2,3</sup>, Whitman<sup>2,3</sup>. Seasonality: Apr<sup>1,2,3</sup>, May<sup>1,2,3</sup> (1977<sup>1,2,3</sup>). Collections: BBSL, INHS
- 516. Osmia (Melanosmia) cyanella Cockerell, 1897. County records: Asotin<sup>3</sup>, Chelan<sup>1,2,3</sup>, King<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Thurston<sup>1,2,3,129</sup>, Yakima<sup>1,2,4</sup>. Seasonality: May<sup>1,2,3,4</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2</sup> (2012<sup>1,2</sup>). Collections: BBSL, EMEC, NMNH, UCRC. Type. USA, Washington, Thurston County, Olympia; May; Kincaid; Type No. 6364

- **517.** *Osmia* (*Melanosmia*) *cyanopoda* Cockerell, 1916. County records: Benton<sup>1,2,3</sup>, Garfield<sup>1,2,3,46</sup>, Walla Walla<sup>1,2</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3</sup> (2012<sup>1,2</sup>). Collections: BBSL. Floral records: FABACEAE: *Astragalus*<sup>3</sup>
- **518.** Osmia (Melanosmia) dakotensis Michener, 1937. County records: Benton<sup>1,2</sup>, Garfield<sup>1,2,46</sup>. Seasonality: May<sup>1,2</sup> (1998<sup>1,2</sup>). Collections: BBSL. [= Osmia (Melanosmia) cockerelli Sandhouse, 1939]. Conservation status: G4 Apparently Secure globally (NatureServe 2024)
- 519. † Osmia (Melanosmia) densa Cresson, 1864. County records: Chelan<sup>1,2,3</sup>, Clallam<sup>3</sup>, Garfield<sup>1,2,3</sup>, Island<sup>1,2,3</sup>, King<sup>1,2,3</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, San Juan<sup>1,2,3</sup>, Spokane<sup>1,2</sup>, Stevens<sup>1,2</sup>, Whatcom<sup>3</sup>, Whitman<sup>1,2,3</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup> (2016<sup>1,2</sup>). Collections: BBSL, JRYA, OSUC, UCRC. Conservation status: G5 Secure globally (NatureServe 2024). Floral records: FABACEAE: Onobrychis<sup>3</sup>, Trifolium repens<sup>3</sup>; MALVACEAE: Sidalcea oregana<sup>3</sup>
- 520. Osmia (Melanosmia) dolerosa Sandhouse, 1939. County records: Chelan<sup>3</sup>, Clallam<sup>3</sup>, King<sup>1,2,3,100</sup>, Kitsap<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3</sup>, Pacific<sup>1,2,3</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>2,3,100,136</sup>, Thurston<sup>100</sup>, Whitman<sup>3</sup>. Seasonality: Apr<sup>1,2,3</sup>, May<sup>1,2,3,100</sup>, Jun<sup>1,2,3,100</sup>, Jul<sup>1,2,3,100</sup>, Aug<sup>3</sup> (2017<sup>136</sup>). Collections: BBSL, JRYA, SEMC, UCRC. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: FA-BACEAE: *Trifolium hybridum*<sup>3</sup>; ROSACEAE: *Rubus bifrons*<sup>136</sup>, *R. ursinus*<sup>3</sup>
- 521. † Osmia (Melanosmia) ednae Cockerell, 1907. County records: Spokane<sup>1,2</sup>, Whitman<sup>1,2,4</sup>. Seasonality: May<sup>1,2,4</sup> (2014<sup>1,2</sup>). Collections: BBSL, PCYU. Conservation status: G4 Apparently Secure globally (NatureServe 2024)
- **522.** Osmia (Melanosmia) exigua Cresson, 1878. County records: Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,59</sup>, **Spokane**<sup>1,2</sup>, **Stevens**<sup>1,2</sup>, Thurston<sup>133</sup>, **Yakima**<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2,3</sup>, May<sup>1,2,133</sup>, Jun<sup>1,2,3,133</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2</sup> (2019<sup>133</sup>). Collections: BBSL. Floral records: ASTERACEAE: Hypochaeris radicata<sup>133</sup>; CAPRIFOLIACEAE: Plectritis congesta<sup>133</sup>; FABACEAE: Lupinus albicaulis<sup>133</sup>, L. lepidus<sup>133</sup>, Trifolium repens<sup>3,59</sup>
- 523. Osmia (Melanosmia) giliarum Cockerell, 1906. County records: Adams<sup>2,101</sup>, King<sup>101</sup>, Kittitas<sup>1,2</sup>, Klickitat<sup>1,2</sup>, Thurston<sup>101</sup>, Walla Walla<sup>1,2,101</sup>, Whitman<sup>1,2,101</sup>, Yakima<sup>1,2,101</sup>. Seasonality: May<sup>1,2,101</sup>, Jun<sup>1,2,101</sup>, Jul<sup>1,2,101</sup> (2012<sup>1,2</sup>). Collections: BBSL, SEMC. [= Osmia physariae Cockerell, 1907]. Conservation status: G4 Apparently Secure globally (NatureServe 2024)
- **524.** †**‡** *Osmia* (*Melanosmia*) *grindeliae* Cockerell, 1910. County records: Chelan<sup>1,2,3</sup>. Seasonality: Jul<sup>1,2,3</sup> (1930<sup>1,2,3</sup>). Collections: BBSL. Conservation status: G4 Apparently Secure globally (NatureServe 2024)
- **525.** *Osmia* (*Melanosmia*) *inermis* (Zetterstedt, 1838). County records: King<sup>1,2,3,31</sup>. Collections: BBSL. Conservation status: G5 Secure globally (NatureServe 2024)
- **526.** Osmia (Melanosmia) integra Cresson, 1878. County records: Adams<sup>7</sup>, Benton<sup>1,2,3</sup>, Chelan<sup>1,2,3</sup>, Garfield<sup>1,2,3,46</sup>, Grant<sup>1,2,3,4</sup>, Kittitas<sup>1,2,3</sup>, Walla Walla<sup>1,2,3,101</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2,3,7,101</sup>, May<sup>1,2,3,4,101</sup> (2014<sup>1,2</sup>). Collections: BBSL, LACM, PCYU, WSUC. Conservation status: G5 Secure globally (NatureServe 2024). Floral records: FABACEAE: Astragalus bungeanus<sup>3</sup>; LAMIACEAE: Salvia dorrit<sup>3</sup>

- **527.** † *Osmia* (*Melanosmia*) *inurbana* Cresson, 1878. County records: Garfield<sup>1,2,3</sup>, Thurston<sup>133</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3</sup>. Seasonality: May<sup>1,2,3,133</sup>, Jun<sup>1,2,3,133</sup>, Jul<sup>133</sup> (2020<sup>133</sup>). Collections: BBSL, SEMC. Conservation status: G4 – Apparently Secure globally (NatureServe 2024). Floral records: ASPARAGACEAE: *Camassia quamash*<sup>133</sup>; ASTERACEAE: *Crepis capillaris*<sup>133</sup>, *Hypochaeris radicata*<sup>133</sup>; CAPRIFOLIACEAE: *Plectritis congesta*<sup>133</sup>; FABACEAE: *Lupinus bicolor*<sup>133</sup>, *L. lepidus*<sup>133</sup>; HYPERICACEAE: *Hypericum perforatum*<sup>133</sup>; ROSACEAE: *Potentilla gracilis*<sup>133</sup>
- 528. Osmia (Melanosmia) juxta Cresson, 1864. County records: Asotin<sup>7</sup>, Chelan<sup>1,2,3</sup>, Ferry<sup>3</sup>, King<sup>1,2,3</sup>, Kittitas<sup>3</sup>, Klickitat<sup>1,2</sup>, Lewis<sup>1,2,4</sup>, Okanogan<sup>1,2,3,4,59</sup>, San Juan<sup>1,2,3</sup>, Spokane<sup>1,2</sup>, Stevens<sup>1,2,3</sup>, Thurston<sup>1,2,3</sup>, Whitman<sup>6</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3,4</sup>, Jun<sup>1,2,3,4,6,7</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3,4</sup> (2015<sup>1,2</sup>). Collections: BBSL, EMEC, LACM, OSUC, PCYU, UCRC, WSDA, WSUC. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Arnica cordifolia<sup>59</sup>, Erigeron speciosus<sup>3,59</sup>, Microseris nutans<sup>59</sup>, Taraxacum officinale<sup>59</sup>; FABACEAE: Trifolium repens<sup>3,59</sup>; HYDROPHYLLACEAE: Phacelia leptosepala<sup>59</sup>; ONAGRACEAE: Chamerion angustifolium ssp. angustifolium<sup>8</sup>; PLANTAGINACEAE: Penstemon confertus<sup>3,59</sup>
- 529. Osmia (Melanosmia) kincaidii Cockerell, 1897. County records: Benton<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2</sup>, Pierce<sup>1,2,3</sup>, Skagit<sup>1,2,3</sup>, Spokane<sup>1,2</sup>, Stevens<sup>1,2</sup>, Thurston<sup>1,2,3,129</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2</sup> (2016<sup>1,2</sup>). Collections: BBSL, NMNH, WSUC. Lectotype. USA, Washington, Thurston County, Olympia; 2 June 1894; Type No. 3710, USNM ENT 00536951. Paratype. USA, Washington, Thurston County, Olympia; Kincaid; Type No. 6867. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: HYDROPHYLLACEAE: Phacelia heterophylla<sup>8</sup>; PLANTAGINACEAE: Collinsia parviflora<sup>8</sup>
- 530. † Osmia (Melanosmia) laeta Sandhouse, 1924. County records: Klickitat<sup>1,2</sup>, Okanogan<sup>2,4</sup>. Seasonality: Jun<sup>1,2</sup>, Jul<sup>2,4</sup>, Aug<sup>2,4</sup> (2012<sup>1,2</sup>). Collections: BBSL. Conservation status: G4 Apparently Secure globally (NatureServe 2024)
- 531. †\$‡ Osmia (Melanosmia) lanei Sandhouse, 1939. County records: Yakima<sup>1,2,3</sup>. Seasonality: Jun<sup>1,2,3</sup> (1927<sup>1,2,3</sup>). Collections: NMNH. Holotype. USA, Washington, Yakima County, Naches River; 8 June 1927; MC Lane; Type No 52872, USNM ENT 00536953. Conservation status: G3 Vulnerable globally, possibly extirpated in Washington (NatureServe 2024)
- 532. Osmia (Melanosmia) longula Cresson, 1864. County records: Benton<sup>1,2,3</sup>, Chelan<sup>136</sup>, Kittitas<sup>1,2,3</sup>, Okanogan<sup>1,2,3,4,59</sup>, Spokane<sup>1,2</sup>, Thurston<sup>129</sup>, Whitman<sup>1,2,6</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2,3</sup>, May<sup>129</sup>, Jun<sup>1,2,3,6</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3,4</sup> (2018<sup>1,2,3</sup>). Collections: BBSL, iNaturalist, WSDA. [= Osmia grandior Cockerell, 1897]. Paratype. USA, Washington, Thurston County, Olympia; 10 May 1894; Kincaid; Type No. 6869, USNM ENT 00536934. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: FABACEAE: Astragalus columbianus<sup>3</sup>, A. miser var. miser<sup>59</sup>; PLANTAGINACEAE: Penstemon washingtonensis<sup>3,59</sup>

- 533. † Osmia (Melanosmia) malina Cockerell, 1909. County records: Chelan<sup>1,2,3</sup>, Clallam<sup>1,2,3</sup>, King<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Wahkiakum<sup>1,2</sup>. Seasonality: May<sup>1,2,3</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2</sup> (2011<sup>1,2</sup>). Collections: BBSL, OSUC. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: MALVACEAE: Sidalcea oregana<sup>3</sup>
- **534.** *Osmia* (*Melanosmia*) *melanopleura* Cockerell, 1916. County records: Klickitat<sup>1,2</sup>, Spokane<sup>1,2</sup>, Stevens<sup>1,2</sup>, Whitman<sup>1,2,3,40</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3,40</sup>, Jun<sup>1,2</sup> (2016<sup>1,2</sup>). Collections: BBSL, INHS, SEMC. [= *Osmia bakeri* Sandhouse, 1924]
- 535. Osmia (Melanosmia) nanula Cockerell, 1897. County records: King<sup>1,2,3,100,129</sup>, Okanogan<sup>1,2</sup>, Skamania<sup>1,2</sup>, Spokane<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3,8</sup>. Seasonality: May<sup>1,2,3,129</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2</sup>, Aug<sup>1,2</sup> (2016<sup>1,2</sup>). Collections: BBSL, INHS, NMNH, SEMC, WSUC. Type. USA, Washington, King County, Seattle; 19 May 1896; Type No. 6865, USNM ENT 00536968. [= Osmia phaceliae Cockerell, 1907]. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: GERANIACEAE: Geranium viscosissimum<sup>8</sup>; RANUNCULACEAE: Ranunculus<sup>8</sup>
- **536.** Osmia (Melanosmia) nemoris Sandhouse, 1924. County records: Benton<sup>1,2</sup>, Klickitat<sup>1,2</sup>, Spokane<sup>1,2</sup>, Thurston<sup>1,2</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3,8</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2</sup>, Aug<sup>1,2</sup> (2014<sup>1,2</sup>). Collections: BBSL, MCZ, SEMC, WSUC. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Arnica cordifolia<sup>8</sup>, Balsamorhiza sagittata<sup>8</sup>
- **537.** ‡ *Osmia (Melanosmia) nifoata* Cockerell, 1909. County records: Whitman<sup>1,2,3,101</sup>, Yakima<sup>1,2,3,101</sup>. Seasonality: Jun<sup>101</sup>, Jul<sup>1,2,3,101</sup> (1904<sup>101</sup>). Collections: BBSL, SEMC, WSUC. Conservation status: G4 – Apparently Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Senecio<sup>3</sup>
- **538.** *Osmia* (*Melanosmia*) *nigrifrons* Cresson, 1878. County records: Adams<sup>7</sup>, Benton<sup>1,2,3</sup>, Garfield<sup>1,2,3,46</sup>, King<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Stevens<sup>1,2</sup>, Whitman<sup>1,2,3,8,101</sup>. Seasonality: Apr<sup>1,2,3</sup>, May<sup>1, 2,3,7,101</sup>, Jun<sup>1,2,3,101</sup> (2012<sup>1,2</sup>). Collections: AMNH, BBSL, EMEC, WSUC. Conservation status: G5 Secure globally (NatureServe 2024). Floral records: ASTERACEAE: *Balsamorhiza sagittata*<sup>8</sup>; FABACEAE: *Astragalus*<sup>3</sup>, *Trifolium*<sup>3</sup>, *Vicia villosa*<sup>8</sup>
- **539.** *Osmia* (*Melanosmia*) *nigriventris* (Zetterstedt, 1838). County records: Okanogan<sup>1,2,3,31,59</sup>, Pierce<sup>1,2,3</sup>, Stevens<sup>1,2</sup>, Whatcom<sup>1,2,3</sup>. Seasonality: Jun<sup>1,2</sup>, Jul<sup>1,2,3,31</sup> (2014<sup>1,2</sup>). Collections: BBSL. Conservation status: G4 Apparently Secure globally (NatureServe 2024)
- **540. §‡** *Osmia (Melanosmia) nigrobarbata* Cockerell, 1916. County records: Walla Walla<sup>1,2,3,101</sup>. Seasonality: May<sup>1,2,3,101</sup> (1937<sup>1,2,3,101</sup>). Collections: SEMC. Conservation status: G3 Vulnerable globally (NatureServe 2024)
- 541. †§ Osmia (Melanosmia) obliqua White, 1952. County records: Klickitat<sup>1,2</sup>, Spokane<sup>1,2</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2</sup> (2014<sup>1,2</sup>). Collections: BBSL. Conservation status: G3 Vulnerable globally (NatureServe 2024)
- 542. § Osmia (Melanosmia) odontogaster Cockerell, 1897. County records: King<sup>1,2,3</sup>, Okanogan<sup>1,2,3,59</sup>, Thurston<sup>1,2,3,101,129</sup>, Whitman<sup>1,2,3,101</sup>. Seasonality: Apr<sup>1,2</sup>,

May<sup>1,2,3,101</sup>, Jun<sup>1,2,3,101</sup>, Jul<sup>1,2,3</sup> (2004<sup>1,2,3,59</sup>). Collections: BBSL, NMNH, SEMC. **Paratype**. USA, Washington, Thurston County, Olympia; Kincaid; Type No. 3709. Conservation status: G2 – Imperiled globally (NatureServe 2024). Floral records: ASTERACEAE: *Erigeron nivalis*<sup>59</sup>, *Senecio hydrophiloides*<sup>3,59</sup>; FABACEAE: *Trifolium pratense*<sup>59</sup>, *T. repens*<sup>3,59</sup>; ROSACEAE: *Potentilla gracilis*<sup>3,59</sup>, *Rubus ursinus*<sup>3</sup>

- 543. Osmia (Melanosmia) paradisica Sandhouse, 1924. County records: Chelan<sup>3</sup>, Okanogan<sup>1,2,3,4,59</sup>, Pierce<sup>1,2,3</sup>, Skagit<sup>3</sup>, Stevens<sup>1,2</sup>, Whatcom<sup>3</sup>. Seasonality: Jun<sup>1,2</sup>, Jul<sup>1,2,3,4</sup>, Aug<sup>1,2,3,4</sup> (2016<sup>1,2</sup>). Collections: BBSL, JRYA. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Anaphalis margaritacea<sup>3,59</sup>, Erigeron speciosus<sup>3,59</sup>, Senecio integerrimus<sup>59</sup>; CRASSU-LACEAE: Sedum lanceolatum<sup>59</sup>; FABACEAE: Lupinus<sup>3,59</sup>; PLANTAGINACEAE: Penstemon washingtonensis<sup>59</sup>; POLEMONIACEAE: Polemonium pulcherrimum<sup>59</sup>; ROSACEAE: Potentilla gracilis<sup>3,59</sup>
- 544. Osmia (Melanosmia) pentstemonis Cockerell, 1906. County records: Clallam<sup>3</sup>, Kittitas<sup>2,3</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,4,59</sup>, Pierce<sup>1,2,3</sup>, Stevens<sup>1,2</sup>, Whitman<sup>1,2,3,8</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Jun<sup>1,2,3</sup>, Jul<sup>1,2,3,4</sup>, Aug<sup>1,2,3,4</sup>, Sep<sup>3</sup> (2016<sup>1,2</sup>). Collections: BBSL, JRYA, SEMC, WSUC. Conservation status: G5 – Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Erigeron speciosus<sup>59</sup>, Senecio triangularis<sup>59</sup>, Taraxacum officinale<sup>59</sup>; FABACEAE: Trifolium repens<sup>3,59</sup>; ONA-GRACEAE: Gayophytum diffusum ssp. parviflorum<sup>3,59</sup>; PLANTAGINACEAE: Penstemon albertinus<sup>8</sup>, P. serrulatus<sup>3</sup>, P. washingtonensis<sup>59</sup>; ROSACEAE: Fragaria virginiana ssp. platypetala<sup>59</sup>
- 545. Osmia (Melanosmia) pikei Cockerell, 1907. County records: King<sup>1,2,3,40</sup>, Okanogan<sup>1,2,3,59</sup>, Thurston<sup>40</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jul<sup>1,2,3</sup> (2004<sup>1,2,3,59</sup>). Collections: BBSL, EMEC. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: ASTERACEAE: *Balsamorhiza sagittata*<sup>8</sup>; ROSACEAE: *Rubus ursinus*<sup>3</sup>
- 546. Osmia (Melanosmia) proxima Cresson, 1864. County records: Clark<sup>1,2</sup>, Garfield<sup>1,2,3,46</sup>, Jefferson<sup>1,2</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,59</sup>, San Juan<sup>136</sup>, Skamania<sup>1,2</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2</sup>, Wahkiakum<sup>1,2</sup>, Whitman<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2</sup>, Aug<sup>1,2,3</sup> (2017<sup>136</sup>). Collections: BBSL. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: CONVOL-VULACEAE: Calystegia soldanella<sup>136</sup>; FABACEAE: Astragalus miser<sup>3</sup>; ROSACEAE: Rubus bifrons<sup>136</sup>
- 547. †§ Osmia (Melanosmia) pulsatillae Cockerell, 1907. County records: King<sup>1,2,3</sup>, Whitman<sup>1,2,3</sup>. Seasonality: May<sup>1,2</sup> (2003<sup>1,2,3</sup>). Collections: BBSL, OSUC, SEMC. Conservation status: G2 Imperiled globally (NatureServe 2024)
- 548. Osmia (Melanosmia) pusilla Cresson, 1864. County records: Benton<sup>1,2,3</sup>, Clallam<sup>3</sup>, Clark<sup>1,2</sup>, Cowlitz<sup>1,2,3</sup>, Garfield<sup>1,2,3,46</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,4,59</sup>, Pierce<sup>1,2,3</sup>, Skamania<sup>1,2</sup>, Spokane<sup>1,2</sup>, Stevens<sup>1,2</sup>, Whatcom<sup>1,2,3</sup>, Whitman<sup>1,2,3,6</sup>. Seasonality: May<sup>1,2,3</sup>, Jun<sup>1,2,3,6</sup>, Jul<sup>1,2,3,4,6</sup>, Aug<sup>1,2,3</sup>, Sep<sup>1,2</sup> (2016<sup>1,2</sup>). Collections: BBSL, INHS, JRYA, WSDA. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Anaphalis margaritacea<sup>3,59</sup>,

*Erigeron speciosus*<sup>3,59</sup>, *Taraxacum officinale*<sup>59</sup>; BORAGINACEAE: *Myosotis laxa*<sup>59</sup>; FABACEAE: *Astragalus chaborasicus*<sup>3</sup>, *Lupinus sericeus*<sup>59</sup>, *Onobrychis*<sup>3</sup>, *Trifolium repens*<sup>3,59</sup>; HYDROPHYLLACEAE: *Phacelia leptosepala*<sup>59</sup>; PLANTAGINACE-AE: *Penstemon confertus*<sup>59</sup>; POLEMONIACEAE: *Polemonium pulcherrimum*<sup>59</sup>; ROSACEAE: *Fragaria virginiana ssp. platypetala*<sup>3,59</sup>, *Potentilla gracilis*<sup>3,59</sup>

- **549.** *Osmia* (*Melanosmia*) *raritatis* Michener, 1957. County records: Klickitat<sup>1,2</sup>, **Spokane**<sup>1,2</sup>, Yakima<sup>40</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,40</sup> (2012<sup>1,2</sup>). Collections: BBSL. Conservation status: G4 Apparently Secure globally (NatureServe 2024)
- 550. † Osmia (Melanosmia) rawlinsi Sandhouse, 1939. County records: Chelan<sup>1,2,3</sup>, Grant<sup>1,2,3</sup>, Walla Walla<sup>1,2</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2,3</sup>, May<sup>1,2,3</sup> (2012<sup>1,2</sup>). Collections: BBSL. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: LAMIACEAE: Salvia dorrii<sup>3</sup>
- 551. Osmia (Melanosmia) regulina Cockerell, 1911. County records: Garfield<sup>1,2,3,46</sup>, Klickitat<sup>1,2</sup>, Walla Walla<sup>1,2,3,71</sup>. Seasonality: Jun<sup>1,2,3</sup>, Aug<sup>1,2,3</sup> (2012<sup>1,2</sup>). Collections: BBSL. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: FABACEAE: Astragalus cicer<sup>3</sup>
- **552.** Osmia (Melanosmia) sculleni Sandhouse, 1939. County records: Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,59</sup>, Spokane<sup>1,2</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2</sup>, Jun<sup>1,2</sup>, Jul<sup>1,2</sup>, Aug<sup>1,2,3</sup> (2015<sup>1,2</sup>). Collections: BBSL. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Arnica cordifolia<sup>3,59</sup>
- 553. † Osmia (Melanosmia) sedula Sandhouse, 1924. County records: Klickitat<sup>1,2</sup>, Thurston<sup>1,2</sup>. Seasonality: May<sup>1,2</sup>, Jun<sup>1,2</sup> (2011<sup>1,2</sup>). Collections: BBSL. [= Osmia claremontensis Michener, 1936]. Conservation status: G5 Secure globally (NatureServe 2024)
- 554. Osmia (Melanosmia) simillima Smith, 1853. County records: Clallam<sup>3</sup>, Garfield<sup>1,2,3,46</sup>, Island<sup>1,2,3</sup>, Jefferson<sup>1,2</sup>, King<sup>1,2,3</sup>, Pacific<sup>1,2,3</sup>, Spokane<sup>1,2</sup>, Stevens<sup>1,2</sup>, Thurston<sup>1,2,3</sup>, Whatcom<sup>7</sup>, Whitman<sup>1,2,3,6</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3</sup>, Jun<sup>1,2,3,67</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3</sup> (2016<sup>1,2</sup>). Collections: BBSL, EMEC, JRYA, SEMC, WSDA, WSUC. Conservation status: G5 – Secure globally (NatureServe 2024). Floral records: FA-BACEAE: Astragalus chaborasicus<sup>3</sup>, Lathyrus japonicus<sup>7</sup>, Trifolium repens<sup>3</sup>
- **555.** Osmia (Melanosmia) tanneri Sandhouse, 1939. County records: Okanogan<sup>1,2,3,4,59</sup>. Seasonality: Jul<sup>1,2,3,4</sup>, Aug<sup>1,2</sup> (2004<sup>1,2,3,4,59</sup>). Collections: BBSL. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: FABACEAE: Oxytropis campestris var. cusickii<sup>59</sup>; PLANTAGINACEAE: Penstemon washingtonensis<sup>59</sup>; POLEMONIACEAE: Polemonium pulcherrimum<sup>59</sup>; ROSACEAE: Dryas hookeriana<sup>59</sup>
- **556.** †§ *Osmia (Melanosmia) thysanisca* Michener, 1957. County records: Whitman<sup>7</sup>, Yakima<sup>1,2</sup>. Seasonality: Apr<sup>7</sup>, Jul<sup>1,2</sup> (1973<sup>7</sup>). Collections: SEMC, WSUC. Conservation status: G3 – Vulnerable globally (NatureServe 2024)
- 557. Osmia (Melanosmia) trevoris Cockerell, 1897. County records: Benton<sup>1,2,3</sup>, Clark<sup>1,2</sup>, Columbia<sup>1,2,3</sup>, Franklin<sup>97</sup>, Garfield<sup>1,2,3,4,46</sup>, King<sup>1,2,3,129</sup>, Kittitas<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Okanogan<sup>1,2,3,4,59</sup>, Skamania<sup>1,2</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2</sup>, Thurston<sup>1,2,3</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3,6,7</sup>. Seasonality: Apr<sup>1,2,3</sup>, May<sup>1,2,3,4,129</sup>, Jun<sup>1,2,3,4,67</sup>,

Jul<sup>1,2,3,6</sup>, Aug<sup>1,2,3,4</sup> (2016<sup>1,2</sup>). Collections: BBSL, INHS, NMNH, PCYU, SEMC, WSDA, WSUC. **Type**. USA, Washington, King County, Seattle; 19 May 1896; Type No. 1895, USNM ENT 00537003. Conservation status: G5 – Secure globally (NatureServe 2024). Floral records: ASTERACEAE: *Erigeron corymbosus*<sup>3,59</sup>, *E. speciosus*<sup>3,59</sup>; FABACEAE: *Astragalus*<sup>3</sup>

- 558. †\$ Osmia (Melanosmia) trifoliama Sandhouse, 1939. County records: Klickitat<sup>1,2</sup>, San Juan<sup>1,2,3</sup>. Seasonality: Jul<sup>1,2</sup>, Aug<sup>1,2</sup> (2011<sup>1,2</sup>). Collections: BBSL, PWRC. Conservation status: G3 – Vulnerable globally, possibly extirpated in Washington (NatureServe 2024)
- 559. Osmia (Melanosmia) tristella Cockerell, 1897. County records: Chelan<sup>3</sup>, Clallam<sup>1,2,3</sup>, King<sup>1,2,3</sup>, Okanogan<sup>1,2,3,459</sup>, Pierce<sup>1,2,3</sup>, Spokane<sup>1,2</sup>, Stevens<sup>1,2</sup>, Thurston<sup>1,2,3,129</sup>, Walla Walla<sup>7</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Jan<sup>1,2</sup>, Mar<sup>1,2</sup>, Apr<sup>1,2,3</sup>, May<sup>1,2,3,7</sup>, Jun<sup>1,2,3</sup>, Jul<sup>1,2,3</sup>, Aug<sup>1,2,3,4</sup> (2015<sup>1,2</sup>). Collections: BBSL, EMEC, JRYA, NMNH, WSUC. Type. USA, Washington, Thurston County, Olympia; Kincaid; Type No. 6863, USNM ENT 00537005. Conservation status: G4 Apparently Secure globally (NatureServe 2024). Floral records: ASTERACEAE: Agoseris glauca var. dasycephala<sup>59</sup>, Arnica cordifolia<sup>59</sup>, Erigeron speciosus<sup>3,59</sup>, Senecio triangularis<sup>59</sup>, Taraxacum officinale<sup>59</sup>; FABACEAE: Lupinus<sup>59</sup>, Trifolium pratense<sup>3,59</sup>, T. repens<sup>59</sup>; HYDRO-PHYLLACEAE: Phacelia leptsepala<sup>59</sup>; ONAGRACEAE: Gayophytum diffusum spp. parviflorum<sup>3,59</sup>; OROBRANCHACEAE: Castilleja miniata<sup>59</sup>; PLANTAGINACE-AE: Penstemon<sup>3</sup>, P. confertus<sup>59</sup>; POLEMONIACEAE: Polemonium pulcherrimum<sup>3,59</sup>; ROSACEAE: Fragaria virginiana ssp. platypetala<sup>59</sup>, Potentilla gracilis<sup>59</sup>
- 560. Osmia (Melanosmia) unca Michener, 1937. County records: Benton<sup>1,2</sup>, Garfield<sup>46</sup>, Walla Walla<sup>1,2,3</sup>, Whitman<sup>1,2,3,101</sup>. Seasonality: Apr<sup>1,2</sup>, May<sup>1,2,3,101</sup>, Jun<sup>1,2,3</sup> (2014<sup>1,2</sup>). Collections: BBSL, SEMC. Conservation status: G4 Apparently Secure globally (NatureServe 2024)
- 561. Osmia (Melanosmia) vandykei Sandhouse, 1924. County records: Benton<sup>1,2</sup>, Klickitat<sup>1,2</sup>, Spokane<sup>1,2</sup>, Whitman<sup>1,2,3,40</sup>. Seasonality: Mar<sup>1,2,3</sup>, Apr<sup>1,2</sup>, May<sup>1,2</sup>, Jun<sup>1,2</sup> (2016<sup>1,2</sup>). Collections: BBSL, SEMC. Conservation status: G4 – Apparently Secure globally (NatureServe 2024)
- 562. †\* Osmia (Osmia) cornifrons (Radoszkowski, 1887). County records: King<sup>2</sup>, Thurston<sup>1,2</sup>. Seasonality: Mar<sup>1,2</sup>, Apr<sup>2</sup> (2021<sup>1,2</sup>). Collections: BugGuide, iNaturalist. Conservation status: G5 Secure globally (NatureServe 2024)
- 563. Osmia (Osmia) lignaria Say, 1837. County records: Adams<sup>3</sup>, Chelan<sup>1,2,3</sup>, Clallam<sup>1,2,3</sup>, Clark<sup>1,2</sup>, Cowlitz<sup>1,2</sup>, Ferry<sup>2</sup>, Grant<sup>1,2,3</sup>, Island<sup>1,2,3</sup>, Jefferson<sup>1,2</sup>, King<sup>1,2,3</sup>, Kitsap<sup>1,2,3</sup>, Klickitat<sup>1,2</sup>, Mason<sup>1,2</sup>, Okanogan<sup>1,2,3</sup>, Pacific<sup>1,2,3</sup>, Pierce<sup>1,2,3</sup>, San Juan<sup>1,2,3</sup>, Skagit<sup>2,3,10</sup>, Snohomish<sup>1,2,3</sup>, Spokane<sup>1,2,3</sup>, Stevens<sup>1,2,3</sup>, Thurston<sup>1,2,3,6,133</sup>, Walla Walla<sup>2,3</sup>, Whatcom<sup>1,2,3</sup>, Whitman<sup>1,2,3</sup>, Yakima<sup>1,2,3</sup>. Seasonality: Feb<sup>1,2</sup>, Mar<sup>1,2,3</sup>, Apr<sup>1,2,3</sup>, May<sup>1,2,3,133</sup>, Jun<sup>1,2,3,6</sup>, Jul<sup>1,2</sup>, Aug<sup>1,2,3</sup>, Nov<sup>3</sup>, Dec<sup>1,2</sup> (2022<sup>1,2</sup>). Collections: BBSL, BugGuide, CUIC, iNaturalist, INHS, NCSU, PMNH, SEMC, UCMC, WSDA, WSUC. Conservation status: G5 Secure globally (NatureServe 2024). Floral records: ASPARA-GACEAE: Camassia quamash<sup>133</sup>; ASTERACEAE: Arnica cordifolia<sup>8</sup>, Taraxacum<sup>3</sup>; FABACEAE: Astragalus sinuatus<sup>3</sup>; HYDROPHYLLACEAE: Phacelia heterophylla<sup>8</sup>

## Genus Protosmia Ducke

564. Protosmia (Chelostomopsis) rubifloris (Cockerell, 1898). County records: Chelan<sup>1,2,130</sup>, King<sup>1,2,96</sup>, Okanogan<sup>1,2</sup>, Thurston<sup>1,2,104</sup>. Seasonality: Apr<sup>130,104</sup>, May<sup>1,2</sup>, Jun<sup>1,2</sup> (2021<sup>1,2</sup>). Collections: BBSL, iNaturalist, NMNH. [= Chelynia rubifloris Cockerell, 1898]. Holotype. USA, Washington, King County, Seattle. Floral records: BORAGINACEAE: Hackelia venusta<sup>7</sup>

## Melittidae: Melittinae: Macropidini

## Genus Macropis Panzer

565. §‡ *Macropis* (*Macropis*) *steironematis opaca* Michener, 1938. County records: Yakima<sup>1,2,45,112</sup>. Seasonality: Jul<sup>1,2,45,112</sup> (1882<sup>1,2,45,112</sup>). Collections: MCZ. Holotype. USA, Washington Territory, Yakima River, Morgan's Ferry; 1 July 1882; MCZ Type 23415, MCZ-ENT 00023415. Conservation status: Critically Endangered (National Research Council 2007)

## Bee species likely to occur in Washington

## Andrenidae

Andrena (Achandrena) angustella Cockerell, 1936 Andrena (Andrena) edwardsi Viereck, 1916 Andrena (Callandrena) vulpicolor Cockerell, 1897 Andrena (Cnemidandrena) apacheorum Cockerell, 1897 Andrena (Derandrena) vandykei Cockerell, 1936 Andrena (Diandrena) ablegata (Cockerell, 1922) Andrena (Melandrena) regularis Malloch, 1917 Andrena (Parandrena) concinnula Cockerell, 1898 Andrena (Parandrena) gibberis Viereck, 1924 Andrena (Parandrena) papagorum Viereck & Cockerell, 1914 Andrena (Ptilandrena) penemisella LaBerge & Ribble, 1975 Andrena (Scaphandrena) cruciferarum Ribble, 1974 Andrena (Scaphandrena) plana Viereck, 1904 Calliopsis (Nomadopsis) anthidius Fowler, 1899 Panurginus beardsleyi (Cockerell, 1904) Perdita (Perdita) claypolei limatula Timberlake, 1962<sup>\*</sup> Perdita (Perdita) exclamans Cockerell, 1895

<sup>\*</sup> We are aware of unpublished records for these species in Washington which could not be included in this checklist.

Perdita (Perdita) fallax Cockerell, 1896 Perdita (Perdita) nuda Cockerell, 1896 Perdita (Perdita) oreophila Timberlake, 1964 Perdita (Perdita) stottleri Cockerell, 1896 Perdita (Perdita) subfasciata Cockerell, 1897 Perdita (Perdita) zebrata Cresson, 1878 Perdita (Pygoperdita) mormonica Timberlake, 1956 Protandrena (Pterosarus) innuptus (Cockerell, 1896) Protandrena (Pterosarus) irregularis (Cockerell, 1922)

## Apidae

Anthophora (Micranthophora) maculifrons Cresson, 1879 Anthophora (Pyganthophora) lesquerellae (Cockerell, 1896) Biastes (Neopasites) fulviventris (Cresson, 1878)\* Bombus (Psithyrus) variabilis (Cresson, 1872)\* Eucera (Synhalonia) chrysophila (Cockerell, 1914) Eucera (Synhalonia) cordleyi (Viereck, 1905) Melecta edwardsii Cresson, 1879 Melissodes (Callimelissodes) lustrus LaBerge, 1961 Melissodes (Callimelissodes) minusculus LaBerge, 1961 Melissodes (Callimelissodes) nigracauda LaBerge, 1961\* Melissodes (Eumelissodes) confusus Cresson, 1878 Melissodes (Melissodes) tepidus yumensis LaBerge, 1956 Nomada accepta Cresson, 1878 Nomada calloxantha Cockerell, 1921 Nomada citrina rufula Cockerell, 1903 Nomada depressa Cresson, 1863 Nomada erythraea Dalla Torre, 1896 Nomada hemphilli Cockerell, 1903 Nomada opposita Cresson, 1878<sup>\*\*\*</sup> Nomada scitiformis Cockerell, 1903 Nomada taraxacella Cockerell, 1903 Nomada ultimella Cockerell, 1903 Nomada valida Smith, 1854 Nomada vicinalis vicinalis Cresson, 1878

<sup>\*\*</sup> Mayer et al. (2000) states that their Moscow Mountain site is located in southeastern Washington; however, further investigation revealed that the Moscow Mountain site may, in fact, be located across the border in Idaho.

<sup>\*\*\*</sup> Discover Life has synonymized these species with other species already in the checklist without reference or explanation. As we are not aware of any publications that synonymize these species, these species are kept separate here.

Triepeolus balteatus Cockerell, 1921 Triepeolus bihamatus (Cockerell, 1907) Triepeolus utahensis (Cockerell, 1921) Xenoglossa (Peponapis) pruinosa (Say, 1837)

## Halictidae

Agapostemon (Agapostemon) melliventris Cresson, 1874 Dieunomia nevadensis (Cresson, 1874) Dufourea dilatipes Bohart, 1948\* Lasioglossum (Dialictus) abundipunctum Gibbs, 2010 Lasioglossum (Dialictus) pavoninum (Ellis, 1913) Lasioglossum (Dialictus) planatum (Lovell, 1905) Lasioglossum (Dialictus) sagax (Sandhouse, 1924) Lasioglossum (Dialictus) subversans (Mitchell, 1960) Lasioglossum (Dialictus) yukonae Gibbs, 2010 Lasioglossum (Hemihalictus) diatretum (Vachal, 1904) Lasioglossum (Hemihalictus) pulveris (Cockerell, 1930) Lasioglossum (Lasioglossum) paraforbesii McGinley, 1986 Lasioglossum (Sphecodogastra) nigrum (Viereck, 1903) Lasioglossum (Sphecodogastra) peraltum (Cockerell, 1901) Sphecodes confertus Say, 1837\*\* Sphecodes eustictus Cockerell, 1906 Sphecodes lautipennis Cockerell, 1908 Sphecodes patruelis Cockerell, 1913

## Megachilidae

Anthidiellum (Loyolanthidium) ehrhorni (Cockerell, 1900) Anthidium (Anthidium) maculosum Cresson, 1878 Anthidium (Anthidium) palliventre Cresson, 1878 Anthidium (Anthidium) placitum Cresson, 1879 Ashmeadiella (Ashmeadiella) gillettei Titus, 1904 Atoposmia (Atoposmia) abjecta (Cresson, 1878) Atoposmia (Atoposmia) oregona (Michener, 1943) Coelioxys (Synocoelioxys) alternatus Say, 1837 Coelioxys (Synocoelioxys) apacheorum Cockerell, 1900 Coelioxys (Boreocoelioxys) banksi Crawford, 1914 Coelioxys (Cyrtocoelioxys) deani Cockerell, 1909 Coelioxys (Paracoelioxys) funerarius Smith, 1854 Coelioxys (Synocoelioxys) hunteri Crawford, 1914 Coelioxys (Boreocoelioxys) porterae Cockerell, 1900 Hoplitis (Proteriades) boharti (Timberlake & Michener, 1950) Hoplitis (Proteriades) linsdalei Michener, 1947

Megachile (Litomegachile) gentilis Cresson, 1872 Megachile (Megachile) inermis Provancher, 1888 Megachile (Litomegachile) lippiae Cockerell, 1900<sup>\*\*\*\*</sup> Megachile (Chelostomoides) odontostoma Cockerell, 1924 Megachile (Megachiloides) pseudonigra Mitchell, 1927 Megachile (Pseudocentron) sidalceae Cockerell, 1897 Osmia (Melanosmia) cyaneonitens Cockerell, 1906<sup>\*</sup> Osmia (Melanosmia) gaudiosa Cockerell, 1907 Osmia (Melanosmia) indeprensa Sandhouse, 1939<sup>\*</sup> Osmia (Osmia) ribifloris Cockerell, 1900 Osmia (Melanosmia) tarsata Provancher, 1888 Stelis (Stelis) interrupta Cresson, 1879

## Melittidae

Hesperapis (Carinapis) carinata Stevens, 1919 Macropis (Macropis) nuda (Provancher, 1882)

## **Records excluded from analysis**

We highlight 38 records as questionable and propose that they require more research to confirm their presence in Washington state. Many of these would be significant and surprising range expansions. Most of these records were obtained from data made available through GBIF, Discover Life, or BOLD, and could represent species that are mislabeled or misidentified in their parent collections. A few records were derived from identifications recorded in older revisions and may reflect outdated taxonomy. We do not include these records in the total bees recorded by state or county and highlight them here to ensure they are treated with appropriate caution.

## Andrenidae

1. ! Andrena (Andrena) mandibularis Robertson, 1892 – Yakima<sup>2,3</sup>; Apr<sup>2,3</sup> (1987<sup>2,3</sup>); INHS

**Comments.** This species is generally eastern in distribution.

2. ! Andrena (Andrena) tridens Robertson, 1902 – Kittitas<sup>2,3</sup>; May<sup>2,3</sup> (1989<sup>2,3</sup>); INHS

**Comments.** This species is generally eastern in distribution.

<sup>\*\*\*\*</sup> Sheffield et al. (2011) raised *Megachile lippiae* from a subspecies of *Megachile texana*. It is possible records of *M. lippiae* in Washington already exist under the name *M. texana*.

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**3.** ! *Andrena* (*Cnemidandrena*) *luteihirta* Donovan, 1977 – Benton<sup>7</sup>; Jul<sup>7</sup> (1994<sup>7</sup>); WSUC

**Comments.** This species is generally restricted to southern California, west of the Sierra Nevada mountains. A positive identification requires examination of genitalia; this specimen (which is a male with the genitalia hidden) is more likely the closely related *A. surda* which occurs east and north of the Sierra Nevada range.

4. ! Andrena (Conandrena) cheyennorum Viereck and Cockerell, 1914 – Whitman<sup>2,3</sup>; (2003<sup>2,3</sup>); BBSL

**Comments.** This species is generally southwestern in distribution

**5.** ! Andrena (Melandrena) sayi Robertson, 1891 – Snohomish<sup>1,3</sup>; Aug<sup>1,3</sup> (1985<sup>1,3</sup>); INHS

**Comments.** This species is generally eastern in distribution.

**6.** ! *Andrena* (*Onagrandrena*) *rozeni* Linsley and MacSwain, 1955 – King<sup>2,3</sup>; May<sup>2,3</sup> (1914<sup>2,3</sup>); INHS

**Comments.** This species is generally southwestern in distribution.

**7.** ! *Andrena* (*Ptilandrena*) *erigeniae* Robertson, 1891 – Kittitas<sup>2,3</sup>; Apr<sup>2,3</sup> (1989<sup>2,3</sup>); INHS

**Comments.** This species is generally eastern in distribution.

8. ! Calliopsis (Nomadopsis) obscurella Cresson, 1879 – Franklin<sup>118</sup>; May<sup>118</sup> (1896<sup>118</sup>)

**Comments.** Older identification - Rozen (1958) recommends these records be taken with caution until the specimens have either been examined or other records in the distributional gap are confirmed.

**9.** ! *Perdita* (*Perdita*) *aridella* Timberlake, 1960 – Benton<sup>1,2</sup>; May<sup>1,2</sup>, Jun<sup>1,2</sup>, Aug<sup>1,2</sup> (2015<sup>1,2</sup>); BBSL

**Comments.** This species is generally southwestern in distribution.

## 10. ! Perdita (Perdita) ashmeadi Cockerell, 1899 – Columbia<sup>1,2,4</sup>; PCYU

**Comments.** This species is generally southwestern in distribution. Additionally, P. ashmeadi is a specialist on Prosopis spp. (Simpson and Neff 1987) which do not occur in Washington state.

# Apidae

**11.** ! Anthophora (Clisodon) furcata (Panzer, 1798) – Grays Harbor<sup>1,2</sup>, Pierce<sup>1,2</sup>; Jul<sup>1,2</sup> (1935<sup>1,2</sup>); SEMC

**Comments.** This species is generally European in distribution. However, *A. terminalis* was sometimes considered a subspecies of *A. furcata* (Muesebeck et al. 1951; Hurd 1979) and sometimes a full species (Mitchell 1962). These records are likely older identifications of *A. terminalis*.

**12.** ! *Anthophorula* (*Anthophorula*) *rufiventris* (**Timberlake**, **1947**) – no location reported<sup>2,4</sup>; PCYU

**Comments.** This species is generally southwestern in distribution.

**13.** ! *Bombus (Alpinobombus) polaris* Curtis, 1835 – Thurston<sup>1,2</sup>, Yakima<sup>1,2</sup>; Jul<sup>1,2</sup>, Aug<sup>1,2</sup> (1971<sup>1,2</sup>); NMNH; Data Deficient (Hatfield et al. 2016b)

**Comments.** This species is generally arctic in distribution.

**14.** ! *Bombus* (*Bombus*) *terricola* Kirby, 1837 – San Juan<sup>1,2,3</sup>, Whitman<sup>1,2</sup>, Yakima<sup>1,2</sup>; May<sup>1,2,3</sup>, Aug<sup>1,2</sup> (1959<sup>1,2</sup>); INHS, PMNH; Vulnerable (National Research Council 2007; Hatfield et al. 2015c); G3 – Vulnerable globally (NatureServe 2024)

**Comments.** Milliron (1971) considered *Bombus occidentalis* a subspecies of *B. terricola*; however, current taxonomy classifies *B. occidentalis* as a distinct species (e.g., Bertsch et al. 2010; Williams et al. 2012; Owen and Whidden 2013). It is probable that these records represent *B. occidentalis*.

**15.** *Bombus (Psithyrus) ashtoni* (Cresson, 1864) – Whitman<sup>1,2,3</sup>; Oct<sup>1,2,3</sup> (1960<sup>1,2,3</sup>); BBSL; Data Deficient (Hatfield et al. 2016c); G4 – Apparently Secure globally (NatureServe 2024)

**Comments.** This species is generally northern and eastern in distribution.

**16.** ! *Bombus* (*Pyrobombus*) *ternarius* Say, 1837 – Whitman<sup>1</sup>; Oct<sup>1</sup> (1950<sup>1</sup>); PSUC; Least Concern (Hatfield et al. 2014i)

Comments. This species is generally northeastern and northcentral in distribution.

**17.** ! *Bombus* (*Subterraneobombus*) *borealis* Kirby, 1837 – Clallam<sup>1,2,3</sup>; Sep<sup>1,2,3</sup> (1955<sup>1,2,3</sup>); CNC; Least Concern (Hatfield et al. 2015o)

**Comments.** This species is generally northeastern and northcentral in distribution.

18. ! *Bombus* (*Thoracobombus*) *pensylvanicus* (DeGeer, 1773) – Mason<sup>1,2,3</sup>, Thurston<sup>1,2,3</sup>; Aug<sup>1,2,3</sup> (1908<sup>1,2,3</sup>); BBSL; Vulnerable (Hatfield et al. 2015q)

**Comments.** This species is generally eastern and southwestern in distribution.

**19.** ! *Habropoda depressa* Fowler, 1899 – Walla Walla<sup>1,2</sup>; May<sup>1,2</sup> (1937<sup>1,2</sup>); SEMC; G4 – Apparently Secure globally (NatureServe 2024)

**Comments.** This species is generally southwestern in distribution.

**20.** ! *Melissodes* (*Eumelissodes*) *bicoloratus* LaBerge, 1961 – Benton<sup>1,2</sup>; Jun<sup>1,2</sup> (2014<sup>1,2</sup>); BBSL

**Comments.** This species is generally southwestern in distribution.

**21.** ! *Melissodes* (*Eumelissodes*) *druriellus* (Kirby, 1802) [= *Melissodes rustica* (Say, 1837)] – **Benton**<sup>1,2</sup>; Jun<sup>1,2</sup> (2014<sup>1,2</sup>); BBSL

Comments. This species is generally eastern and midwestern in distribution.

**22.** ! *Melissodes* (*Eumelissodes*) *utahensis* LaBerge, 1961 – Yakima<sup>2,3</sup>; Sep<sup>2,3</sup> (1993<sup>2,3</sup>); INHS

**Comments.** This species is generally southwestern in distribution.

23. ! Nomada argentea (Schwarz, 1966) – Walla Walla<sup>1,2,3</sup>; Jun<sup>1,2,3</sup> (1951<sup>1,2</sup>); BBSL

**Comments.** This species is Middle Eastern in distribution.

24. ! Triepeolus lunatus (Say, 1824) – Klickitat<sup>1,2</sup>; Aug<sup>1,2</sup> (2011<sup>1,2</sup>); BBSL

Comments. This species is generally eastern and midwestern in distribution.

**25.** ! *Triepeolus verbesinae* (Cockerell, 1897) – Klickitat<sup>1,2</sup>, Stevens<sup>3</sup>; Jul<sup>3</sup>, Sep<sup>1,2</sup> (2011<sup>1,2</sup>); BBSL, NMNH

**Comments.** This species is generally southwestern in distribution.

Halictidae

**26.** ! *Agapostemon* (*Agapostemon*) *sericeus* (Forster, 1771) [= *Agapostemon radiatus* Say, 1837] – **Douglas**<sup>1,2</sup>, Franklin<sup>119</sup>; May<sup>1,2</sup> (1905<sup>1,2</sup>); FMNH

**Comments.** This species is normally distributed east of the Rocky Mountains.

**27.** ! Augochloropsis (Paraugochloropsis) sumptuosa (Smith, 1853) – Spokane<sup>1,2,3</sup>; Jun<sup>1,2</sup>, Jul<sup>1,2</sup> (2007<sup>1,2,3</sup>); BBSL

**Comments.** This species is generally eastern and midwestern in distribution.

28. ! Halictus (Nealictus) parallelus Say, 1837 – Kittitas<sup>1,2</sup>; Aug<sup>1,2</sup> (1967<sup>1,2</sup>); FMNH

**Comments.** This species is generally eastern and midwestern in distribution.

Megachilidae

**29.** ! *Anthidium* (*Anthidium*) *collectum* Huard, 1896 – G3 – Vulnerable globally (NatureServe 2024)

**Comments.** Gonzalez and Griswold (2013) make note of an isolated record from south central Washington well outside the expected distribution, but do not provide a specific locality.

30. ! Coelioxys (Boreocoelioxys) insita Cresson, 1872 – Columbia<sup>1,2,4</sup>; PCYU

**Comments.** This species is generally midwestern in distribution.

**31.** ! *Dianthidium* (*Dianthidium*) *dubium* H. F. Schwarz, 1928 – Spokane<sup>1,2</sup>; Jun<sup>1,2</sup>, Jul<sup>1,2</sup> (2015<sup>1,2</sup>); BBSL

**Comments.** This species is generally southwestern in distribution.

**31a.** ! *Dianthidium* (*Dianthidium*) *dubium mccrackenae* Timberlake, 1943 – Benton<sup>1,2</sup>, Walla Walla<sup>1,2</sup>; Jun<sup>1,2</sup>, Jul<sup>1,2</sup> (2014<sup>1,2</sup>); BBSL

**Comments.** This subspecies is generally southwestern in distribution.

**32.** ! *Hoplitis* (*Hoplitis*) *samarkanda* (Warncke, 1991) – Garfield<sup>1,2,3</sup>; (1998<sup>1,2,3</sup>); BBSL

**Comments.** This species is generally Palearctic in distribution.

**33.** ! *Megachile (Xanthosarus) latimanus* Say, 1823 [= *Megachile vidua* Smith, 1853] – San Juan<sup>24</sup>, Thurston<sup>24</sup>, Whitman<sup>1,2</sup>, Yakima<sup>1,2</sup>; Jul<sup>1,2,24</sup>, Aug<sup>24</sup> (1949<sup>1,2</sup>); CMNH, MCZ; G5 – Secure globally (NatureServe 2024)

**Comments.** This species is generally only found east of the 100<sup>th</sup> meridian. *Megachile latimanus* and *M. perihirta* are considered an eastern and western sibling pair with only subtle characters distinguishing *M. latimanus* females from *M. perihirta* females.

**34.** ! *Osmia* (*Diceratosmia*) *subfasciata* Cresson, 1872 – King<sup>1,2,3</sup>; Jul<sup>1,2,3</sup> (1929<sup>1,2,3</sup>); BBSL; G5 – Secure globally (NatureServe 2024); LAMIACEAE: *Prunella vulgaris*<sup>3</sup>

**Comments.** This species is generally southern in distribution.

**35.** ! *Osmia (Melanosmia) crassa* Rust and Bohart, 1986 – Walla Walla<sup>1,2,3</sup>; May<sup>1,2,3</sup> (1937<sup>1,2,3</sup>); BBSL

**Comments.** This species is generally southwestern in distribution.

**36.** ! *Osmia* (*Melanosmia*) *granulosa* Cockerell, 1911 – Walla Walla<sup>2,3</sup>; May<sup>2,3</sup> (1937<sup>2,3</sup>); BBSL; G4 – Apparently Secure globally (NatureServe 2024)

**Comments.** Hurd (1979) synonymized *O. granulosa* with *O. exigua* without explanation. As this record and a single record from Wyoming are the only records of *O. granulosa* outside of California, NatureServe (2024) suggests that these records could possibly be *O. exigua*.

**37.**! *Osmia (Melanosmia) phenax* Cockerell, 1897 [= *Osmia titusi* Cockerell, 1905] – Stevens<sup>1,2</sup>; Jun<sup>1,2</sup>, Jul<sup>1,2</sup> (2015<sup>1,2</sup>); BBSL

**Comments.** This species is generally southwestern in distribution.

38. ! Stelis (Stelis) robertsoni Timberlake, 1941 – Spokane<sup>1</sup>; Jul<sup>1</sup> (2015<sup>1</sup>); BBSL

**Comments.** This species is generally southwestern in distribution.

## Acknowledgements

We are grateful to Dr. Katie Buckley, Dr. Karen Wright, and the Washington State Pollinator program for ongoing support and input. We thank Nate Green, Dr. Thor Hansen, and Dr. Julie Combs for the use of records from their personal collections, and the National Park Service for the use of records from their data. We recognize Dr. Richard Zack, Curator at the WSUC, for the decades of effort in surveys of the state of Washington. His work has added many county records from the Hanford site in Benton County. We also thank Dr. Julie Combs and Dr. Jack Neff for suggestions on this manuscript. Funding for this work was provided by the Washington State Legislature as part of SSB 5253 and from NSF DBI-2216934 to EAM.

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## Supplementary material I

## Life history data for each species

Authors: Chanda S. Bartholomew, Elizabeth A. Murray, Silas Bossert, Joel Gardner, Chris Looney

Data type: xlsx

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Link: https://doi.org/10.3897/jhr.97.129013.suppl1

## Supplementary material 2

## Species by ecoregion

Authors: Chanda S. Bartholomew, Elizabeth A. Murray, Silas Bossert, Joel Gardner, Chris Looney

Data type: csv

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Link: https://doi.org/10.3897/jhr.97.129013.suppl2



# First detection of *Trissolcus japonicus* (Ashmead) (Hymenoptera, Scelionidae) in southwestern France

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Academic editor: Elijah Talamas | Received 18 July 2024 | Accepted 3 October 2024 | Published 4 November 2024

https://zoobank.org/8B42E7A2-41CD-4DE7-A075-00AA4B9412B0

**Citation:** Martel G, Bout A, Tortorici F, Hamidi R, Tavella L, Thomas M (2024) First detection of *Trissolcus japonicus* (Ashmead) (Hymenoptera, Scelionidae) in southwestern France. Journal of Hymenoptera Research 97: 1123–1139. https://doi.org/10.3897/jhr.97.132433

#### Abstract

We report the first detection of *Trissolcus japonicus* in southwestern France. A total of almost 3000 sentinel and 700 field-laid egg masses of *Halyomorpha halys* were exposed or collected in the administrative region of Nouvelle-Aquitaine in 2022 and 2023. A total of 12 and 44 specimens of *T. japonicus* emerged from one and two egg masses in 2022 and 2023, respectively. Morphologic analysis confirmed the identification of this egg parasitoid, while molecular analysis of COI matched the haplotype of the French population to the population of *T. japonicus* released in Italy. *Trissolcus japonicus* may have arrived in Nouvelle-Aquitaine from introduction pathways similary to *T. mitsukurii*, detected in 2020, although these pathways cannot be clearly defined. The co-occurrence of these two major parasitoids of BMSB should now be surveyed as possible competition can arise. In the frame of the biological control program currently running in France against BMSB, the use of one or two parasitoid species is also considered.

#### **Keywords**

Biological control, brown marmorated stink bug, DNA barcoding, exotic species

## Introduction

Herbivorous stink bugs are a good example of increasing economic loss by invasive insects; many of these species are agricultural pests in their native and invasive range (McPherson 2018; Conti et al. 2021). The Brown Marmorated Stink Bug (BMSB), Halyomorpha halys (Stål) (Hemiptera: Pentatomidae) is one of the main invasive stink bug species in recent decades. Native to eastern Asia, BMSB arrived in North America in the mid-1990's (Leskey and Nielsen 2018) and in Europe in the 2000's where it spread quickly in Switzerland, Georgia, Italy and, more recently, France (Bosco et al. 2018; Kereselidze et al. 2022). Like many invasive Pentatomidae species, BMSB is highly polyphagous, feeding on more than one hundred host plants (Lee et al. 2013; Bergmann et al. 2016) from wild and ornamental to cultivated species, including peach, peer, apple, grape and hazelnut. Thus, it can incur considerable damages on a wide range of agricultural systems, like in northern Italy (Maistrello et al. 2017; Bosco et al. 2018) where outbreaks in 2019 caused more than € 356 million damage on pear, peach, and nectarine productions, with up to 80-100% yield losses (Centro Servizi Ortofrutticoli 2019). In hazelnut orchards, the absence of insecticide treatment can lead to 23-40% of damaged hazelnuts (de Benedetta et al. 2023). In France, the presence of BMSB is increasing since first identified in 2012, and this species represents an important risk for many French crops, according to the French Agency for Food, Environmental, and Occupational Health and Safety (Haye et al. 2014). In the case of hazelnut orchards, average bug damage increased continuously from 0.2% in 2015 to 2% in 2018, with peaks that reached 14% and up to 30% in 2022 (unpublished data, Unicoque). To control BMSB, the use of broad-spectrum insecticides can no longer be considered due to the ecological and sanitary risks, the growing societal demand that results in the progressive suppression of authorized chemicals, and the possibility of resistance in BMSB populations, as has happened in other pentatomid species (Sosa-Gomez et al. 2001). Classical biological control (CBC) appears as a possible alternative strategy to the use of insecticides. CBC aims at restoring ecosystem balance by introducing exotic natural enemies to better control an invasive pest, which often lacks efficient natural enemies in its invasive range. In Europe for instance, BMSB can be parasitized by parasitoid wasps in the genera Trissolcus Ashmead, Telenomus Haliday, Ooencyrtus Ashmead or Anastatus Motchoulsky, but parasitism often leads to egg abortion, incomplete development of parasitoids or low parasitism rates (Haye et al. 2016; Roversi et al. 2016). Among the natural enemies of the BMSB in its native range, Trissolcus japonicus (Ashmead) (Hymenoptera: Scelionidae) is considered as one of the most promising candidates for CBC (Yang et al. 2009; Zhong et al. 2017). Numerous studies have been conducted to assess the parasitoid's efficiency and biosafety as part of the requirements for its legal introduction in the USA (Hedstrom et al. 2017), Canada (Abram et al. 2019), New Zealand (Charles et al. 2019), and Europe (Haye et al. 2020). Trissolcus mitsukurii (Ashmead) is also known as a natural enemy of the BMSB in Japan
(Arakawa and Namura 2002) and is considered as a valid candidate for its control in Italy together with *T. japonicus* (Sabbatini Pevereri et al. 2020). Since *T. mitsukurii* is absent in North America, Europe (especially Italy) has been the only known place where the control of BMSB by both parasitoid species could be studied (Moraglio et al. 2020).

Legislative restrictions in the USA and Europe may be a limiting factor for the introduction of exotic species by focusing on perceived risks for non-targets organisms rather than the benefits of pest reduction (van Lenteren et al. 2006; Rondoni et al. 2021). However, unintentional introduction of exotic natural enemies is likely to happen more often than expected (Mason et al. 2017). Parasitoids often move along the same routes as their hosts, and this phenomenon can lead to unintentional biological control as defined by Beers et al. (2022) and has been documented several times, for instance in the USA, Germany and Italy: Leptopilina japonica Novković and Kimura (Hymenoptera: Figitidae) against Drosophila suzukii (Matsumura) (Diptera: Drosophilidae) (Puppato et al. 2020; Beers et al. 2022; Martin et al. 2023); as well as Scelionidae species, Paratelenomus saccharalis (Hym. Platygastridae) (Dodd) (Gardner et al. 2013) against Megacopta cribraria (F.) (Hem. Plataspidae), with Trissolcus hyalinipennis Rajmohana and Narendran and Grvon aetherium Talamas (Ganjisaffar et al. 2018; Hogg et al. 2021) against Bagrada hilaris (Burmeister) (Hem. Pentatomidae). Fortuitious populations of T. japonicus were found in the USA (Talamas et al. 2015; Milnes et al. 2019), Canada (Abram et al. 2019), Switzerland, Italy (Sabbatini Peverieri et al. 2018; Stahl et al. 2019; Moraglio et al. 2020), Germany (Dieckhoff et al. 2021) and Slovenia (Rot et al. 2021), while T. mitsukurii was detected in Italy (Sabbatini Peverieri et al. 2018), France (Bout et al. 2021) and Serbia (Konjević et al. 2024).

The discovery of adventive populations of T. japonicus in the USA and Italy probably led to lower constraints for releases (Talamas et al. 2015). In France, the discovery of an adventive population of T. mitsukurii (Bout et al. 2021) led to the obtainment of a release permit that opened the way to a biological control program against BMSB in 2022. The detection of T. japonicus in France should help in the same way and represents a unique opportunity to study possible interactions of both parasitoid species. Despite surveys conducted in southeastern and southwestern France since 2017 and multiple releases in northern Italy since 2020, T. japonicus has not been detected yet in France. Meanwhile, the geographical proximity with the Piedmont region (Italy) where T. japonicus is released and the important commercial and human connection between northern Italy and southeastern France could lead to unintentional dispersion of this parasitoid. This dispersion is also expected to reach southwestern France where an adventive population of *T. mitsukurii* already established, likely from the Italian population (Bout et al. 2021). In the region Nouvelle-Aquitaine (France), where the current study took place, releases of T. mitsukurii were initiated in 2022 in the frame of the project RIPPOSTE and field monitoring was conducted with a focus on T. mitsukurii and T. japonicus.

# Materials and methods

## Field surveys

Exposure of BMSB sentinel egg masses and collection of field-laid egg masses of Pentatomidae and Coreidae were used to assess the diversity of egg parasitoids in France. The field surveys took place in 2022 and 2023 and covered 11 sampling sites in Nouvelle-Aquitaine (southwestern France) in three departments: Lot-et-Garonne, Dordogne and Gironde. In this sampling area, opportunistic collection of egg masses from *H. halys* and other pentatomid species on localities that are not part of the 11 chosen sites were also included in the samples.

# Laboratory colony of the BMSB

The monitoring of egg parasitoids of BMSB requires the use of sentinel egg masses that can be produced in laboratory conditions. To obtain these egg masses, a laboratory colony of BMSB was constituted from adult individuals collected in Cancon (France) during fall 2021 using pheromone traps (Trece<sup>®</sup>) and transferred to laboratory conditions (T:  $25 \pm 2$  °C, RH:  $50 \pm 10\%$ , L:D: 16:8 h). They were reared in nylon net cages (47.5 × 47.5 × 47.5 cm, Bugdorm<sup>®</sup>, MegaView Science Co., Ltd., Taichung, Taiwan) containing fresh beans and apples, complemented with fresh maize and hazelnuts. Egg masses were collected daily and stored under the same laboratory conditions until hatching of the first instars. These were transferred to new cages so that each cage was homogeneous in developmental stage.

# Field parasitoid monitoring

Sentinel egg masses were obtained from fresh BMSB egg masses (< 24 h) collected from the laboratory colony and were directly exposed in the field or stored in a fridge (c.a. 8 °C) for up to 2 days. Frozen eggs were not used as they can be less detectable or acceptable for egg parasitoids and lead to sampling bias (Jones et al. 2014). Each egg mass was glued on a cardboard piece  $(1 \times 3 \text{ cm})$  and stapled to the under- side of the leaves of a wide variety of host plants, mostly woody trees (e.g., Prunus spp., Acer spp., Catalpa bigninoides Walt., Paulownia tomentosa (Thunb.), and Corylus avellana L.). Sentinel egg masses were removed from the field three days after deployment. They were exposed in the field every two weeks on each monitored site from June 10th to September 16th in 2022 and every week from April 28th to September 15th in 2023. Field-laid egg masses from BMSB and other heteropteran species (Pentatomidae, Coreidae) were collected in the sampling area in N-A from May 18th to September 16th, 2022, and from May 10<sup>th</sup> to September 8<sup>th</sup>, 2023. During the surveys, egg masses of stink bug species were visually located on various host plants and collected by hand. All egg masses, sentinel and field-laid, were kept in the laboratory under controlled

conditions ( $22 \pm 1$  °C; RH 50 ± 5%; L:D: 16:8 h) until the emergence of bug nymphs or adult parasitoids. Egg masses were individually stored in Petri dishes and checked daily for emergence since the first observation of external indication of parasitoid development (grey or black coloration of the egg). Emerged parasitoids were stored in 70% ethanol while non-emerged eggs were dissected under a stereomicroscope (Nikon SMZ 1270) to determine whether they were parasitized or not (presence of an identifiable larvae, nymph, or adult parasitoid). When the egg content was not identifiable, the egg was considered as non-parasitized.

### Molecular analysis

DNA-barcoding characterization consisted in a double identification based on the Cytochrome Oxydase I (COI) amplification and sequencing, and morphological identification of the corresponding voucher (exoskeleton of the specimen). Molecular analyses were performed as describe in Bout et al. (2021) for T. mitsukurii identification. Extraction of DNA was performed using the DNA kit extraction MA150E - QuickExtract - DNA, following company specifications. This non-destructive method allowed the vouchers to remain intact for morphological identifications. PCR amplifications were performed on a portion of the Cytochrome Oxydase I subunit (COI) locus using the LCO-HCO primer: HCO2198 (5'-TAAA CTT CAG GGT GAC CAA AAA ATC A-3'), LCO1490 (5'- GGTC AAC AAA TCA TAA AGA TAT TGG-3') (Folmer et al. 1994), allowing amplification of an approximately 600-700 bp portion of DNA on this locus. The product was sent to Genewiz (Leipzig, Germany) for a double, single read sequencing with the HCO2198 primer. All residual DNAs are archived at INRAE Sophia-Antipolis (France). Correction, annotation and alignment were performed manually using BioEdit Geneious R10 software. The comparison of nucleotide sequences with sequences available in the NCBI database (GenBank) was performed using Blastn (Altschul et al. 1990) with standard settings. From GenBank (NCBI), all COI sequences (72) clearly identified as T. japonicus species were downloaded. Two sequences from CREA-Italy were added to the study and compiled with the ten sequences obtained from French population of T. japonicus collected in 2022 (7 sequences) and 2023 (3 sequences) (Table 2), resulting in a final table of 84 sequences (Suppl. material 2). Analysis of sequences data was done with the MegaX software (Tamura et al. 2013), using the neighbor joining (NJ) method (Saitou et al. 1987), with bootstrap values based on 500 replications. Nucleotide distances in NJ trees were estimated by the Kimura's two-parameters method (Kimura, 1980). Some sequences were significantly shorter than the others. Hence, analyses exclude the 22 shorter sequences and work only on the common part of the 62 other sequences (fragment of 575 pb). A fast alignment file was used with DnaSP6 to create all haplotypes of T. japonicus sequences. The resulting nexus file was analyzed with PopArt software (Otago University, Dunedin, New Zeland) to organize haplotype networks.

# Morphological identification

All parasitoid wasps emerged were morphologically identified using a Wild M5 stereomicroscope with the appropriate taxonomic key. Species of Scelionidae were identified using Kozlov and Kononova (1983), Javahery (1968), Moraglio et al. (2021), Talamas et al. (2017), Tortorici et al. (2019). Eupelmidae wasps were identified using Askew and Nieves-Aldrey (2004) and Peng et al. (2020). Images of the specimens were taken using a Canon 90D camera (Canon Inc., Tokyo, Japan) equipped with extension tube, 10× and 20× LWD microscope lenses mounted on a macro-rail. The final pictures were processed with Zerene Stacker (PMax algorithm, Zerene Systems LLC, Richland, WA, USA) and with Photoshop (Adobe Systems Inc, USA). The specimens used for morphological analysis were deposited in the collection of the Dipartimento di Scienze Agrarie, Forestali e Alimentari, University of Turin, Italy.

# Results

## Parasitism on BMSB egg masses

Various species of native egg parasitoids belonging to Scelionidae (*Trissolcus* spp. and *Tel-enomus* spp.), Eupelmidae (*Anastatus bifasciatus* (Geoffroy)), and Encyrtidae (*Ooencyrtus* spp.) emerged from egg masses of BMSB collected during the surveys, as well as sentinel egg masses (data not shown). The parasitism rate of sentinel egg masses was lower than naturally-laid ones in 2022 and 2023 (Table 1). In early August 2022, one parasitized egg mass of BMSB laid on *Ailanthus altissima* L. was collected in Castillonnès (N-A, France) and produced 12 specimens of *T. japonicus*. In early July and late August 2023 respectively, two sentinel egg masses were found parasitized by *T. japonicus* in Sainte Foy la grande (N-A, France; 42 km far from Castillonnès) and produced together 44 specimens. However, no specimen was further recovered from 2023 survey in Castillonnès.

### Morphological identification

Females and males of *T. japonicus* specimens detected in Castillonnès and Sainte Foy la grande had typical morphological features of this species as described by Talamas

**Table 1.** Parasitism rates of sentinel and naturally laid egg masses of BMSB in 2022 and 2023 in Nouvelle-Aquitaine (France). (1) All parasitism occurrences; (2) *Trissolcus japonicus* occurrences.

Monitoring period (in	Type of	Number of	Number of	(1) % of egg	(2) % of egg
Nouvelle-Aquitaine, France)	egg mass	collected egg masses	parasitized egg masses	masses parasitized	masses parasitized
June–September 2022	< 24 h sentinel	1169	40	3.4	0
May–September 2022	Natural	155	26	19.2	0.6
April–September 2023	< 24 h sentinel	1822	83	4.6	0.1
May–September 2023	Natural	181	18	9.9	0

et al. (2017): a uniform, well-defined hyperoccipital carina on the vertex between lateral ocelli (Figs 1B, C, 2) and females had a clypeus with four setae and well-defined episternal foveae that extend from the postacetabular sulcus to the mesopleural pit (Fig. 1A). In addition, the absence of rugae on the mesoscutum and the absence of a smooth area below the median ocellus (Fig. 1A, B) confirm that it is neither of the Palearctic species closest to *T. japonicus, Trissolcus kozlovi* Rjachovskij and *Trissolcus plautiae* (Watanabe).

# Molecular identification

Molecular characterization of the specimens collected in Nouvelle-Aquitaine, resulted in one specific haplotype: haplotype Hap02 (Fig. 3; Suppl. material 2). These sequences match with *T. japonicus* cluster (Fig. 3; Suppl. material 1). The haplotype analyses highlights that these specimens are the same haplotype that the Asian



**Figure I.** *Trissolcus japonicus* female, voucher n° DISAFA-FT HYM651 **A** head and mesopleuron **B** habitus in dorsal **C** habitus in lateral view; of = orbital furrow; cs = clypeal seteae; eps = episternal foveae; ats = postacetabular sulcus; mpp = mesopleural pit; hoc = hyperoccipital carina; A7–A11 = Antenomeres 7–11 (clavomeres).



**Figure 2.** *Trissolcus japonicus* male, voucher n° DISAFA-FT HYM652 **A** habitus in latero-dorsal view **B** habitus in dorsal view.

**Table 2.** GenBank accession number and sample information for COI sequences of French *Trissolcus japonicus* presented in this study.

Collection Code	Department country	Year of collection	GPS coordinates (DMS)	GenBank accession number
ISA45651	Lot et Garonne, France	2022	44.65474, 0.5883531	PP766189
ISA45652	Lot et Garonne, France	2022	44.65474, 0.5883531	PP766190
ISA45653	Lot et Garonne, France	2022	44.65474, 0.5883531	PP766191
ISA45654	Lot et Garonne, France	2022	44.65474, 0.5883531	PP766192
ISA45671	Lot et Garonne, France	2022	44.65474, 0.5883531	PP766193
ISA45672	Lot et Garonne, France	2022	44.65474, 0.5883531	PP766194
ISA45673	Lot et Garonne, France	2022	44.65474, 0.5883531	PP766195
ISA47499	Gironde, France	2023	44.8405337, 0.212578	PP766196
ISA47500	Gironde, France	2023	44.8405337, 0.212578	PP766197
ISA47501	Gironde, France	2023	44.8405337, 0.212578	PP766198

strain labelled "Beijing USDA", recently released in Italy for the official CBC program (Suppl. material 2). In addition, translation of all COI sequences into protein resulted in homogeneous protein sequences, with no stop codons. The few changes in amino acid composition observed are between amino acids of the same structural group (Suppl. material 3). Two sequences, corresponding to haplotype Hap01, show a change of amino acid at position 92 *i.e.* Alanine instead of Serine, which belong to two different structural groups (Alanine being the simplest amino acid, while Serine which derived from alanine, has an alcohol function).

### Discussion

The sampling of egg parasitoids of BMSB using natural and fresh sentinel egg masses has been effective for the detection of exotic *Trissolcus* species in several countries including France (Talamas et al. 2015; Milnes et al. 2019; Stahl et al. 2019; Moraglio et al. 2020; Bout et al. 2021; Dieckhoff et al. 2021). In Nouvelle-Aquitaine, where



**Figure 3.** Haplotype network obtained from the 62 COI sequences (575 bp) of *Trissolcus japonicus*. Countries of origin were indicated by colors. POP ART program (Leigh and Bryant 2015).

T. mitsukurii was previously collected from natural egg masses, T. japonicus was equally collected from natural and fresh sentinel egg masses. This indicates that both are physiologically suitable for the parasitoid, although the low general parasitism rate on sentinel egg masses suggests they are more difficult to detect or exploit. Regarding the geographic range of our sampling, we likely detected the first non-intentional introduction of T. japonicus in France. A migration of the two exotic species T. japonicus and T. mitsukurii in southwestern France has been expected as (i) they are widespread in Italy and Switzerland, and (ii) the growing density of BMSB provides an invasion opportunity for its native parasitoids (Zapponi et al. 2020). The shared distribution of T. mitsukurii and T. japonicus in Asia, as well as their co-occurrence in Italy (Zapponi et al. 2020; Falagiarda et al. 2023), reveals similar ecological preferences. French climatic conditions, as those of Europe, are favorable for widespread establishment of *T. japonicus* following the presence of BMSB (Avila and Charles 2018). The detection of T. japonicus in Nouvelle-Aquitaine also matches with its modelized distribution proposed by Tortorici et al. (2023). On the other hand, T. japonicus has not been collected in the French region of Alpes-Maritimes which is close to Italy, or the regions close to Switzerland as no sampling was performed along an East-West gradient. Thus, it cannot be concluded whether the presence of T. japonicus in Nouvelle-Aquitaine results from human activities or natural dispersion, although it is likely to have used similar dispersal ways than T. mitsukurii.

Very low recorded parasitism levels are characteristic of the initial detections in other areas where adventive *T. japonicus* populations have since been confirmed and spread (Talamas et al. 2015; Abram et al. 2019; Milnes et al. 2019). Detections of *T. japonicus* and *T. mitsukurii* in France always occurred in urban areas or in proximity to ornamental trees. This was also the case in the USA and Italy (Hedstrom et al. 2017; Sabbatinni Peverieri et al. 2018; Lowenstein et al. 2019). While *T. mitsukurii* was first discovered in France peri-urban area BMSB egg masses laid on cherry laurel, *T. japonicus* was collected in a residential area where BMSB established at high densities on preferred host plants *A. altissima* and *C. bigninoides*. In North America, BMSB is highly associated with *A. altissima*, as well as in Italy (Zapponi et al. 2020; Dyer et al. 2022) so that these tree species are relevant sampling spot (Quinn et al. 2019).

All of the samples of *T. japonicus* collected between 2022 and 2023 in Nouvelle-Aquitaine present the same haplotype Hap02. This haplotype corresponds to strains of *T. japonicus* present in China previously collected by USDA and introduced in Europe *i.e.* Cabi quarantine (Switzerland) and CREA-DC (Consiglio per la ricerca in agricoltura e l'analisi dell'economia agraria – Difesa e Certificazione, Italy). In the same way as for *T. mitsukurii* (Bout et al. 2021) the most probable origin of the French population of *T. japonicus* appears to be Italy, likely from material or plants moved from Italy to France which would support the common introduction way. The collection of specimens between 2022 and 2023 would indicate that this population of *T. japonicus* is established, although it was collected on two different sites. Hence, the question of multiple introductions remains. Molecular sequences used in this study are of good quality: translation of sequences into proteins are preserved and homogeneous, without stop codon. These sequences reflect a genetic polymorphism present within the species. The two sequences representing the haplotype Hap01, with a more significant amino acid replacement at position 92, could reflect a DNA amplification (or correction) error. These sequences could probably be part of the haplotype Hap06.

# Conclusion

The detection of *T. japonicus* in 2023, even on a different site than 2022, encourages new prospects and may indicate establishment of the parasitoid. How populations of T. japonicus will manage to establish and spread will depend on their ability to survive and reproduce after winter, as well as finding suitable hosts when temperatures rise. In Oregon (USA), T. japonicus was able to survive average winter lows of -3 °C (Lowenstein et al. 2019) and it could establish in Italy despite winter reaching -5 °C (Falagiarda et al. 2023). With similar thermal conditions in southwestern France, it is likely to overcome winter, which is currently under investigation. Regarding possible hosts, in addition to BMSB, surveys should continue to include non-target host species. In Italy, surveys one year after releases of T. japonicus indicated that Pentatoma rufipes (L.), Graphosoma lineatum (L.) and Palomena prasina (L.) were parasitized (up to 26% parasitized eggs for G. lineatum) (Falagiarda et al. 2023). The monitoring of non-target pentatomid species also provides data on egg parasitoid diversity and prevalence, with some of species like A. bifasciatus or Trissolcus belenus (Walker) able to apply a "natural" regulation of BMSB. Finally, the co-occurrence of T. japonicus and T. mitsukurii should be investigated both in terms of parasitism rate and geographical dispersion, since monitoring in Italy highlighted that the natural spread of *T. japonicus* was of lower importance than T. mitsukurii (Falagiarda et al; 2023).

# Acknowledgements

This study took place in the frame of the project RIPPOSTE with the financial support of the Nouvelle-Aquitaine Region (FR). We acknowledge Emeric Poret, Léa Tournier and Amandine Jagueneau for their involvement in the project and the field monitoring during summers 2022 and 2023. This study was also carried out within the Agritech National Research Center and received funding from the European Union Next-Generation EU (PIANO NAZIONALE DI RIPRESA E RESILIENZA (PNRR)—MISSIONE 4 COMPONENTE 2, INVESTIMEN-TO 1.4—D.D. 1032 17/06/2022, CN0000022). We acknowledge the reviewers for their comments and language revision that improved the quality of the manuscript. This manuscript reflects only the authors' views and opinions; neither the European Union nor the European Commission can be considered responsible for them.

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# Supplementary material I

# Phylogenetic tree based on molecular clustering of worldwid *Trissolcus japonicus* vouchers including French samples

Authors: Guillaume Martel, Alexandre Bout, Francesco Tortorici, Rachid Hamidi, Luciana Tavella, Maud Thomas

Data type: pdf

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Link: https://doi.org/10.3897/jhr.97.132433.suppl1

# Supplementary material 2

# Sequences references of *Trissolcus japonicus* vouchers used to build the Haplotype network

Authors: Guillaume Martel, Alexandre Bout, Francesco Tortorici, Rachid Hamidi, Luciana Tavella, Maud Thomas

Data type: xlsx

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Link: https://doi.org/10.3897/jhr.97.132433.suppl2

# Supplementary material 3

# COI proteine translation from Trissolcus japonicus sequences used in the study

Authors: Guillaume Martel, Alexandre Bout, Francesco Tortorici, Rachid Hamidi, Luciana Tavella, Maud Thomas

Data type: pdf

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Link: https://doi.org/10.3897/jhr.97.132433.suppl3

RESEARCH ARTICLE



# Five new species of *Passaloecus* Shuckard (Hymenoptera, Crabronidae) from China, with a key to Chinese species

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Academic editor: Michael Ohl	Received 25 August 2024   Accepted 25 October 2024   Published 12 November 2024
http:	

**Citation:** Li J, Ma L, Li Q (2024) Five new species of *Passaloecus* Shuckard (Hymenoptera, Crabronidae) from China, with a key to Chinese species. Journal of Hymenoptera Research 97: 1141–1161. https://doi.org/10.3897/jhr.97.135489

### Abstract

Based on the key diagnostic characteristics such as petiole, clypeus, and hypersternaulus, five new species of *Passaloecus* from China are identified: *P. clypearcuatus* Li & Ma, **sp. nov.**, *P. clypeconvexus* Li & Ma, **sp. nov.**, *P. edentutus* Li & Ma, **sp. nov.**, and *P. sternoleios* Li & Ma, **sp. nov.** Detailed descriptions, diagnoses, and photographs of diagnostic characteristics are provided for these new species. Additionally, a key to the known species of *Passaloecus* in China is updated and illustrated, further enhancing the understanding of biodiversity within this genus.

### Keywords

Digger wasps, identification key, morphology, Pemphredoninae, taxonomy

### Introduction

In 1837, Shuckard placed *Pemphredon insignis* within the genus *Passaloecus*, establishing *Passaloecus* as a new taxon and designating *Passaloecus insignis* (Vander Linden, 1829) as its type species (Shuckard 1837). The classification system used in this study integrates research findings from Pulawski (2024) incorporating the studies of Brothers (1999) and Melo (1999). *Passaloecus* belongs to Hymenoptera: Crabronidae: Pemphredoninae: Pemphredonini: Pemphredonina. The main diagnostic characteristics of Pemphredonina include the presence of two submarginal cells and three discal cells on the forewing (Kim and Yang 2010). The Pemphredonina comprises four genera, with Passaloecus resembling Polemistus and Pemphredon resembling Diodontus. Passaloecus can be readily distinguished from Pemphredon and *Diodontus* by the following characteristics: episternal sulcus well-developed, distinctly crenate; mesopleuron nearly smooth, lacking complex characteristics; mandible apex with 2-3 teeth; females without pygidial plate. The difference between Passaloecus and its closely related genus Polemistus lies in the following characteristics: inner orbits nearly parallel, with less pronounced aggregation in the lower frons; gena without long, erect setae ventrally; mesopleuron often without omaulus (Yasumatsu 1934; Bohart and Menke 1976). Passaloecus are small (4-9 mm) predatory wasps that primarily feed on aphids. Females of this genus nest in existing cavities, such as tree stems previously excavated by other insects, old galls, or by excavating their own burrows in soft, pithy wood. The cells within the nest are separated by resin and arranged linearly (Finnamore 1982; Antropov and Perkovsky 2009; Kaplan and Yildirim 2023). Based on our field collection experience, species of this genus are commonly found in environments such as wooden houses, dead wood, and nature reserves. These locations provide abundant wood resources and suitable nesting habitats, fulfilling their nesting and predation needs.

*Passaloecus* is represented by 46 species and five subspecies worldwide, with the majority of species distributed in the Palearctic region (30 species and three subspecies) and the Nearctic region (19 species and one subspecies). The Oriental region has a relatively lower diversity, with 13 species and one subspecies, while only one species occurs in the Neotropical region (Tsuneki 1955, 1967, 1974; Vincent 1979; Amarante and Vincent 1993; Vardy 2017; Kejval et al. 2020; Shorenko 2020; Saure 2021; Pulawski 2024). Scholars such as Qiang Li, Li Ma, and Bashir have conducted extensive diversity and taxonomic studies on Chinese Pemphredoninae, describing and documenting numerous new species and records. Their research has increased the known diversity of *Passaloecus* in China to 18 species and one subspecies (Ma and Li 2012; Ma et al. 2013, 2018; Bashir et al. 2019, 2020, 2021, 2023).

This study provides detailed descriptions and illustrations of five new species from China: *P. clypearcuatus* sp. nov., *P. clypeconvexus* sp. nov., *P. edentutus* sp. nov., *P. margdentatus* sp. nov., and *P. sternoleios* sp. nov. Additionally, an illustrated key to all known *Passaloecus* species in China is provided.

### Materials and methods

The specimens examined in this study were collected using malaise traps, yellow plates, sweep nets, and flight intercept traps, and were deposited in the Insect Collections of Yunnan Agricultural University, Kunming, Yunnan, China (**YNAU**). Observations were conducted under an Olympus stereomicroscope (SZ Series) with an ocular

micrometer. Measurements were taken at  $5 \times$  magnification, except for body length, which was measured at  $2 \times$  magnification and subsequently converted. Photographs were captured using a VHX-5000 and edited with Adobe Photoshop 8.0. Morphological terminology follows Bohart and Menke (1976), Vincent (1979), and Bashir et al. (2023). The description of the five new species is based on holotypes. The abbreviations and definitions used are as follows:

- **AOD** Distance from inner eye margin to antennal socket, frontal view;
- **BL** Body length;
- EDL Distance between inner eye margins at base of clypeus, frontal view;
- **EDU** Distance between inner eye margins at base of vertex, dorsally;
- **EL** Eye length in lateral view, maximum;
- **EW** Eye width in lateral view, maximum;
- **EWd** Eye width in frontal view, maximum;
- HLD Head length in dorsal view, the distance from occipital margin to frons, medially;
- **HLF** Head length in front view, the distance from the clypeal margin to the vertex, medially;
- HW Head width, dorsally;
- IAD Distance between antennal sockets, frontal view;
- **LFI** Length of flagellomere I;
- **LFII** Length of flagellomere II;
- LTI Length of gastral tergum I, maximum, dorsally;
- **OCD** Ocello-occipital distance, distance between posterior margin of hind ocellus and occipital margin, dorsally;
- **OOD** Ocellocular distance, distance between outer margin of hind ocellus and nearest inner orbit, dorsally;
- PL Pedicel length;
- **PLL** Petiole length laterally, maximum;
- **POD** Postocellar distance, distance between inner margins of hind ocelli, dorsally;
- **PW** Petiole width, maximum, dorsally;
- **SL** Scape length;
- **TW** Gena width in lateral view, maximum;
- **WAS** Width of antennal socket, frontal view;
- **WFI** Width of flagellomere I;
- **WFII** Width of flagellomere II;
- WTI Width of gastral tergum I, maximum, dorsally.

# Taxonomy

# Genus Passaloecus Shuckard, 1837

Type species. Pemphredon insignis Vander Linden, 1829.

## Key to the species of Passaloecus from China, including males and females

Females of *P. multituberculatus* Ma & Li, *P. petiolatus* Ma & Li and *P. tuberculi-formis* Bashir & Ma and males of *P. frontirugatus* Bashir & Ma, *P. labrinigratus* Ma & Li, *P. monilicornis taiwanus* Tsuneki, *P. clypearcuatus* sp. nov., *P. clypeconvexus* sp. nov., *P. edentutus* sp. nov., *P. margdentatus* sp. nov., and *P. sternoleios* sp. nov. remain unknown.

1	Clypeus deeply concave, free margin not produced (Fig. 1A)
	<i>P. clypearcuatus</i> Li & Ma, sp. nov.
_	Clypeus flat or raised, free margin slightly or broadly produced (Fig. 2A)2
2	Mandible tridentate apically
-	Mandible bidentate apically (Fig. 2A)5
3	Interantennal tubercle narrow and short; free margin of clypeus toothless, females truncate, males nearly arcuate
_	Interantennal tubercle robust, forming columned or conical projection; free margin of clypeus with three small teeth
4	Pronotal collar without anterior, transverse carina and antero-lateral corner;
	posterior area of mesopleuron smooth, without rugae; hypersternaulus shal-
	low, short, inconspicuously crenate; gaster distinctly constricted between
	terga I and II
_	Pronotal collar with robust, anterior, transverse carina, antero-lateral cor-
	ner slightly produced; posterior area of mesopleuron with dense, short,
	longitudinal rugae; hypersternaulus deep, normal length, distinctly cre-
	nate; gaster slightly constricted between terga I and II
5	Petiole slightly to distinctly longer than wide (Fig. 3F)6
-	Petiole not longer than wide (Fig. 2F)11
6	Hypersternaulus smooth, not crenate (Fig. 4D)7
-	Hypersternaulus distinctly crenate (Fig. 5D)
7	Free margin of clypeus slightly produced, with three distinct, conical teeth
	medially (Fig. 4A); posterior area of mesopleuron smooth, without rugae
	(Fig. 4D); scrobal suture broad, shallow, slightly crenate (Fig. 4D); labrum
	hardly constricted subapically; pronotal lobe black (Fig. 4D)
	<i>P. margdentatus</i> Li & Ma, sp. nov.
-	Free margin of clypeus broadly produced, with distinct emargination medi-
	ally (Fig. 3A); posterior area of mesopleuron with sparse, indistinct, short,
	longitudinal rugae (Fig. 3D); scrobal suture vestigial, only with single trace
	(Fig. 3D); labrum distinctly constricted subapically; pronotal lobe ivory
	(Fig. 3D) P. edentutus Li & Ma, sp. nov.

8	Inner orbital furrow broad, smooth, and with conspicuous, inner margin-
	al carina (Fig. 5A), outer orbital furrow broad, conspicuously crenate, and
	with conspicuous, find marginal carina (Fig. 5H); occipital carina broad,
	conspicuously crenate (Fig. 5B); notaulus absent (Fig. 5C); sternum I smooth,
	without rugae (Fig. 5G)
-	Inner and outer orbital furrows lacking; occipital carina narrow, not crenate;
	notaulus slightly or distinctly impressed; sternum I with several, short, longi-
	tudinal rugae
9	Lateral surface of propodeum with dense, slender, oblique rugae anteriorly;
	sternum I in anterior half with slender, median, longitudinal carina; gaster
	not constricted between terga I and II P. birugatus Bashir & Chen
-	Lateral surface of propodeum smooth, without rugae anteriorly; sternum I
	without median, longitudinal carina; gaster slightly or distinctly constricted
	between terga I and II10
10	Admedian line slightly impressed; gaster distinctly constricted between terga
	I and II; gena with dense, fine punctures ventrally; clypeus with dense, mid-
	size punctures
_	Admedian line distinctly impressed; gaster slightly constricted between terga
	I and II; ventral gena with sparse, fine punctures; clypeus with sparse, fine
	punctures
11	Scrobal suture distinct, weakly to distinctly crenate (Fig. 2D)12
_	Scrobal suture absent or weakly impressed, not crenate
12	Omaulus present: ocellar triangle flat
_	Omaulus absent (Fig. 2D): ocellar triangle slightly convex (Fig. 2B) <b>13</b>
13	Antero-lateral corner markedly produced: hypersternaulus and episternal sul-
10	cus distinctly broadened: frontal median carina absent
_	Antero-lateral corner absent (Fig. 2C): hypersternaulus and episternal sulcus
	of normal width (Fig. 2D): frontal median carina distinct (Fig. 2A) <b>15</b>
14	Females with south natches: interantennal tubercle reduced to one point:
17	labrum slightly constricted subanically: proposal lobe black
	<i>D labuinimatus</i> Mo & Li
	Formales without south patchess interantennal typerale distinct alightly alon
_	remaies without south patches; interantennal tubercie distinct, slightly con-
	gated; fabrum distinctly constricted subapically; pronotal tobe yellow
1.5	<i>P. frontirugatus</i> Bashir & Ma
15	Occipital carina distinctly crenate; labrum distinctly constricted subapically;
	anterior part of scutum normal; scutum with sparse, short, longitudinal rugae
	posteriorly
_	Occipital carina not crenate (Fig. 2B); labrum not constricted subapically;
	anterior part of scutum nearly right angle, significantly higher than prono-
	tum (Fig. 2C); scutum smooth, without rugae posteriorly (Fig. 2C)
	<i>P. clypeconvexus</i> Li & Ma, sp. nov.

16 _	Anterior part of scutum normal
17	tum
1/	clypeus distinctly convex medially; lateral surface of propodeum with dense, slender, oblique rugae anteriorly; antero-lateral corner moderately to distinct-
	ly produced; pronotal lobe white; in females, head from above with temples distinctly convergent posteriorly
_	Clypeus nearly flat medially; lateral surface of propodeum smooth anteriorly;
	from above with temples slightly convergent posteriorly
	<i>P. singularis</i> Dahlbom
18	Females with scutal patches; in males, posterior area of tergum VI without
	spinose tubercles P. turanicus Gussakovskij
_	Females without scutal patches; in males, posterior area of tergum VI with conspicuous spinose tubercles
19	Propodeal enclosure and posterior surface of propodeum irregularly reticu-
_	Propodeal enclosure with irregular rugae or reticulation medially and with
	sparse or dense, oblique rugge on each side: posterior surface of propodeum
	with irregular rugae
20	Pronotal collar with robust, anterior, transverse carina, antero-lateral corner
	markedly produced; occipital carina not crenate; lateral surface of propode-
	um with dense, slender, irregular, oblique rugae anteriorly, and with sparse,
	sturdy, oblique rugae posterioriy; body predominantly black
	Proposal coller without antorior transverse carina or antoro lateral corner oc
_	cipital carina distinctly crenate ventrally lateral surface of propodeum chiny
	nearly smooth anteriorly, and with sturdy reticulation posteriorly; body pre-
	dominantly vellowish-brown to reddish-brown
	<i>P tuberculiformis</i> Bashir & Ma
21	Occipital carina distinctly crenate: parapsidal line weakly impressed: metano-
	tum with sparse, tiny punctures; flagellum mostly vellow
	<i>P. koreanus</i> Tsuneki
_	Occipital carina not crenate; parapsidal line distinctly impressed; metanotum
	with dense, fine punctures; flagellum dark brown to black
22	Antero-lateral corner markedly produced; propodeal enclosure reticulated
	medially; frontal median carina weakly impressed; in male, flagellum nor-
	mal
_	Antero-lateral corner slightly produced; propodeal enclosure irregularly ru-
	gose medially; frontal median carina absent; in male, flagellum slightly mon- iliform
23	Pronotal lobe ivory to vellowish <i>P. monilicornis monilicornis</i> Dahlbom
_	Pronotal lobe black

### Species accounts

### Passaloecus clypearcuatus Li & Ma, sp. nov.

https://zoobank.org/28B30E12-2206-4FA6-8D22-4F71D2DCE5C2 Figs 1A–G

**Type material.** *Holotype*: CHINA •  $\bigcirc$ ; Yunnan, Shangri-La City, Pudacuo National Park; 27°55'13"N, 99°52'46"E; 3515 m elev.; 16.VII.2022; coll. Zhizhi Liu; sweep net (**YNAU**). *Paratype*: CHINA • 1 $\bigcirc$ ; Shaanxi, Baoji City, Tiantai Mountain Scenic Area; 34°17'10"N, 107°10'55"E; 852 m elev.; 8–10.VI.1998; NO.983654; coll. Yun Ma; sweep net (**YNAU**).

**Diagnosis.** This species differs from the similar species *P. labrinigratus* Ma & Li, 2012 and other congeners in the following characteristics: free margin of clypeus with two robust, triangular teeth medially, distinctly reflected, area between two teeth deeply concave; scutal patches absent; scutum with sparse, irregular, short, longitudinal rugae posteriorly; scapal hollow coriaceous, shiny and clearly defined; gaster not constricted between terga I and II. *Passaloecus labrinigratus* has the following characters: free margin of clypeus broadly produced, truncate medially; scutal patches ovate; scutum smooth, without rugae posteriorly; scapal hollow constricted between terga I and II.

**Description. Female.** *Measurements.* ♀, BL: 7.7 mm; HLF: HW: HLD = 63: 80: 51; HW: EWd: EW: TW: EL = 80: 15: 20: 28: 49; POD: OOD: OCD = 13: 13: 23; SL: PL: LFI: LFII: WFII: WFII = 29: 7: 12: 11: 6: 6; WAS: AOD: IAD = 6: 10: 14; EDU: EDL = 47: 49; PLL: PW: LTI: WTI = 10: 13: 55: 48.

**Color pattern.** Body black; mandible inner margin pale yellow, remainder reddish-brown to dark brown; labrum ivory medially, central part dark brown; ventral scape ivory to pale yellow; tegula, palpi and forewing veins dark brown; fore tibia and tarsus dark brown; mid leg: inner margin of femur, tibia, and tarsus pale yellow to yellowish-brown, remainder of femur and trochanter dark brown; basal 1/4 of hind tibia dark brown; clypeus with scattered, silvery, short setae.

*Head.* Mandible bidentate apically, inner tooth large (Fig. 1A). Labrum slightly narrower than clypeal lobe, V-shaped, apex bluntly rounded, slightly constricted sub-apically (Fig. 1A). Clypeus flat, with sparse, fine punctures, slightly coriaceous; free margin of clypeus with two robust, triangular teeth medially, distinctly reflected, area between two teeth deeply concave (Fig. 1A). Sides of lower frons slightly coriaceous; scapal hollow coriaceous, shallow, clearly defined; interantennal tubercle very short; frontal median carina absent; median and upper frons distinctly coriaceous, with dense, large punctures, sometimes contiguous (Fig. 1A). Ocellar triangle coarsely coriaceous, slightly coriaceous, with dense, midsize punctures (Fig. 1B). Vertex distinctly coriaceous, with dense, midsize punctures and weakly transverse striations (Fig. 1B). Dorsal gena coarsely coriaceous, with dense, fine to midsize punctures; ventral gena coarsely coriaceous, with midsize punctures. Occipital carina narrow, not crenate (Fig. 1B). Inner and outer orbital furrows lacking (Fig. 1A).



Figure 1. *Passaloecus clypearcuatus* Li & Ma, sp. nov. (female) A head, frontal view B head, dorsal view
C collar, scutum, scutellum and metanotum, dorsal view D thorax, lateral view E propodeum, dorsal view
F petiole and tergum I dorsal view G habitus, lateral view. Scale bars: 1 mm.

Mesosoma. Pronotal collar with robust, anterior, transverse carina, antero-lateral corner slightly produced (Fig. 1C). Scutum coarsely coriaceous, with dense, midsize punctures, anterior area nearly right angle, significantly higher than pronotum, posterior area with sparse, irregular, short, longitudinal rugae; scutal patches absent; admedian line distinctly impressed, extending to 1/3 of scutum length; notaulus shallowly impressed, indistinctly crenulate, extending to 1/3 of scutum length; parapsidal line distinct, longer than admedian line (Fig. 1C). Scutellum slightly coriaceous, with dense, midsize punctures (Fig. 1C). Metanotum slightly coriaceous, with dense, fine punctures (Fig. 1C). Mesopleuron coarsely coriaceous, with dense, midsize punctures, posterior area with sparse, very short, longitudinal rugae; scrobal suture deeply impressed, not crenate; hypersternaulus and episternal sulcus distinctly crenate; omaulus absent (Fig. 1D). Metapleuron shiny and smooth (Fig. 1D). Propodeal enclosure not delimited by carina, with irregular rugae medially, and several, robust oblique rugae laterally; posterior surface of propodeum with irregular rugae, interspersed with several, robust, transverse rugae (Fig. 1E); lateral surface of propodeum with dense, slender, irregular, oblique rugae anteriorly, and sparse, robust, oblique rugae posteriorly (Fig. 1D).

*Metasoma*. Petiole short, not longer than width; dorsal surface of petiole with median, longitudinal groove (Fig. 1F); lateral surface of petiole with two short,

longitudinal carinae (Fig. 1G). Gaster moderately matte, slightly coriaceous, with dense, fine punctures (Fig. 1G); sternum I with several, longitudinal rugae; median, longitudinal carina lacking; sternum II deeply impressed basally; gaster not constricted between terga I and II (Fig. 1G); pygidial plate lacking.

Male. Unknown.

Distribution. China (Yunnan, Shaanxi).

**Etymology.** The name *clypearcuatus* is derived from the Latin *clype-* (= clypeus) and the Latin word *arcuatus* (= arcuate), referring to the area between two teeth on free margin of clypeus with an arcuate, deep concavity.

### Passaloecus clypeconvexus Li & Ma, sp. nov.

https://zoobank.org/A0D16311-C339-4BCC-BD26-219213486496 Figs 2A–G

**Type material.** *Holotype*: CHINA •  $\bigcirc$ ; Xinjiang, Gongliu County, Qiaxi Forest Park; 43°5'44"N, 82°39'18"E; 1713.8 m elev.; 7.VII.2023; coll. Lili Dong; sweep net (**YNAU**). *Paratype*: CHINA • 1 $\bigcirc$ ; Xinjiang, Gongliu County, Hetaogou Scenic Area; 43°22'59"N, 82°16'10"E; 913 m elev.; 30.VI.2016; coll. Yicheng Li; sweep net (**YNAU**).

**Diagnosis.** This species can be distinguished from the similar species *P. bisulcatus* Bashir & Ma, 2019 and other congeners by: occipital carina not crenate; labrum not constricted subapically; anterior part of scutum nearly right angle, significantly higher than pronotum; scutum smooth, without rugae posteriorly; propodeal enclosure with irregular rugae medially, and with sparse, oblique rugae on each side. *Passaloecus bisulcatus* has the following characters: occipital carina distinctly crenate; labrum distinctly constricted subapically; anterior part of scutum normal; scutum with sparse, short, longitudinal rugae posteriorly; propodeal enclosure with sturdy, irregular reticulation.

**Description. Female.** *Measurements.* ♀, BL: 5.3 mm; HLF: HW: HLD = 53: 54: 36; HW: EWd: EW: TW: EL = 54: 13: 15: 25: 40; POD: OOD: OCD = 8: 9: 12; SL: PL: LFI: LFII: WFII: WFII = 20: 6: 6: 6: 3: 3; WAS: AOD: IAD = 4: 5: 6; EDU: EDL = 32: 22; PLL: PW: LTI: WTI = 6: 10: 38: 36.

**Color pattern.** Body black; mandible predominantly reddish-brown, basal inner margin grayish-white; palpi and tegula brown to dark brown; scape ventrally and pronotal lobe ivory; fore and mid tibiae and tarsis brown to dark brown; hind leg: tibia brown, except basal 1/4 ivory, tarsus brown; sides of lower frons and clypeus with scattered, silvery, short setae; outer margin of mandible with several golden, long setae.

*Head.* Mandible bidentate apically, inner tooth large (Fig. 2A). Labrum heartshaped, not constricted subapically. Clypeus conspicuously convex medially, coriaceous; free margin of clypeus broadly produced, truncate medially; sides of lower frons coarsely coriaceous (Fig. 2A). Scapal hollow coriaceous, shallow, not clearly defined (Fig. 2A). Interantennal tubercle narrow and short; frontal median carina slightly impressed; median and upper frons coarsely coriaceous, slightly convex, with dense, midsize punctures (Fig. 2A). Ocellar triangle shiny, moderately convex, with dense,



Figure 2. *Passaloecus clypeconvexus* Li & Ma, sp. nov. (female) A head, frontal view B head, dorsal view
C collar, scutum, scutellum and metanotum, dorsal view D thorax, lateral view E propodeum, dorsal view
F petiole and tergum I dorsal view G habitus, lateral view. Scale bars: 1 mm.

midsize punctures (Fig. 2B). Vertex shiny, coriaceous, with dense, weakly transverse striations (Fig. 2B). Gena shiny, coriaceous and impunctate. Occipital carina narrow, not crenate (Fig. 2B). Inner and outer orbital furrows lacking (Fig. 2A).

*Mesosoma.* Pronotal collar with robust, anterior, transverse carina, antero-lateral corner absent (Fig. 2C). Scutum shiny, with dense, midsize to large punctures, anterior area nearly right angle, significantly higher than pronotum and with sparse, transverse striations; scutal patches nearly ovate, slightly raised; admedian line weakly impressed, extending to 2/7 of scutum length; notaulus distinct and crenulate, slightly longer than admedian line; parapsidal line distinct, long (Fig. 2C). Scutellum shiny, with dense, fine punctures. Metanotum shiny and smooth (Fig. 2C). Mesopleuron shiny, with sparse, midsize punctures, posterior area with contiguous, very short, longitudinal rugae; scrobal suture narrow, shallowly impressed and weakly crenate;

hypersternaulus and episternal sulcus deep, conspicuously crenate; omaulus absent (Fig. 2D). Metapleuron shiny and smooth (Fig. 2D). Propodeal enclosure matte, not delimited by carina, with irregular rugae medially, and irregular, sparse, oblique rugae laterally, area between rugae with contiguous, fine punctures; posterior surface of propodeum coarsely coriaceous, shiny, and with reticulation posteriorly (Fig. 2E); lateral surface of propodeum with dense, slender, oblique rugae anteriorly, and irregular reticulation posteriorly (Fig. 2D).

*Metasoma*. Petiole short, not longer than width (Fig. 2F); dorsal surface of petiole with median, longitudinal groove (Fig. 2F); lateral surface of petiole with two short, longitudinal carinae (Fig. 2G). Gaster shiny, with sparse, tiny punctures; sternum I matte, with several, longitudinal rugae, median, longitudinal carina lacking; sternum II deeply impressed basally; gaster distinctly constricted between terga I and II (Fig. 2G); pygidial plate lacking.

Male. Unknown.

Distribution. China (Xinjiang).

**Etymology.** The name *clypeconvexus* is derived from the Latin *clype-* (= clypeus) and the Latin word *convexus* (= convex), referring to the clypeus conspicuously convex medially.

### Passaloecus edentutus Li & Ma, sp. nov.

https://zoobank.org/6F867050-BE09-41CA-A4F9-48D9A725A406 Figs 3A–G

**Type material.** *Holotype*: CHINA •  $\bigcirc$ ; Tibet, Shigatse City, Yadong County, Shang Yadong County, Galingang Village; 27°30'28"N, 88°57'40"E; 3445 m elev.; 24.VII.2018; NO.202006141; coll. Shijie Du; sweep net (**YNAU**). *Paratype*: CHINA • 1 $\bigcirc$ ; Tibet, Shigatse City, Gyirong County, Gyirong Town, Madun Bridge; 28°23'35"N, 85°19'45"E; 2795 m elev.; 1.VIII.2018; coll. Shijie Du; sweep net (**YNAU**).

**Diagnosis.** This species differs from *P. tuberangustus* Bashir & Ma, 2019 and other congeners by these characteristics: hypersternaulus smooth, not crenate; pronotal collar with weak, anterior, transverse carina laterally; lateral surface of propodeum with dense, slender, oblique rugae anteriorly; propodeal enclosure with irregular rugae medially, and sparse, irregular, oblique rugae laterally; mesopleuron coriaceous, posterior area with sparse, indistinct, very short, longitudinal rugae. *Passaloecus tuberangustus* has the following characters: hypersternaulus conspicuously crenate; pronotal collar without anterior, transverse carina; lateral surface of propodeum smooth and shiny anteriorly; propodeal enclosure with dense, slender, longitudinal rugae, and interspersed with several, short, transverse rugae medially; mesopleuron coarsely coriaceous, posterior area smooth, without rugae.

**Description. Female.** *Measurements.* ♀, BL: 6.9 mm; HLF: HW: HLD = 58: 67: 40; HW: EWd: EW: TW: EL = 67: 16: 16: 35: 43; POD: OOD: OCD = 7: 11: 18; SL: PL: LFI: LFII: WFI: WFII = 25: 7: 8: 8: 4: 5; WAS: AOD: IAD = 7: 10: 9; EDU: EDL = 49: 43; PLL: PW: LTI: WTI = 30: 7: 42: 35.



Figure 3. *Passaloecus edentutus* Li & Ma, sp. nov. (female) A head, frontal view B head, dorsal view
C collar, scutum, scutellum and metanotum, dorsal view D thorax, lateral view E propodeum, dorsal view
F petiole and tergum I dorsal view G habitus, lateral view. Scale bars: 1 mm.

**Color pattern.** Body black; mandible ivory except apex reddish-brown; palpi ivory to brown; ventral scape and pronotal lobe ivory; tegula and forewing veins dark brown; all tibiae and tarsis brown to dark brown; sides of lower frons and clypeus with scattered, silvery, short setae; outer margin of the mandible with scattered golden, long setae.

*Head.* Mandible bidentate apically, inner tooth large (Fig. 3A). Labrum broadly V-shaped, slightly wider than clypeal lobe, apex bluntly rounded, distinctly constricted subapically (Fig. 3A). Clypeus smooth medially, coriaceous elsewhere; free margin of clypeus broadly produced, distinctly emarginated medially (Fig. 3A). Sides of lower frons coarsely coriaceous; scapal hollow coriaceous, shallow, clearly defined; interantennal tubercle narrow and short; frontal median carina distinct, slightly impressed;

median and upper frons coarsely coriaceous, slightly convex, with dense, fine punctures (Fig. 3A). Ocellar triangle coarsely coriaceous, nearly flat, with dense, fine punctures (Fig. 3B). Vertex coriaceous, with dense, weak, transverse striations (Fig. 3B). Gena coriaceous, shiny, impunctate. Occipital carina narrow, not crenate (Fig. 3B). Inner and outer orbital furrows lacking (Fig. 3A).

*Mesosoma.* Pronotal collar with weak, anterior, transverse carina laterally, without antero-lateral corner (Fig. 3C). Scutum coarsely coriaceous, with dense, fine punctures, anterior area nearly right angle, significantly higher than pronotum, posterior area smooth, without rugae; scutal patches absent; admedian line distinctly impressed, extending to 1/3 of scutum length; notaulus indistinctly impressed, slightly shorter than admedian line; parapsidal line distinctly impressed, long (Fig. 3C). Scutellum and metanotum coriaceous and impunctate (Fig. 3C). Mesopleuron coriaceous, posterior area with sparse, indistinct, very short, longitudinal rugae; scrobal suture reduced to single trace; hypersternaulus narrowly, weakly impressed, smooth and not crenate; episternal sulcus broad, deeply impressed and distinctly crenate; omaulus absent (Fig. 3D). Metapleuron shiny and smooth (Fig. 3D). Propodeal enclosure matte, not delimited by carina, with irregular rugae medially, and sparse, irregular, oblique rugae laterally; posterior surface of propodeum coarsely coriaceous and with sparse, irregular rugae (Fig. 3E); lateral surface of propodeum with dense, slender, oblique rugae anteriorly, and sparse, robust, oblique rugae posteriorly (Fig. 3D).

*Metasoma*. Petiole long, conspicuously longer than width; dorsal surface of petiole with indistinct, median, longitudinal groove (Fig. 3F); lateral surface of petiole with two short, longitudinal carinae (Fig. 3G). Gaster shiny, with sparse, tiny punctures; sternum I with median, longitudinal carina and two longitudinal rugae; sternum II deeply impressed basally; gaster slightly constricted between terga I and II (Fig. 3G); pygidial plate lacking.

Male. Unknown.

Distribution. China (Tibet).

**Etymology.** The name *edentutus* is derived from the prefix *e*- (= without) and the Latin word *dentutus* (= dentate), referring to the hypersternaulus smooth, not crenate.

### Passaloecus margdentatus Li & Ma, sp. nov.

https://zoobank.org/63C7B755-BA33-4305-94EE-CD715B93EC7B Figs 4A–G

**Type material.** *Holotype*: CHINA •  $\bigcirc$ ; Yunnan, Shangri-La City, Jiantang Town, Lindu Village; 27°47'24"N, 99°48'36"E; 3321 m elev.; 13.VII.2022; coll. Huifen Jiang; Yellow Plates (**YNAU**). *Paratype*: CHINA • 1 $\bigcirc$ ; Yunnan, Shangri-La City, Jiantang Town, East Ring Road; 27°50'24"N, 99°46'48"E; 3373 m elev.; 14.VII.2022; coll. Lili Dong; sweep net (**YNAU**).

**Diagnosis.** This species is distinguished from *P. tuberangustus* Bashir & Ma, 2019 and other congeners by the following characteristics: in female, free margin of clypeus

with 3 distinct teeth; hypersternaulus smooth, not crenate; anterior margin of pronotal collar with slender, transverse carina; propodeal enclosure with irregular rugae medially, and sparse, irregular, oblique rugae laterally; pronotal lobe black. *Passaloecus tuberangustus* has the following characters: in female, free margin of clypeus with shallow emargination medially, in male, free margin of clypeus truncate; hypersternaulus distinctly crenate; pronotal collar without anterior, transverse carina; propodeal enclosure with dense, slender, longitudinal rugae, and interspersed with several, short, transverse rugae medially; pronotal lobe ivory.

**Description. Female.** *Measurements.* ♀, BL: 8.5 mm; HLF: HW: HLD = 77: 85: 42; HW: EWd: EW: TW: EL = 85: 20: 25: 50: 58; POD: OOD: OCD = 9: 12: 26; SL: PL: LFI: LFII: WFII = 35: 7: 11: 10: 6: 7; WAS: AOD: IAD = 6: 7: 7; EDU: EDL = 38: 37; PLL: PW: LTI: WTI = 20: 13: 52: 55.

**Color pattern.** Body black; mandible ivory except apex reddish-brown; margin of labrum ivory, central part brown; palpi brown to reddish-brown; scape ventrally ivory; tegula and forewing veins dark brown; fore leg: femur reddish-brown basally, tibia and tarsus yellowish-brown to dark brown; mid and hind tibiae and tarsis dark brown; sides of lower frons and clypeus with scattered, silvery, short setae; outer margin of mandible with scattered, golden, long setae.

*Head.* Mandible with two blunt teeth apically, inner tooth large (Fig. 4A). Labrum broad V-shaped, apex thickened, weakly constricted subapically (Fig. 4A). Clypeus coriaceous, nearly flat, with several, fine punctures basally; free margin of clypeus slightly produced, with three distinct teeth medially, all teeth moderately upturned, median tooth large, area between teeth deeply emarginated (Fig. 4A). Sides of lower frons coarsely coriaceous; scapal hollow shiny, coriaceous, shallow, clearly defined; interantennal tubercle narrow and short; frontal median carina very weakly impressed; median and upper frons coarsely coriaceous, slightly convex, with dense, midsize punctures (Fig. 4A). Ocellar triangle coriaceous, moderately convex, with sparse, fine to midsize punctures (Fig. 4B). Occipital carina narrow, not crenate (Fig. 4B). Inner and outer orbital furrows lacking (Fig. 4A).

*Mesosoma.* Anterior margin of pronotal collar with weak, transverse carina, anterolateral corner absent (Fig. 4C). Scutum coarsely coriaceous, with dense, fine to midsize punctures, anterior area nearly right angle, significantly higher than pronotum; scutal patches absent; admedian line distinct, weakly impressed, extending to 2/5 of scutum length; notaulus distinct, weakly impressed, extending to 1/3 of scutum length; parapsidal line distinctly impressed, long (Fig. 4C). Scutellum shiny, with dense, fine to midsize punctures (Fig. 4C). Metanotum shiny, with sparse, tiny punctures (Fig. 4C). Mesopleuron coriaceous, with sparse, fine to midsize punctures, posterior area smooth, without rugae; scrobal suture broad, shallowly impressed and weakly crenate; episternal sulcus broad, deeply impressed and conspicuously crenate; hypersternaulus with broad, deeply impressed, smooth, not crenate; omaulus absent (Fig. 4D). Metapleuron shiny, coarsely coriaceous (Fig. 4D). Propodeal enclosure matte, not delimited by carina, with irregular rugae medially, and sparse, irregular, oblique rugae laterally; posterior surface of propodeum coarsely coriaceous, with median, longitudinal rugae and



Figure 4. *Passaloecus margdentatus* Li & Ma, sp. nov. (female) A head, frontal view B head, dorsal view
C collar, scutum, scutellum and metanotum, dorsal view D thorax, lateral view E propodeum, dorsal view
F petiole and tergum I dorsal view G habitus, lateral view. Scale bars: 1 mm.

several, irregular, transverse rugae (Fig. 4E); lateral surface of propodeum with dense, slender, oblique rugae, anteriorly, and with sturdy oblique rugae posteriorly (Fig. 4D).

*Metasoma*. Petiole long, conspicuously longer than width (Fig. 4F); dorsal surface with conspicuous median, longitudinal groove (Fig. 4F); lateral surface of petiole with two sturdy, longitudinal, carinae (Fig. 4G). Gaster shiny, impunctate; sternum I with distinct, median, longitudinal carina and several, short, longitudinal rugae; sternum II shallowly impressed basally; gaster distinctly constricted between terga I and II (Fig. 4G); pygidial plate lacking.

Male. Unknown.

Distribution. China (Yunnan).

**Etymology.** The name *margidentatus* is derived from the Latin *marg-* (= margin), and the Latin word *dentatus* (= dental), referring to the free margin of clypeus with three distinct teeth medially.

#### Passaloecus sternoleios Li & Ma, sp. nov.

https://zoobank.org/DFE6A4EA-0E4A-48C6-AD7A-AE2D6C87DE65 Figs 5A–H

**Type material.** *Holotype*: CHINA •  $\bigcirc$ ; Guangdong, Qingyuan City, Fogang County, Guanyin Mountain; 23°58'12"N, 113°33'49"E; 353 m elev.; 15–16.IX.2007; Yellow Plates (**YNAU**). *Paratype*: CHINA • 1 $\bigcirc$ ; Guangdong, Shaoguan City, Nanling National Nature Reserve; 24°54'49"N, 113°2'30"E; 845 m elev.; 23.V.2020; coll. Fei Ye; flight intercept traps (**YNAU**).

**Diagnosis.** This species differs from *P. insignis* (Vander Linden, 1829) and other congeners by these characteristics: petiole conspicuously longer than width; inner and outer orbital furrows broad, marginal carina conspicuous, outer orbital furrow distinctly crenate; occipital carina broad, conspicuous crenate; notaulus lacking; sternum I smooth, without carina and rugae. *Passaloecus insignis* has the following characters: petiole not longer than width; inner and outer orbital furrows lacking; occipital narrow, not crenate; notaulus shallowly impressed, crenate; sternum I with sturdy, median, longitudinal carina and several, short, longitudinal rugae.

**Description. Female.** *Measurements.* ♀, BL: 7.8 mm; HLF: HW: HLD = 73: 78: 30; HW: EWd: EW: TW: EL = 78: 20: 26: 33: 60; POD: OOD: OCD = 10: 13: 16; SL: PL: LFI: LFII: WFII = 28: 6: 7: 7: 5: 5; WAS: AOD: IAD = 6: 5: 7; EDU: EDL = 42: 32; PLL: PW: LTI: WTI = 25: 10: 40: 52.

**Color pattern.** Body black; mandible ivory except apex yellowish-brown to reddish-brown; central part of labrum with ivory, V-shaped stripe, remainder yellowishbrown; palpi ivory to pale yellow; ventral scape and pronotal lobe ivory; dorsal scape, pedicel, flagellum, tegula, forewing veins yellowish-brown to dark brown; fore leg: apex of trochanter ivory, remainder dark brown, femur dark brown except base and apex yellowish-brown to brown, tibia and tarsus pale yellow to yellowish-brown; mid and hind legs: apex of trochanter, base of femur, ventral tibia and tarsus yellowish-brown, remainder dark brown; sides of lower frons and clypeus with scattered, silvery, short setae; clypeus with sparse, golden, short setae, and interspersed with several golden, long setae apically; labrum with several, golden, long setae apically.

*Head.* Mandible bidentate apically, inner tooth large (Fig. 5A). Labrum slightly narrower than clypeal lobe, heart-shaped, distinctly constricted subapically (Fig. 5A). Clypeus slightly convex medially, coriaceous; free margin of clypeus broadly produced, semicircular (Fig. 5A). Sides of lower frons coarsely coriaceous, and with irregular, longitudinal rugae; scapal hollow coriaceous, shiny, slightly deep, clearly defined; interantennal tubercle narrow and short; median and upper frons coarsely coriaceous, with sparse, irregular, transverse rugae, frontal median carina strong, extending to anterior ocellus (Fig. 5A). Ocellar triangle shiny, moderately convex, with sparse, fine to midsize punctures (Fig. 5B). Vertex shiny, with sparse, fine punctures (Fig. 5B). Gena shiny, coriaceous, with sparse, indistinct, midsize punctures. Occipital carina broad, conspicuously crenate (Fig. 5B). Inner orbital furrow broad, smooth, shiny, boundary carina distinct (Fig. 5A); outer orbital furrow broad, distinctly crenate, boundary carina distinct (Fig. 5H).



**Figure 5.** *Passaloecus sternoleios* Li & Ma, sp. nov. (female) **A** head, frontal view **B** head, dorsal view **C** collar, scutum, scutellum and metanotum, dorsal view **D** thorax, lateral view **E** propodeum, dorsal view **F** petiole and tergum I dorsal view **G** petiole and sternum I ventral view **H** habitus, lateral view. Scale bars: 1 mm.

*Mesosoma.* Anterior margin of pronotal collar with strong, arcuate, transverse carina, antero-lateral corner markedly produced (Fig. 5C). Scutum coarsely coriaceous, with dense, fine to midsize punctures, posterior area with several, indistinct, very short, longitudinal rugae; scutal patches absent; admedian line robust, distinctly raised, extending to 1/3 of scutum length; notaulus lacking; parapsidal line distinctly impressed, slightly shorter than admedian line (Fig. 5C). Scutellum shiny, with dense, fine punctures (Fig. 5C). Metanotum smooth and shiny (Fig. 5C). Mesopleuron shiny, with scattered fine punctures, posterior area with contiguous, short, longitudinal rugae; scrobal suture lacking; hypersternaulus and episternal sulcus broad, conspicuously crenate; omaulus absent (Fig. 5D). Metapleuron shiny and smooth (Fig. 5D). Propodeal enclosure shiny, not delimited by carina, with sturdy, irregular rugae medially, and sparse, sturdy, oblique rugae laterally; posterior surface of propodeum reticulated (Fig. 5E); lateral surface of propodeum with dense, slender, oblique rugae anteriorly, and irregular reticulation posteriorly (Fig. 5D).

*Metasoma*. Petiole long, conspicuously longer than width, smooth, without carina or rugae (Fig. 5F). Gaster shiny, and with sparse, tiny punctures; sternum I smooth and shiny, without carina or rugae (Fig. 5G); sternum II deeply impressed basally (Fig. 5G); gaster slightly constricted between terga I and II (Fig. 5H); pygidial plate lacking.

Male. Unknown.

Distribution. China (Guangdong).

**Etymology.** The name *sternoleios* is derived from the Greek *stern-* (= sternum), and the Greek word *leios* (= smooth), referring to the sternum I smooth and shiny, without carina or rugae.

### Discussion

The genus *Passaloecus* comprises 46 species and 5 subspecies globally, primarily distributed across the Palearctic, Nearctic, and Oriental regions. China boasts the highest diversity of this genus, with 18 species and 1 subspecies recorded across its Provinces (Ma and Li 2012; Bashir et al. 2021; Pulawski 2024). Furthermore, the identification of 5 new species in this study enhances the existing species records in China, indicating that many more undiscovered species likely exist in regions that remain insufficiently explored. This significant diversity is closely associated with China's unique geographical position, which spans both the Palearctic and Oriental regions. It reflects a rich ecosystem and diverse climatic conditions that provide favorable environments for the survival and reproduction of *Passaloecus* (Fan et al. 2024).

Notably, all 13 known species and one subspecies of *Passaloecus* in the Oriental region are exclusively distributed in China, with no records found in other Oriental countries, such as those in Southeast Asia (Bashir et al. 2023). However, the climate of China's Oriental region closely resembles that of neighboring Southeast Asian countries, both classified as subtropical and tropical climate types, and there are no significant geographical barriers separating them (Yang et al. 2020; Meng and Song 2023). Consequently, it can be inferred that the *Passaloecus* genus may also be present in Southeast Asia.

From a global perspective, further collection and research efforts are essential. Although only one species of the *Passaloecus* genus is currently recorded in the Neotropical region, the climatic conditions there are highly conducive to species diversification, suggesting the potential existence of additional undiscovered species (Amarante and Vincent 1993; Vardy 2017). Furthermore, there are currently no distribution records for this genus in the Afrotropical and Australian regions, which may be attributed to a combination of factors, including climatic conditions, historical geographical isolation, and ecological competition (Machac 2023). Additionally, the inadequacy of collection efforts and research may hinder the accuracy of current species records. Increased investigations in these regions could lead to the discovery of new distributions of this genus, which is crucial for understanding the global diversity of *Passaloecus*.

### Acknowledgements

We extend our heartfelt thanks to Wojciech J. Pulawski (California Academy of Sciences, California) for providing us with numerous valuable references, and to Prof. Zhiqiang Li and Dr. Fei Ye from the Institute of Zoology, Guangdong Academy of Sciences, for supplying the specimens. We also express our sincere gratitude to the section editor and all anonymous reviewers for their valuable and constructive comments, which have greatly improved this article. This work was supported by the National Natural Science Foundation of China under Grant number 32270485 and the Agricultural Basic Research joint project of Yunnan Province under Grant number 202101BD070001-004.

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CHECKLIST



# Checklists of the Ceraphronoidea, Cynipoidea, Evanioidea, Stephanoidea and Trigonalyoidea (Hymenoptera) of Canada, Alaska and Greenland

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Academic editor: Miles Zhang   Received 25 June 2024   Accepted 9 October 2024   Published 22 November 2	2024

**Citation:** Bennett AMR, Buffington ML, Deans AR, Forshage M, Melika G, Mikó I, Smith DR (2024) Checklists of the Ceraphronoidea, Cynipoidea, Evanioidea, Stephanoidea and Trigonalyoidea (Hymenoptera) of Canada, Alaska and Greenland. Journal of Hymenoptera Research 97: 1163–1220. https://doi.org/10.3897/jhr.97.130428

#### Abstract

Distributional checklists of the extant, described species of five superfamilies of Hymenoptera of Canada, Alaska and Greenland are presented. In total, 296 species in 79 genera in 12 families are recorded: 55 species of Ceraphronoidea, classified in 10 genera in 2 families, 205 species of Cynipoidea in 58 genera in 5 families, 30 species of Evanioidea in 5 genera in 3 families of Evanioidea, 2 species of Stephanoidea in 2 genera in 1 family and 4 species of Trigonalyoidea in 4 genera in 1 family. Of the reported species, 281 (in 79 genera in 12 families) are listed from Canada, 31 (in 16 genera in 6 families) from Alaska, and 7 (in 5 genera in 2 families) from Greenland. The list includes 8 new generic records for Canada (1 Ceraphronoidea, 6 Cynipoidea and 1 Evanioidea) and 43 new Canadian species records (13 Ceraphronoidea, 28 Cynipoidea and 2 Evanioidea). For each species in Canada, distribution is tabulated by province or territory, except the province

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of Newfoundland and Labrador is divided into the island of Newfoundland and the region of Labrador. These checklists are compared with previous Nearctic and Palaearctic surveys, checklists and catalogues. *Klei-dotoma minima* Provancher, 1883 (Figitidae) is moved from this genus to *Hexacola* Förster, 1869 to form *H. minimum* (Provancher, 1883), **comb. nov.** *Amblynotus slossonae* Crawford, 1917 (Figitidae) is moved from *Melanips* Walker, 1835 to *Amphithectus* Hartig, 1840 forming *A. slossonae* (Crawford, 1917), **comb. nov.** 

#### Keywords

Hymenoptera superfamilies, northern North America, species distributions

#### Introduction

Following publication of the introduction of the checklists of the Hymenoptera of Canada, Alaska and Greenland (Bennett 2021) as well as the checklists of the sawflies (Goulet and Bennett 2021) and the Chalcidoidea and Mymarommatoidea (Huber et al. 2021), the fourth installment in the series presents checklists of five more superfamilies. Most species in this paper (205 of 296) belong to the Cynipoidea, but species of four relatively small superfamilies (at least in terms of described species in the northern Nearctic region) are also included, rather than deal with these in one or more separate papers. Other than the total species counts detailed in Tables 1, 2 and the summary, each superfamily is treated separately.

#### Ceraphronoidea

Ceraphronoidea (Figs 4–9) is a cosmopolitan, but relatively poorly studied superfamily classified in two extant families: Ceraphronidae and Megaspilidae (Johnson and Musetti 2004). Species are small-bodied (5 mm or less), predominantly black (not metallic) with reduced wing venation (lacking closed cells) (Figs 4, 5). In this respect, they superficially resemble Scelionidae (Platygastroidea) and non-metallic Chalcidoidea. See Goulet and Huber (1993) for characters to distinguish these three superfamilies. Ceraphronoidea have been reared from many insect orders and with varied life histories. Within Ceraphronidae, Aphanogmus thylax Polaszek and Dessart was reared as an obligate hyperparasitoid of bagworm larvae (Lepidoptera: Psychidae) via Dolichogenidea metesae (Nixon) (Hymenoptera: Braconidae), but also via a tachinid fly (Diptera: Tachinidae) (Kamarudin et al. 1996), A. flavigastris Matsuo has been reared as a solitary or gregarious parasitoid of gall midges (Feltiella spp.) (Diptera: Cecidomyiidae) (Matsuo et al. 2016), A. albicoxalis Evans and Dessart was reared as a gregarious ectoparasitoid of prepupae and pupae of cybocephalid beetles (Coleoptera: Cybocephalidae) (Evans et al. 2004) and an undescribed species has been reared as an ectoparasitoid of pupae of caddisflies (Trichoptera: Hydroptilidae) (Luhman et al. 1998). Within Megaspilidae, species of Conostigmus Dahlbom (Fig. 7) have been most commonly reared as solitary endoparasitoids in puparia or pupae of Diptera (Kamal 1926 in Syrphidae; Guppy 1961 in Cecidomyiidae). Conostigmus species have also been reared as endoparasitoids of a snow scorpionfly (Mecoptera: Boreidae) (Cooper and Dessart 1975) and have been collected from nests of ants (Hymenoptera: Formicidae) (Panis 2008). See Trietsch et al. (2020) for a summary of known biology of *Conostigmus*. Species of the sister genus *Dendrocerus* Ratzeburg (Fig. 8) have been reared as gregarious ectoparasitic hyperparasitoids developing on prepupae and pupae of the primary parasitoid *Aphidius* spp. (Hymenoptera: Braconidae) inside mummies of parasitized aphids (Hemiptera: Aphididae) (Haviland 1920; Fergusson 1980; Mackauer 2017). Rearings of ceraphronoids from Neuroptera and Thysanoptera are also reported (Johnson and Musetti 2004), for example *D. conwentziae* Gahan (Fig. 8) has been reared from a dustywing *Conwentzia* sp. (Neuroptera: Coniopterygidae) (Muesebeck 1979).

The phylogenetic placement of Ceraphronoidea within Hymenoptera has been historically equivocal (see Heraty et al. 2011; Sharkey et al. 2012). Recent molecularbased study places Ceraphronoidea as the sister group of Ichneumonoidea (Peters et al. 2017) or as sister group to Evanioidea + Stephanoidea (Blaimer et al. 2023). In terms of previous surveys, Johnson and Musetti (2004) published a world catalog with species distributions by region that totalled 603 extant described species up to September 2003. Muesebeck (1979) provided the last catalogue for North America north of Mexico including distributions by state and province. Masner et al. (1979) summarized the species number of Ceraphronoidea for Canada and this was updated by Bennett et al. (2019). Buhl (2015) listed the species from Greenland. For identification, Dessart and Cancemi (1987) provided keys to world genera.

#### Cynipoidea

Cynipoidea (gall wasps and allies) (Figs 10–33) is a moderately diverse superfamily. There are about 3200 described species globally (Huber 2017) currently classified into 7 extant families (Buffington et al. 2020; Hearn et al. 2024). Austrocynipidae has only 1 species from Australia (Ronquist 1999) and Ibaliidae is known from 20 extant species in 3 genera in the Holarctic and Oriental regions including Papua New Guinea (Nordlander et al. 1996; Liu 1998; Buffington et al. 2020). Liopteridae is moderately speciose with 175 species in 10 genera and most species are tropical or subtropical (Buffington et al. 2020). Figitidae is the largest family, but also the most poorly known, with estimates of described species ranging from 1423 (Buffington et al. 2020) to 1570 (Huber 2017), depending on differing opinions on the validity of some taxa. The family is cosmopolitan including species in the high Arctic. Until recently, there was only one other cynipoid family recognized: Cynipidae; however, the phylogenomic study of Blaimer et al. (2020) suggested the lack of monophyly of Cynipidae and more recent phylogenomic work by Hearn et al. (2024) formally divided Cynipidae into three families: Cynipidae sensu stricto, Diplolepididae (previously Cynipinae: Diplolepidini and Pediaspidini) and Paraulacidae (previously Cynipinae: Paraulacini). Following the removal of Diplolepididae and Paraulacidae, Cynipidae has more than 1400 described, extant species, all belonging to subfamily Cynipinae (Buffington et al. 2020). Diplolepididae has 63 described species in 4 genera including Diplolepis Geoffrey that has species in northern North America. Paraulacidae is comprised of two genera, each with three species, all from southern South America (Hearn et al. 2024). Within Hymenoptera, phylogenomic studies place Cynipoidea within the

"Proctotrupomorpha" with Chalcidoidea, Diaprioidea, Mymarommatoidea, Platygastroidea and Proctotrupoidea. Peters et al. (2017) found Cynipoidea to be the sister group to all other superfamilies within Proctotrupomorpha, whereas Blaimer et al. (2023) hypothesized that Cynipoidea + Platygastroidea was sister group to the other superfamilies.

Morphologically, cynipoids can generally be distinguished from other superfamilies by having moderately reduced wing venation with a characteristic, triangular, radial (= marginal) cell in the fore wing, as well as a laterally flattened metasoma and they generally lack metallic colouration (Ritchie 1993). They are also unique within Hymenoptera in that the radicle of the antenna is absent (not distinguishable from the scape) (Ronquist 1995). With respect to biology, Austrocynipidae, Ibaliidae and Liopteridae are parasitoids of wood-boring or cone-boring larvae of Lepidoptera, Hymenoptera or Coleoptera that pupate inside hard substrates and consequently have adaptations for boring in wood, for example, strongly sclerotized mandibles, transverse ridges on the mesoscutum and an elongate body (Ronquist 1999). Cynipidae, Diplolepididae, Figitidae and Paraulacidae have a characteristic high, compact mesosoma and short, rounded metasoma and lack the characteristics for living in wood (Ronquist 1999). Diplolepididae and most Cynipidae are gall makers (Shorthouse 2010; Melika and Abrahamson 2002) although some Cynipidae are phytophagous inquilines living in galls made by other insects (Ritchie 1993; Nastasi et al. 2024b). All Figitidae are parasitoids of larvae of Hymenoptera, Diptera or Neuroptera (Ronquist 1999; Buffington et al. 2020). Paraulacidae appear to be parasitoids of gall-inducing Melanosomellidae (Hymenoptera: Chalcidoidea) on southern beech (Nothofagus: Nothofagaceae) (Rasplus et al. 2022).

In terms of previous Nearctic catalogues and faunal surveys, Burks (1979) provided the last complete catalogue of all species of Cynipoidea of North America north of Mexico and various authors have published updated catalogues of particular groups, for example, a catalogue of the Nearctic rose gall, herb gall and inquiline gall wasps (Cynipidae and Diplolepididae) (Nastasi and Deans 2021) as well as illustrated keys to these groups in North America (Nastasi et al. 2024b). In addition, a world catalogue for Charipinae is available (Ferrer-Suay et al. 2012) and a Nearctic catalogue for Eucoilinae (Forshage et al. 2013). Masner et al. (1979) summarized the species numbers for Canada and these numbers were updated for Canada by Bennett et al. (2019) Vilhelmsen and Forshage (2015) summarized the Cynipoidea fauna of Greenland. With respect to taxonomic revisions, the Nearctic species of Ibaliidae are well-known (Liu and Nordlander 1992) as is the one genus of Liopteridae (Paramblynotus Cameron) known from northern North America (Liu et al. 2007). Within Cynipidae, many studies treating Nearctic species have been published in the last few years. For example, Melika and Abrahamson (2007) revised Bassettia Ashmead and Lobato-Vila and Pujade-Villar (2019) treated the tribe Ceroptresini including the genus Ceroptres Hartig, but some of the larger genera, e.g., Andricus Hartig (Fig. 11) and Aulacidea Ashmead (Fig. 13) have not been revised at all and some of those that have still require additional study (e.g., Nastasi et al. 2024c described an additional 22 species of Ceroptres, most of which are Nearctic and suggested that hundreds more undescribed species may be present in the genus). Some generic definitions may also require clarification (e.g., Cuesta-Porta et al.

2023 that resurrected Druon Kinsey out of Andricus). Finally, newly recognized associations of sexual and asexual forms, especially using DNA barcoding continues to result in new synonymies and new combinations (e.g., Nicholls et al. 2022), highlighting the taxonomic challenges of Cynipidae. In terms of Dipolepididae, some of the species definitions of *Diplolepis* Geoffrey (Fig. 15) also require clarification (Zhang et al. 2019). In Figitidae, two subfamilies have been the subject of several recent studies including revisions of all major genera: Aspicerinae (Ros-Farré and Pujade-Villar 2009a, 2011a, 2011b, 2013) and Charipinae (Paretas-Martinez et al. 2011; Ferrer-Suay et al. 2013, 2019). In contrast, the subfamily Anacharitinae has only been partially revised for the Neartic region (e.g., Mata-Casanova et al. 2014 for Xyalaspis Hartig), but other genera such as Aegilips Walker and Anacharis Dalman (Fig. 22) are in the process of being revised as of 2024. The majority of Nearctic species of Eucoilinae are still undescribed and working keys to all the Nearctic genera are not available (Forshage et al. 2013), although some genera have been revised for the region, for example, Banacuniculus Buffington (Buffington 2010a) and Ganaspidium Weld (Buffington 2010b). This is true as well for Figitinae, although some genera have been at least partially revised for the Nearctic including Neralsia Cameron (Jiménez et al. 2008a) (Fig. 29) and Xyalophora Kieffer and Xyalophoroides Jiménez and Pujade-Villar (Jiménez et al. 2008b) (Fig. 30).

# Evanioidea

Evanioidea (ensign wasps and allies) (Figs 34-39) is a relatively small superfamily with 1,130 species globally (Huber 2017; Deans et al. 2023). It is mostly a tropical group with a limited number of taxa having ranges that extend to northern latitudes (Mason 1993; Bennett et al. 2019). There are three extant families (Li et al. 2018), all of which are present in northern North America: Aulacidae (Figs 34, 35), Evaniidae (ensign or hatchet wasps) (Figs 36, 37), and Gasteruptiidae (Figs 38, 39). Evanioidea are nonmetallic in colour and have wing lengths in Nearctic species ranging from 2.3 mm in one species of Evaniidae (Townes 1949b) to over 13 mm in some Aulacidae (Townes 1950). Evanioidea possess the synapomorphy of having the metasoma attached high on the propodeum (Goulet and Huber 1993; Li et al. 2018). In terms of biology, Aulacidae are parasitoids of wood-boring insects, although hosts are not certain for many species. Some species of Aulacus Jurine (e.g., Fig. 34) are associated with species of Xiphydria Latreille (Hymenoptera: Xiphydriidae), for example, A. burquei (Provancher) has been reared from branches infested with X. maculata Say (Smith 1996a). Species of Pristaulacus Kieffer (Fig. 35) are also associated with Xiphydria, but also beetles (Coleoptera), for example, Pristaulacus californicus (Townes) has been reared from logs infested with Paratimia conicola Fisher (Cerambycidae) and Chrysophana placida (Leconte) (Buprestidae) (Townes 1950). Evaniidae lay their eggs in the oothecae of cockroaches (Dictyoptera: Blattaria) (Deans 2005; Deans et al. 2023) and the larvae generally consume more than one egg during development which makes them predators, not parasitoids. Similar to Aulacidae, it is difficult to be certain of the precise hosts of most species of Gasteruptiidae (Figs 38, 39), but they have been reared from nests of solitary bees (Zhao et al. 2012) and it is assumed that they are predators of these bees, and perhaps also of solitary wasps. The larval gasteruptiid preys on one or more eggs or larvae to complete development (Mason 1993).

The phylogenomic study of Peters et al. (2017) recovered Evanioidea as the sister group of Stephanoidea with these two superfamilies placed as the sister group to Trigonalvoidea + Aculeata. Blaimer et al. (2023) also recovered the sister group relationship with Stephanoidea which along with Ceraphronoidea was sister group to (Trigonalyoidea + Megalyroidea) + Aculeata. Keys to the Nearctic species of Aulacidae are available (Townes 1950) and a more recent key to eastern species was provided by Smith (1996a) with updated valid names and combinations, for example Aulacostethus Phillipi of Townes (1950) = Pristaulacus Kieffer. A key to the Nearctic species of Gasteruptiidae is available (Townes 1950) and Smith (1996b) presented a more recent key to the eastern species with valid names, e.g., all species of Rhydinofoenus Bradley in Townes (1950) are now placed in Gasteruption Latreille. A key to world genera of Evaniidae is available (Deans and Huben 2003) and a key to Nearctic species has been published (Townes 1949b). Carlson (1979b) provided the Nearctic catalogue for Evanioidea, Deans (2005) updated the world catalogue for Evaniidae, and Smith (2001) published a world catalogue of Aulacidae. An online catalogue for Evanioidea including lists of all world species of Aulacidae and Evaniidae (Gasteruptiidae to be completed in the future) and an extensive list of references is available at Evanioidea Online (Deans et al. 2023).

#### Stephanoidea

Stephanoidea (Figs 40, 41) is a small, widespread superfamily of Hymenoptera comprised of one extant family: Stephanidae (Mason 1993). There are more than 360 described species worldwide (Aguiar 2004; Ceccolini 2021). Specimens are rarely collected with 95% of species being described from singletons (Aguiar 2004). They are long, slender insects with body length up to 3.5 cm (Hong et al. 2011) and are idiobiont ectoparasitoids of wood-boring insect larvae (Mason 1993). Most substantiated rearings are from Cerambycidae (Coleoptera) (Visitpanich 1994) and Buprestidae (Coleoptera) (Townes 1949a), but other families of beetles can also serve as hosts, as well as Siricidae (Hymenoptera) (Kirk 1975). See above (Evanioidea) for hypotheses of their placement in Hymenoptera. Most species of stephanids occur in tropical and subtropical forests (Hong et al. 2011), but species are also known from cooler regions as well as drier habitats such as deserts (Benoit 1984). Keys to genera are provided by van Achterberg (2002) (for the Old World, but including all genera) and Li et al. (2017) (including fossils). A key to the Nearctic species is provided by Aguiar and Johnson (2003). Aguiar (2004) published a world catalog including species distributions by country.

#### Trigonalyoidea

Trigonalyoidea (Figs 42, 43) includes one extant family (Trigonalyidae). The correct spelling of the family group name is controversial (Trigonalidae, Trigonalyidae or Trigonalydidae). For now, we follow Engel and Lelej (2020), although a future decision

from the International Commission on Zoological Nomenclature may be needed to establish one universally accepted family group name. The family is cosmopolitan with the exception of very high latitudes and alpine regions, but most species occur in tropical regions (Carmean and Kimsey 1998). Trigonalyids are not generally commonly collected (but see Smith 1996c) and are sometimes mistaken for Aculeata or Ichneumonidae because of similar wing venation and because most species have aposematic black and yellow body colour like many aculeates, whereas some have white-banded antennae like some ichneumonids (Chen et al. 2014). Trigonalyidae females lay eggs directly on leaves or detritus which may be eaten by caterpillars (Lepidoptera) (e.g., Clausen 1931), sawfly larvae (Hymenoptera) (e.g., Li et al. 2012) or crane fly larvae (Diptera: Tipulidae) (e.g., Gelhaus 1987). Because of the low chance of an egg being consumed, fecundity of female trigonalyids is very high, with females being observed to lay thousands of eggs, for example, Clausen (1929) reported a female of Taeniogonalos (= Poecilogonalos) thwaitesii (Westwood) lay 10,641 eggs in 14 days. Once ingested, the eggs hatch and the larvae bore through the intestinal wall of the host in search of an endoparasitoid larva such as an ichneumonid wasp as used by P. thwaitesii (Clausen 1929) or a tachinid fly as used by Orthogonalys pulchella (Cresson) (Carlson 1979c) (Fig. 42). If the host is not parasitized, then it is thought that trigonalyid larvae do not continue development (Smith 1996c). If it is parasitized, then the trigonalyid larva is presumed to be either ingested by the parasitoid larva or the trigonalyid larva directly penetrates the parasitoid larva (Weinstein and Austin 1991). The exceptions to this situation are for species of several genera including Bareogonalos Schulz and Nomadina Westwood that are known to develop in the nests of Vespinae and Polistinae (Vespidae), respectively, following provisioning of the vespid larval cells with caterpillar or sawfly larvae parasitized by trigonalyid larvae (Carmean 1991; Carmean and Kimsey 1998). In addition, some specimens of Lycogaster pullata Shuckard have been known to develop in a similar way in the nests of Eumeninae (Vespidae) (Cooper 1954), although this species also develops via ichneumonid-parasitized caterpillars (Bischoff 1909). Finally, eggs of two species of Australasian Taeniogonalos that are ingested by larvae of Perga spp. (Hymenoptera: Pergidae) are known to be able to develop as primary parasitoids in these hosts (Raff 1934) but can also develop as facultative hyperparasitoids (Weinstein and Austin 1995).

Phylogenetically, Carmean and Kimsey (1998) performed a morphology-based analysis of the internal relationships of Trigonalyidae, recognizing two subfamilies, although some later authors, for example, Chen et al. (2014), do not recognize these subfamilies. Trigonalyoidea are generally recovered as the sister group to Aculeata (Peters et al. 2017) or as the sister group of Megalyroidea which together form the sister group to Aculeata (Blaimer et al. 2023). Peters et al. (2017) did not include a representative of Megalyroidea in their study. Worldwide, there are about 120 described species of Trigonalyidae (Chen et al. 2020). A key to the Nearctic species is provided by Townes (1956), although one species (from the southeastern USA) has been described since then (Smith and Stocks 2005). Weinstein and Austin (1991) published a species catalogue for Trigonalyidae and an updated list of described species was provided by Carmean and Kimsey (1998). An online resource to the family is maintained by Carmean (2023).

# Methods

#### Sources of data

The starting point of this study was based on examination of specimens deposited in the Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, ON, Canada (A. Bennett) (CNC). Other examined specimens are deposited in the following collections (with current curators and acronyms used in Table 2): American Museum of Natural History, New York, NY, USA (J. Carpenter) (AMNH); Centre for Biodiversity Genomics, University of Guelph, Guelph, Ontario, Canada (J. deWaard) (BIOUG); California Academy of Sciences, San Francisco, CA, USA (B. Zuparko) (CAS); Lyman Entomological Museum, McGill University, Montréal, QC, Canada (S. Boucher) (LEMQ); North Carolina State University, Raleigh, NC, USA (M. Bertone) (NCSU); Natural History Museum, London, United Kingdom (G. Broad) (NHMUK); Plant Health Diagnostic National Reference Laboratory, National Food Chain Safety Office, Budapest, Hungary (G. Melika) (PHDNRL); Royal Alberta Museum, Edmonton, AB, Canada (M. Buck) (PMAE); Frost Entomological Museum, University Park, PA, USA (A. Deans) (PSUC); Royal Ontario Museum, Toronto, ON, Canada (D.C. Darling) (ROM); Royal Saskatchewan Museum, Regina, SK, Canada (C. Sheffield) (RSKM); Texas A&M University, College Station, TX, USA (J. Oswald) (TAMU); University of Alaska Museum, Fairbanks, AK, USA (D. Sikes) (UAM); Provancher Collection, University of Laval, Laval, QC, Canada (C. Cloutier) (ULQC); United States National Museum, Washington, DC, USA (M. Buffington) (USNM). Some records are based on literature sources for which specimens could not be examined (literature citations shown in Table 2). In addition, several records were included based on verified photos from iNaturalist (iNat) or BugGuide (BugG) taken by individuals noted in the acknowledgements. We only include described species, not undescribed taxa or specimens identified only to genus. Fossils are not included in the checklist. All records published or in press up to October 1, 2024 were evaluated for the current checklist.

#### Presentation of data

Distributional data are presented as follows: Table 1 is a summary of the numbers of described, recorded species of the treated five superfamilies in Canada, Alaska and Greenland totalled for each family for all distributional regions of northern (mostly north of 45° latitude) North America. Table 2 is the species checklist arranged alphabetically by superfamily for these same regions. Species recorded in the literature but of uncertain taxonomy are included in Table 3 and these species are not included in the totals in Table 1. Distributions are indicated in these tables using acronyms of 17, mostly political regions. For practical purposes the province of Newfoundland and Labrador is divided into the island of Newfoundland and the region of Labrador on mainland Canada. The acronyms used for the regions are: AK = Alaska (USA), GL = Greenland, CAN = Canada and, within Canada, AB = Alberta, BC = British

Columbia, LB = Labrador, MB = Manitoba, NB = New Brunswick, NF = the island of Newfoundland, NS = Nova Scotia, NT = Northwest Territories, NU = Nunavut, ON = Ontario, PE = Prince Edward Island, QC = Quebec, SK = Saskatchewan, YT = Yukonterritory. These regions are shown in Figs 1-3. In addition to the regions included in Tables 1-3, Figs 1-3 also show the French Overseas Collectivity of Saint Pierre and Miguelon Islands (SPM) located 25 km from the southern coast of Newfoundland. In the tables, the absence of a provincial or territorial acronym for a species recorded from Canada indicates that the taxon was recorded from Canada but no province was specified. The regions listed in Tables 1-3 are approximately from West to East beginning with northernmost continental North America (AK to NU) and then across more southern Canada (BC to NF), to Greenland, which provides a pictorial representation of the species' overall west-to-east distribution across northern North America. It contains three types of distributional records: 1) a published record for which we have examined a specimen; 2) a new (unpublished) record for which we have examined a specimen; and 3) a published record for which we have not examined a specimen, but trust its veracity. The different types of records are indicated by different colours and fonts in Tables 2, 3 (see Table headings).

Literature references (shown in the far-right column of Tables 2, 3) are only noted for previously published records for which no specimens were examined. Relevent major references for higher taxa (e.g., revisions of genera, regional checklists) are cited directly under the higher taxon names in Table 2. Our list is not a catalogue, therefore other than for recently changed or commonly misapplied names, synonyms and previous combinations are generally not included. These can be found in the catalogues and online sources cited in the respective sections of the Introduction. In addition, references for all of the original descriptions are not included; however, all genus and species names in Table 2 are listed with author and year of publication to facilitate reference to the original descriptions, if required. Formal taxonomic changes are noted in Table 2 and summarized in the abstract.

# Classification

Classification for Ceraphronoidea follows the catalogue of Johnson and Musetti (2004). For Cynipoidea, the checklist mostly follows the family and subfamily classification of Buffington et al. (2020) with the changes proposed by Hearn et al. (2024) (i.e., recognition of Diplolepididae and Paraulacidae) as well as changes to the generic and species-level classification of Cynipidae proposed since 2020 (i.e., Russo 2021; Cuesta-Porta et al. 2022, 2023; Nicholls et al. 2022). Family and subfamily classification for Evanioidea follows Li et al. (2018) and generic and species classification follows Deans et al. (2023). Higher level classification of Stephanidae follows Li et al. (2017) whereas generic and species level classification follows Aguiar (2004). Higher level classification of Trigonalyoidea follows Carmean and Kimsey (1998) with the spellings of family group names following Lelej (2003), namely Trigonalyidae, Orthogonalyinae and Trigonalyinae.

#### **Results and discussion**

This checklist records a total of 296 extant, described species of Hymenoptera in northern North America in 79 genera in 12 families and 5 superfamilies (Tables 1, 2 and Figs 1-3). Within Canada, the inventory records 281 species in the same 79 genera, 12 families and 5 superfamilies, Alaska has 31 species in 16 genera in 6 families and Greenland has 7 species in 5 genera in 2 families. There are no species of any of the treated five superfamilies of Hymenoptera recorded from the French Overseas Collectivity of St. Pierre and Miquelon islands located 25 km from the southern coast of Newfoundland based on the list from the TAXREF database (Gargominy et al. 2021). In terms of new Canadian records of genera, there are 8 reported (1 Ceraphronoidea, 6 Cynipoidea and 1 Evanioidea) (Table 2), as well as 43 new species records from Canada (13 Ceraphronoidea, 28 Cynipoidea and 2 Evanioidea) (Table 1). Table 3 lists 23 additional species of uncertain taxonomy that have previously been recorded from northern North America in the literature but are excluded from the checklist until their status can be evaluated further. Finally, the family Figitidae is so poorly known in northern North America that we felt it necessary to comment on the overall knowledge of the subfamilies and genera in this family. This summary is at the end of the Figitidae section of the Results and Discussion and includes relative estimated species richness, generic

Table 1. Described, recorded species of Ceraphronoidea, Cynipoidea, Evanioidea, Stephanoidea and
Trigonalyoidea in Canada, Alaska and Greenland totalled for each taxon and in each region. See
Methods (Presentation of data) for description of distributional acronyms and Figs 1-3 for maps of
their locations.

TAXON	CAN + AK + GL	CAN (New)	AK	ΥT	NT	NU	BC	AB	SK	MB	ON	QC	NB	PE	NS	LB	NF	GL
CERAPHRONOIDEA	55	49(13)	6	0	0	0	15	3	3	6	28	17	1	0	2	0	0	2
Ceraphronidae	24	24(7)	0	0	0	0	9	0	1	0	10	9	0	0	1	0	0	0
Megaspilidae	31	25(6)	6	0	0	0	6	3	2	6	18	8	1	0	1	0	0	2
CYNIPOIDEA	205	196(28)	22	18	4	0	79	59	26	36	119	49	26	5	15	1	8	5
Cynipidae	89	89(12)	1	1	0	0	24	13	5	19	57	17	4	1	4	0	3	0
Diplolepididae	24	24(3)	2	3	0	0	13	13	13	8	18	8	3	3	2	1	2	0
Figitidae	87	78(13)	19	14	3	0	40	32	8	8	41	21	16	1	6	0	3	5
Ibaliidae	4	4(0)	0	0	1	0	2	1	0	1	2	3	3	0	3	0	0	0
Liopteridae	1	1(0)	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0
EVANIOIDEA	30	30(2)	3	1	3	0	15	6	3	7	21	16	7	4	9	0	1	0
Aulacidae	18	18(0)	1	1	2	0	9	3	1	5	12	10	4	2	6	0	0	0
Evaniidae	4	4(2)	0	0	0	0	0	0	0	0	4	1	0	0	0	0	0	0
Gasteruptiidae	8	8(0)	2	0	1	0	6	3	2	2	5	5	3	2	3	0	1	0
STEPHANOIDEA	2	2(0)	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0
Stephanidae	2	2(0)	0	0	0	0	1	0	0	0	1	1	0	0	0	0	0	0
TRIGONALYOIDEA	4	4(0)	0	0	0	0	1	1	1	0	3	2	1	0	1	0	0	0
Trigonalyidae	4	4(0)	0	0	0	0	1	1	1	0	3	2	1	0	1	0	0	0
CHECKLIST TOTAL	296	281(43)	31	18	7	0	111	69	33	49	173	85	35	9	28	1	9	7



**Figure 1.** Map of Canada, Alaska and Greenland showing number of described, recorded Ceraphronoidea species and percentage of total species by region. Canada is comprised of all regions except for Alaska (AK), Greenland (GL) and St. Pierre and Miquelon (SPM). See Methods, Presentation of data section for all acronyms of regions treated in the checklist.

revisions (or the lack thereof), biology and overall distributions of taxa including genera that may not appear in Table 2 because, for example, they do not have reliable records of described species in northern North America.

# Ceraphronoidea

There are 55 described species of Ceraphronoidea recorded in Canada, Alaska and Greenland in 10 genera in 2 families: Ceraphronidae (24 species) and Megaspilidae (31 species) (Table 1, Fig. 1). Within Canada, there are 49 species of Ceraphronoidea recorded in 10 genera (24 species of Ceraphronoidea and 25 species of Megaspilidae). Alaska has six species of Ceraphronoidea (all Megaspilidae) recorded: *Lagynodes peckorum* Dessart, four species of *Conostigmus* and *Dendrocerus alaskensis* (Ashmead). Greenland has two species, both in *Dendrocerus* as reported in Buhl (2015). In addition to the 55 species in Table 2, the revision of *Conostigmus* by Trietsch et al. (2020) provided discussion about 4 species of uncertain status which were treated as *species inquirenda* (Table 3).

**Table 2.** Checklist of described species of Ceraphronoidea, Cynipoidea, Evanioidea, Stephanoidea and Trigonalyoidea of Canada, Alaska and Greenland. See Methods for description of acronyms of regions and Figs 1–3 for their locations. Black, regular font records are previously published and a specimen or diagnostic photograph has been examined. Red, boldfaced records are new (unpublished) records and a specimen or diagnostic photograph has been examined. All specimens examined are deposited in the CNC, except if a depository acronym is noted in the far right column. Blue, italicized records are previously published but no specimen has been examined. Literature references are only noted for "blue" records, except for *Conostigmus* (Megaspilidae) (see notes in row for genus). For species with multiple "blue" records based on multiple references, the references are listed in order from left to right, corresponding with the distributional records depicted from left to right, unless otherwise noted. An asterisk (\*) denotes a record for which it is uncertain whether the record is from Labrador or the island of Newfoundland.

OPDED HVMENODTEDA

ORDER HIMLINDI ILIOI																		
SUPERFAMILY CERAPHRONOID	EA																	
FAMILY CERAPHRONIDAE																		
Nearctic catalogue – Muesebeck 1979; wor	ld catalo	gue –	Johns	son ar	nd Mi	usetti 2	2004;	keys	to gen	era – I	Dessart	and	Cance	emi 19	87.			
Genus Aphanogmus Thomson, 1858																		
A. abdominalis (Thompson, 1858)	CAN	_	_	_	_	_	_	_	_	_	QC	_	_	_	_	_	_	
A. bicolor Ashmead, 1893	CAN	_	_	_	_	_	_	_	_	ON	QC	_	_	_	_	_	_	Ashmead 1893
A. canadensis Whittaker, 1930	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	Whittaker 1930b
A. dorsalis Whittaker, 1930	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	Whittaker 1930b
A. fulmeki Szelényi, 1940	CAN	-	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	Gilkeson et al. 1993
A. fumipennis (Whittaker, 1930) (species complex)	CAN	-	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	Whittaker 1930a
A. harringtoni Muesebeck, 1979	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	
A. marylandicus Ashmead, 1893	CAN	_	_	_	_	_	_	_	_	_	<b>OC</b>	_	_	NS	_	_	_	
A. microneurus Kieffer, 1907	CAN	_	_	_	_	BC	_	_	_	_	2	_	_	_	_	_	_	Whittaker 1930b
A. subapterus Whittaker, 1930	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	Whittaker 1930b
Genus Ceraphron Jurine, 1807																		
C. amplus Ashmead, 1893	CAN	_	_	_	_	_	_	_	_	_	QC	_	_	_	_	_	_	
C. auripes Ashmead, 1893	CAN	_	_	_	_	_	_	_	_	ON	QC	_	_	_	_	_	_	Ashmead 1893
C. barbieri Dessart, 1975	CAN	_	_	_	_	_	_	_	_	ON	QC	_	_	_	_	_	_	
C. bispinosus (Nees von Esenbeck, 1834)	CAN	-	-	-	-	-	-	SK	-	ON	QC	-	-	-	-	-	-	
C. concinnus (Whittaker, 1930)	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	Whittaker 1930a
C. flaviscapus Ashmead, 1893	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	
C. macroneurus Ashmead, 1887	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	
C. melanocerus Ashmead, 1893	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	Ashmead 1893
C. melantatocephalus Dessart, 1967	CAN	_	_	_	_	_	_	_	_	_	QC	_	_	_	_	_	_	
C. minutus (Ashmead, 1888)	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	Ashmead 1888
C. pacificus Whittaker, 1930	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	Whittaker 1930b
C. pedalis Ashmead, 1893	CAN	_	_	_	_	_	_	_	_	_	QC	_	_	_	_	_	_	
C. whittakeri (Fouts, 1927)	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	Fouts 1927
Genus Pteroceraphron Dessart, 1981																		
P. mirabilipennis Dessart, 1981	CAN	_	-	-	-	_	_	_	_	ON	_	_	_	_	_	_	-	
FAMILY MEGASPILIDAE																		
SUBFAMILY LAGYNODINAE																		
Key to genera – Dessart 1987.																		
Genus Lagynodes Förster, 1840																		
Key to species - Dessart 1987.																		
L. acuticornis (Kieffer, 1906)	CAN	-	-	-	-	-	-	-	-	ON	QC	-	-	-	-	-	-	
L. pallidus (Boheman, 1832)	CAN	-	-	-	-	-	AB	-	-	-	QC	-	-	-	-	-	-	
L. peckorum Dessart, 1987	-	AK	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
L. xanthus Whittaker, 1930	CAN	-	-	-	-	BC	-	-	MB	ON	_	-	-	-	-	-	-	Whittaker 1930a
SUBFAMILY MEGASPILINAE																		
Genus Conostigmus Dahlbom, 1858																		
Nearctic revision – Trietsch et al. 2020. Not	te: Triets	ch et a	d. 202	20 dic	l not	genera	lly lis	prov	inces f	for Ca	nadian	recor	ds, th	erefore	e depo	ositori	es of :	specimens are listed
that support all records in this revision.																		

*C. abdominalis* (Boheman, 1832) CAN – – – BC – – – – – – – – – – – CNC

C. bipunctatus Kieffer, 1907	CAN	AK	-	-	-	BC	-	-	MB	ON	-	-	-	-	-	-	-	AK,BC-AMNH, MB-PSUC,
	CAN									ON								ON-ROM
<i>C. dessarti</i> Trietsch & Miko, 2020	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	IAMU
C. aimiaiatus (Thomson, 1858)	CAN	-	-	-	-	BC	-	-	-	-	-	-	-	_	-	-	-	RIVINE
C. franzinii Trietsch & Miko, 2020	CAN	AK	-	-	-	_	-	-	MB	-	_	-	-	_	-	-	-	PSUC
C. johnsont Irietsch & Miko, 2020	CAN	-	-	-	-	-	-	-	MB	-	-	-	-	_	-	-	-	POM
C. <i>Laeviceps</i> (Ashmead, 1895)	CAN	_	-	_	-	_	-	-	_	ON	_	-	_	_	-	_	-	CNC
C. nigrorufus Dessart, 1997	CAN	-	-	-	-	_	-	-	-	ON	_	-	-	_	-	-	-	LIAM
C. buscurus (Inomson, 1838)	CAN	AK	-	-	-	PC	-	-	_	_	_	-	_	_	-	-	-	DSLIC
C. pucheuus winttakei, 1950	CAN	ЛК	_	-	_	bC	-	_	-	-	-	-	_	-	-	_	_	NHMUK
Genus Creator Alekseev, 1980 Generic status uncertain.																		
C. spissicornis (Hellén, 1966)	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	
Genus Dendrocerus Ratzeburg, 1852																		
D. arietinus (Provancher, 1887)	CAN	_	_	_	_	_	_	_	_	_	OC	_	_	_	_	_	_	
Moved from Conostigmus by Trietsch et											<b>C</b> -							
al. 2020. Maybe syn. with <i>D. penmaricus</i> (Ashmead)																		
D. alaskensis (Ashmead, 1902)	_	AK	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	Ashmead 1902
D. aphidum (Rondani, 1877)	_	_	_	-	_	-	_	_	_	_	_	_	_	_	-	_	GL	Buhl 2015
D. bifoveatus (Kieffer, 1907)	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	GL	Buhl 1995
D. carpenteri (Curtis, 1829)	CAN	_	_	_	_	_	AB	_	MB	ON	_	NB	_	_	_	_	_	
D. conwentziae Gahan, 1919	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	Marshall 2023
D. laticeps (Hedicke, 1929)	CAN	_	_	_	_	_	_	SK	MB	ON	_	_	_	_	_	_	_	SK,ON-BIOUG
D. leucopidis (Muesebeck, 1959)	CAN	_	_	-	_	-	_	_	_	ON	_	_	_	_	-	_	_	
D. pallipes (Harrington, 1899)	CAN	_	_	_	_	_	_	_	_	_	QC	_	_	_	_	_	_	
D. penmaricus (Ashmead, 1893)	CAN	_	_	-	_	-	_	_	_	ON	_	_	_	_	-	_	_	Ashmead 1893
D. picipes (Ashmead, 1893)	CAN	_	_	-	_	-	_	_	_	ON	_	_	_	_	-	_	_	Ashmead 1893
D. stigmatus (Say, 1836)	CAN	_	_	-	_	-	_	_	_	ON	_	_	_	_	-	_	_	Ashmead 1893
Genus Megaspilus Westwood, 1829																		
Nearctic species descriptions – Dessart 198	1.																	
M. armatus (Say, 1836)	CAN	-	-	-	-	-	-	-	-	ON	QC	-	-	-	-	-	-	Muesebeck 1979
Genus Platyceraphron Kieffer, 1906																		
P. artideterens Dessart, 1981	CAN	-	-	-	-	-	-	-	-	ON	QC	-	-	-	-	-	-	
P. sulcatocarinatus Dessart, 1981	CAN	-	-	-	-	-	-	-	-	ON	QC	-	-	-	-	-	-	
Genus Trichosteresis Förster, 1856																		
T. glabra (Boheman, 1832)	CAN	-	-	-	-	BC	AB	SK	-	ON	QC	-	-	NS	-	-	-	
SUPERFAMILY CYNIPOIDEA																		
FAMILY CYNIPIDAE																		
Nearctic catalogue – Burks 1979; review of	world g	enera (	of oak	c gall v	vasps	– Mel	lika ar	nd Ab	orahan	nson 2	002; k	ey to s	ubfa	nilies :	and tr	ibes –	Buffi	ngton et al. 2020;
Nearctic catalogue of rose and herb gall was	ps and t	heir ir	quili	nes – I	Nasta	si and	Dear	is 202	21; key	rs to N	earctio	gener	a of I	ierb, r	ose, b	rambl	e and	inquiline gall
Cenus Acractis Mayr 1881																		
A erinacei (Beutenmüller 1909)	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	Burks 1979
A peramachaides (Osten Sacken 1862)	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	Burks 1979
A quercushirta (Bassett 1864)	CAN	_	_	_	_	_	AB	SK	MB	ON	00	NR	_	_	_	_	_	Nicholls et al.
= A. macrocarbae Bassett, 1890	0/11 1						110	on	10110	011	60	110						2022
A. villosa Gillette, 1888	CAN	-	-	-	-	-	AB	_	MB	ON	-	-	_	-	-	-	-	MB-Nicholls et
Genus Amphibalips Reinhard, 1865																		al. 2022
A. confluentus (Harris, 1841)	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	
A. cookii Gillette, 1888	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	
A. quercusinanis (Osten-Sacken, 1861)	CAN	_	_	_	_	_	_	_	_	ON	OC	_	_	_	_	_	_	
A. quercusostensackenii (Bassett, 1863)	CAN	_	_	_	_	_	_	_	_	_	0C	_	_	_	_	_	_	Burks 1979
= Andricus quercussingularis (Bassett, 1863)											~							
A. quercusspongifica (Osten Sacken, 1862)	CAN	_	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	Burks 1979
Genus Andricus Hartig, 1840																		
A. columbiensis Melika, Nicholls & Stone, 2021	CAN	_	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	Melika et al. 2021
A. dimorphus (Beutenmüller, 1913)	CAN	_	_	_	_	_	_	_	MB	_	_	_	_	_	_	_	_	PHDNRL
A. favosus (Bassett, 1890)	CAN	_	_	_	_	_	_	_	_	_	QC	_	_	_	_	_	_	

A. foliaformis Gillette, 1888	CAN	_	_	_	_	_	_	_	MB	_	_	_	_	_	_	_	_	PHDNRL
A. occultatus (Weld, 1926)	CAN	_	-	_	_	BC	_	_	_	_	_	_	-	-	_	_	_	PHDNRL
A. opertus (Weld, 1926)	CAN	-	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	Evans 1972
A. quercuscalifornicus (Bassett, 1881)	CAN	-	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	Earley, in press.
A. quercuscornigera (Osten Sacken, 1862)	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	
A. quercusfrondosa (Bassett, 1865)	CAN	-	-	-	-	-	-	-	MB	-	-	-	-	-	-	-	-	PHDNRL
A. quercusoperator (Osten-Sacken, 1862)	CAN	-	-	-	-	-	-	-	-	-	-	-	-	NS	-	-	-	Burks 1979
A. quercuspetiolicola (Bassett, 1863)	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	
A. quercusstrobilanus (Osten Sacken, 1862)	CAN	-	-	-	-	-	-	-	MB	ON	-	-	-	-	-	-	-	PHDNRL, Burks 1979
<i>A. schickae</i> Nicholls, Melika & Stone, 2021	CAN	-	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	Melika et al. 2021
A. verensis Weld, 1957	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	Evans 1985
A. weldi (Beutenmüller, 1913)	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	_	Burks 1979
Genus Antistrophus Walsh, 1870																		
A. lygodesmiaepisum Walsh, 1870	CAN	-	-	-	-	-	AB	SK	-	-	-	-	-	-	-	-	-	Nastasi and Deans 2021
Genus Atrusca Kinsey, 1930 A. trimaculosa (McCracken & Egbert, 1922)	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	Evans 1985
Genus Aulacidea Ashmead, 1897																		
Nearctic revision – Beutenmüller 1910; Ne	arctic dis	tribut	ions a	und no	omen	clature	e – Na	istasi	and D	eans 2	.021.							
A. abdita Kinsey, 1920	CAN	_	_	_	_	_	_	_	_	_	QC	_	_	_	_	_	_	Kinsey 1920
A. follioti Barbotin, 1972	CAN	-	-	-	-	BC	-	-	-	ON	-	-	-	-	-	-	-	Nastasi and Deans 2024
A. harringtoni (Ashmead, 1887)	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	Ashmead 1887
A. nabali (Brodie, 1892)	CAN	-	-	-	-	-	-	-	-	ON	QC	-	-	-	-	-	-	Beutenmüller 1910
A. podagrae (Bassett, 1890)	CAN	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Beutenmüller 1910
A. subterminalis Niblett, 1946	CAN	-	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	Nastasi and Deans 2021
A. tumida (Bassett, 1890) Genus Aylax Hartig, 1840	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	
A. quinquecostatus (Provancher, 1883) Genus Bassettia Ashmead, 1887	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	Provancher 1883
B. flavipes (Gillette, 1889)	CAN	-	-	-	_	-	AB	-	-	ON	-	_	-	-	-	-	_	Nicholls et al.
B. lignii Kinsey, 1922	CAN	_	_	_	_	BC	_	_	-	-	-	_	-	-	_	-	_	Evans 1972
Genus Besbicus Kinsey, 1922																		
B. mirabilis (Kinsey, 1922) = Cynips mirabilis Kinsey, 1922	CAN	-	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	
Genus Callirhytis Förster, 1869																		
C. clavula (Osten-Sacken, 1865)	CAN	-	-	-	-	-	-	-	-	-	-	-	-	NS	-	-	-	
C. quercusfutilis (Osten-Sacken, 1861)	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	
C. quercuspunctata (Bassett, 1863)	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	Burks 1979
C. quercuspunctatus (Osten Sacken, 1862)	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	Burks 1979
C. seminator (Harris, 1841) Genus Ceroptres Hartig, 1840	CAN	-	-	-	-	-	-	-	-	ON	QC	-	-	-	-	-	-	Burks 1979
World revision and species key - Lobato-Vi	ila and P	ujade-	Villar	2019	; key	to Ne	arctic	speci	es and	new s	pecies	descr	iption	ıs — Na	astasi	et al. 2	024c	
C. lokii Nastasi, Smith & Davis, 2024	CAN	-	-	-	-	-	-	-	MB	-	-	-	-	-	-	-	-	Nastasi et al. 2024c
C. petiolicola (Osten Sacken, 1861)	CAN	-	-	-	-	-	-	-	-	ON	QC	-	-	-	-	-	-	Provancher 1887; Nastasi and
<i>C. tikoloshei</i> Nastasi, Smith & Davis, 2024	CAN	-	-	-	-	-	-	-	MB	-	-	-	-	-	-	-	-	Nastasi et al. 2024c
Genus <i>Diastrophus</i> Hartig, 1840	Nastasi a	nd D	eans 7	021														
D. cuscutaeformis Osten-Sacken, 1863	CAN				_	_	_	_	_	ON	00	_	_	_	_	NF*	_	ON-Burks 1979:
2. enconnegormus Osten-Sacken, 1003	C2 11 V	-	-	-	-		-	-		014	<b>~</b> ~	-	-	-	-	. 14	-	NF-Nastasi and Deans 2021
D. fragariae Beutenmüller, 1915	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	Nastasi and Deans 2021

D. fusiformans Ashmead, 1890	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	Burks 1979
D. kincaidii Gillette, 1893	CAN	_	_	_	_	BC	_	_	_	ON	_	-	_	-	_	_	_	Nastasi and
																		Deans 2021
D. nebulosus (Osten Sacken, 1861)	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	Burks 1979
D. piceus Provancher, 1887	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	Burks 1979
D. potentillae Bassett, 1864	CAN	-	-	-	-	-	-	-	-	ON	-	NB	-	NS	-	-	-	Nastasi and
D undiana Passatt 1870	CAN									ON								Deans 2021 Burks 1979
D. tumefactus Kinesy 1920	CAN	-	-	-	-	_	-	-	-		00	-	-	_	-	-	-	Kinsey 1920
D. turniduc Bassett 1870	CAN	_	_	_	_	_	_	_			00	_	_	_	_	NE*	_	Nastasi and
D. turguus Dassett, 1070	C/IIV	_	_	_	_	_	_	_	WID	011	QC	-	_	_	_	111	_	Deans 2021
Genus Disholcaspis Dalla Torre & Ke	iffer, 18	881																
D. eldoradensis (Beutenmüller, 1909)	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	
D. mellifica Weld, 1957	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	PHDNRL
D. quercusmamma (Walsh & Riley, 1860)	CAN	-	-	-	AB	-	-	-	MB	ON	-	-	-	-	-	-	-	AB-PHDNRL
D simulata Kinsey 1922	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	
Genus Druon Kinsey, 1922	0/111					DC												
Revision and key – Cuesta-Porta et al. 2022	2																	
D. ignotum (Bassett, 1881)	CAN	_	_	_	_	_	AB	SK	MB	ON	ос	_	_	_	_	_	_	SK,ON,QC-
8																		iNat
Genus Dryocosmus Giraud, 1859																		
D. kuriphilus Yasumatsu, 1951	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	
D. quercuspalustris (Osten-Sacken,	CAN	-	-	-	-	-	-	-	-	ON	QC	-	-	-	-	-	-	Burks 1979
1861)																		
Genus Feron Kinsey, 1937																		
Revision and key – Cuesta-Porta et al. 2023																		6 P
F. rucklei Melika, Nicholls & Stone,	CAN	-	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	Cuesta-Porta et
Cenus Kakharmins Puiade-Villar & I	Melika	201	3															al. 2025
K imbricariae (Ashmend 1896)	CAN	, 201	<i></i>	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	Nieves-Aldrev et
= Dryocosmus imbricariae (Ashmead, 1896)	0/11 V									011								al. 2021
Genus <i>Liposthenes</i> Förster, 1869																		
L. glechomae (Linnaeus, 1758)	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	Burks 1979
Genus Neavlax Nieves-Aldrey, 1994																		
N. verbenacus (Nieves-Aldrey, 1988)	CAN	_	_	_	_	_	_	_	MB	_	_	_	_	_	_	_	_	Nastasi et al.
																		2024a
Genus Neuroterus Hartig, 1840																		
N. floccosus (Bassett, 1881)	CAN	-	-	-	-	BC	AB	-	-	ON	-	-	-	-	-	-	-	Nicholls et al.
N	CAN									ON								2022 Bueleo 1070
N. minutus (Dassett, 1881)	CAN	-	-	-	-	_	- 1 D	-	-		-	-	-	_	-	-	_	Nicholls et al
<i>Iv. niger</i> Gliette, 1888	CAIV	-	-	_	-	_	ΛD	_	-	ON	-	-	_	_	_	-	-	2022: Burks
																		1979
N. quercusirregularis (Osten Sacken,	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	Burks 1979
1861)																		
= N. quercusmajalis (Bassett, 1864)																		
N. saltarius Weld, 1926	CAN	-	-	-	-	BC	-	-	-	ON	-	-	-	-	-	-	-	BC-PHDNRL
N. vesicula (Bassett, 1881)	CAN	-	-	-	-	_	-	-	MB	ON	-	-	-	-	-	-	-	Burks 1979
N. washingtonensis Beutenmüller, 1913	CAN	-	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	
N. umbilicatus Bassett, 1900	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	Burks 1979
Genus <i>Periclistus</i> Förster, 1869	~~~					D.C.	4.0											71 1
P. piceus Fullaway, 1911	CAN	-	ΥI	-	-	BC	AB	-	-	ON	-	-	-	-	-	-	-	Zhang et al.
P. pirata (Osten-Sacken, 1863)	CAN	_	_	_	_	_	AB	SK	_	ON	_	_	_	_	_	_	_	Zhang et al.
																		2019
Genus Phanacis Förster, 1860	.т. т	15		0.2.1														
Nearctic distributions and nomenclature –	Nastasi a	nd D	eans 2	:021.		DC												No
r: nypocnoertais (Nieffer, 188/)	CAIV	-	-	-	-	DU	-	-	-	-	-	-	-	-	-	-	-	Deans 2021
P. taraxaci (Ashmead, 1897)	CAN	AK	_	_	_	BC	AB	SK	MB	ON	0C	_	_	_	_	NF	_	AK, BC, MB,
											0							QC-Earley 2024;
																		AB-Paquette
																		et al. 1993;
																		NF-iNat

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Genus Philonix Fitch, 1859																		
P. fulvicollis Fitch, 1859	CAN	-	-	-	-	-	AB	-	MB	ON	QC	NB	-	-	-	-	-	Nicholls et al. 2022
Genus Phylloteras Ashmead, 1897																		
P. poculum (Osten Sacken 1862)	CAN	-	-	-	-	-	AB	-	MB	-	-	-	-	-	-	-	-	Nicholls et al. 2022
Genus Synergus Hartig, 1840		1. 17:1	1	21. N	r							NL		10	202	1		
S diment hus Octop Sector 1865		10- V II	lar 20	21; 1	earct	ic dist	ributic	ons ai	ia nor		ture –	Inasta	si and	1 Dear	15 202	.1.		
S. aumorphus Osten-Sacken, 1803	CAN	-	_	_	-	_	_	-	_	ON	_	-	_	_	_	_	_	Numeri and
S. erinacei Gillette, 1896	CAIV	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	Deans 2021
S. oneratus (Harris, 1841)	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	Nastasi and Deans 2021
<i>S. pacificus</i> McCracken & Egbert, 1922	CAN	-	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	
Genus Synophromorpha Ashmead, 1	903																	
Nearctic distributions and nomenclature -	Nastasi a	und D	eans 2	2021														
S. rubi Weld, 1952	CAN	_	_	_	_	_	_	_	_	ON	QC	_	_	_	_	_	_	
S. sylvestris (Osten-Sacken, 1861)	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	Burks 1979
Genus Xanthoteras Ashmead, 1897																		
X. pulchellum (Beutenmüller, 1911)	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	
X. radicola (Ashmead, 1896)	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	Burks 1979
Genus Zopheroteras Ashmead, 1897																		
Z. guttatum Weld	CAN	-	-	-	-	-	-	-	-	ON	QC	NB	PE	NS	-	-	-	ON-Marshall 2023, QC,NB,PE,NS- iNat
FAMILY DIPLOLEPIDIDAE																		
Genus Diplolepis Geoffroy, 1785																		
Ecology – Shorthouse 2010; molecular spe	cies limit	s – Z	hang	et al. 2	2019;	Near	ctic dis	stribu	tions a	and no	mencl	ature -	– Nas	stasi ar	nd De	ans 20	)21.	
D. bassetti (Beutenmüller, 1918)	CAN	_	_	_	_	BC	AB	SK	_	_	_	_	_	_	_	_	_	Shorthouse 2010
D. bicolor (Harris, 1852)	CAN	-	-	-	-	BC	AB	SK	MB	ON	QC	NB	-	NS	-	-	-	Nastasi and Deans 2021
D. dichlocera (Harris, 1852)	CAN	-	_	-	-	_	_	_	_	ON	_	_	_	_	_	_	_	
D. eglantariae (Hartig, 1840)	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	Zhang et al. 2019
D. fulgens (Gillete, 1894)	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	Burks 1979
D. fusiformans (Ashmead, 1890)	CAN	_	_	_	_	BC	AB	SK	MB	ON	_	_	_	_	_	_	_	Shorthouse 2010
D. gracilis (Ashmead, 1896)	CAN	-	-	-	-	BC	AB	SK	MB	ON	-	-	-	-	-	-	_	BC-Nastasi and Deans 2019; MB-Friesen and

8 (														
D. ignota (Osten-Sacken, 1862)	CAN	_	_	_	_	_	AB	SK	MB	ON	QC	_	_	_
D. inconspicua Dailey & Campbell, 1973	CAN	-	-	-	-	-	AB	-	_	-	-	-	-	-
D. mayri (Schlechtendal, 1877)	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_
D. nebulosa (Bassett, 1890) May be j. syn. of D. ignota (Friesen & Zhang, 2021)	CAN	-	-	-	-	-	AB	SK	-	ON	-	-	-	-
D. nervosa (Curtis, 1838)	CAN	-	-	-	-	-	-	-	-	ON	QC	-	-	_
D. nodulosa (Beutenmüller, 1909) D. oregonensis (Beutenmüller, 1918)	CAN <i>CAN</i>	-	_	-	-	BC -	AB -	SK <i>SK</i>	МВ _	ON -	QC -	NB -	РЕ —	_
D tolita (Ashmead, 1890)	CAN	AK	YΤ	_	_	BC	AB	SK	MR	ON	00	_	_	_

											~							
D. oregonensis (Beutenmüller, 1918)	CAN	-	-	-	-	-	-	SK	-	-	-	-	-	-	-	-	-	Zhang et al.
																		2019
D. polita (Ashmead, 1890)	CAN	AK	ΥT	-	-	BC	AB	SK	MB	ON	QC	-	-	-	-	-	_	Shorthouse 2010
D. radicum (Osten-Sacken, 1862)	CAN	_	_	_	_	BC	AB	SK	MB	ON	QC	_	_	_	_	_	_	Shorthouse 2010
D. rosae (Linnaeus, 1758)	CAN	_	_	_	_	_	_	_	-	ON	QC	_	_	_	_	NF	_	
D. rosaefolii (Ashmead, 1890)	CAN	AK	YT	_	_	BC	AB	SK	MB	ON	QC	NB	PE	NS	LB	NF	_	Shorthouse 2010
D. spinosa (Ashmead, 1887)	CAN	_	_	_	_	BC	AB	SK	MB	ON	_	_	_	_	_	_	_	
D. triforma Shorthouse & Ritchie,	CAN	_	YT	_	_	BC	AB	SK	MB	ON	_	_	_	_	_	_	_	Shorthouse 2010
1984																		

Zhang 2021; ON-Burks 1979

Zhang 2021; ON-Burks 1979

Nastasi and

Deans 2021

Shorthouse 2010

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\_ \_ \_ \_ MB-Friesen and

D. tuberculator (Cockerell, 1888)	CAN	-	-	-	-	BC	-	-	MB	-	-	-	-	-	-	-	-	Friesen and Zhang 2021
D. tumida (Bassett, 1890)	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	Zilang 2021
D. variabilis (Bassett, 1890)	CAN	-	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	
D. verna (Osten Sacken, 1863)	CAN	-	-	-	-	-	-	-	-	ON	-	-	PE	-	-	-	-	Burks 1979
FAMILY FIGITIDAE																		
Nearctic catalogue – Burks 1979; key to ge	nera of G	reenla	and –	Vilhe	lmsei	n and	Forsha	ige 20	15; k	ey to s	ubfam	ilies a	nd tril	bes – l	Buffin	igton e	t al. 2	2020.
SUBFAMILY ANACHARITINAE																		
Key to genera – Restrepo-Ortiz and Pujade	-Villar 20	010.																
Genus Anacharis Dalman, 1823																		
A. eucharioides (Dalman, 1818)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	GL	Vilhelmsen and
																		Forshage 2015
Genus Hexacharis Kieffer, 190/			<b>.</b>															
Generic status and included species – Restr	epo-Orti	z and	Pujac	le-V111	ar 20	10.												
H. Javipes Kieffer, 1907	-	AK	-	_	-	_	_	-	-	-	-	-	-	-	-	-	-	
Genus <i>Xyalaspis</i> Hartig, 1843	2017																	
New World revision – Mata-Casanova et al	. 2014.									ON								Mata Casanam
A. flavipes Ashmead, 1896	CAIV	-	-	_	-	_	_	-	-	ON	_	-	-	_	-	-	-	at al 2014
X himuta Mata-Casapova Selfa &	CAN	_	_	_	_	_	_	_	_	_	_	MR	_	_	_	_	_	Mata-Casanova
Puiade-Villar, 2014	C2 II V											110						et al. 2014
SUBFAMILY ASPICERINAE																		
Kev to genera – Ros-Farré 2007.																		
Genus Aspicera Dahlbom, 1842																		
World revision – Ros-Farré and Pujade-Vill	ar 2013.																	
A. carinata Ros-Farré & Pujade-Villar,	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	
2013																		
A. carlestolrai Ros-Farré & Pujade-	CAN	_	_	_	_	_	AB	_	_	_	_	_	_	_	_	_	_	
Villar, 2013																		
A. gemmae Ros-Farré & Pujade-Villar,	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	
2013																		
A. jantonii Ros-Farré, 2013	CAN	_	_	_	_	_	AB	_	_	_	_	_	_	_	_	_	_	
A. marginata Ros-Farré & Pujade-	-	AK	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	
Villar, 2013																		
A. mireiae Ros-Farré & Pujade-Villar,	CAN	-	-	_	_	BC	_	-	_	_	_	_	-	_	-	_	_	
2013																		
A. santamariai Ros-Farré & Pujade-	CAN	-	ΥT	-	-	BC	AB	-	-	-	-	-	-	-	-	-	-	Ratzlaff 2018
Villar, 2013																		
A. singularica Ros-Farré & Pujade-	CAN	-	-	-	-	BC	AB	-	-	-	-	-	-	-	-	-	-	
Villar, 2013																		
A. teresae Ros-Farré, 2013	CAN	-	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	
Genus Callaspidia Dahlbom, 1842																		
World revision – Ros-Farré and Pujade-Vill	ar 2009a					_										_		
C. defonscolombei Dahlbom, 1842	CAN	-	ΥT	NT	-	BC	AB	-	-	ON	QC	NB	-	NS	-	NF	-	Ros-Farré and
= C. provancheri Ashmead, 1887																		Pujade-Villar
Conversion Circuit 1860																		2009a
Holarctic revision – Ros-Farré and Puiade.	Villar 201	12																
O brandaoi Puiade-Villar & Ros-	CAN		_	_	_	_	AB	_	_	ON	00	_	_	_	_	_	_	
Farré, 2011	0/11 1						110			011	Qυ							
O. cavroi (Hedicke, 1914)	CAN	AK	ΥT	_	_	BC	AB	_	_	ON	OC	NB	_	_	_	_	_	Ros-Farré and
																		Pujade-Villar
																		2011a; Ratzlaff
																		2018
O. curvilineata Ros-Farré & Pujade-	CAN	-	-	-	-	-	-	-	-	-	-	NB	-	-	-	-	-	
Villar, 2011																		
Genus Paraspicera Kieffer, 1907																		
World revision – Ros-Farré and Pujade-Vill	ar 2011b	,																
P. bakeri Kieffer, 1907	CAN	-	-	-	-	-	-	-	-	ON	QC	NB	-	-	-	-	-	Ros-Farré and
																		Pujade-Villar
	0.022		1.000			D.C.	4.75											2011b
1: orandaoi Kos-Farré & Pujade-Villar,	CAN	-	ΥI	-	-	вC	AB	-	-	-	-	-	-	-	-	-	-	Ratzian 2018;
2011																		Nos-rarre and Puiade-Villar
																		2011b

#### SUBFAMILY CHARIPINAE

Nearctic catalogue of "Alloxystidae" – Andrews 1978; key to Nearctic genera and species checklist – Menke and Evenhuis 1991; world catalogue with key to genera – Ferrer-Suay et al. 2012.

#### Genus Alloxysta Förster, 1869

Revision of Nearctic type specimens with re-description of species – Ferrer-Suay et al. 2013.

A. arcuata (Kieffer, 1902)	CAN	AK	_	-	_	BC	-	-	_	ON	_	_	_	-	-	_	GL	AK,BC-Ferrer- Suay et al. 2014; GL-Vilhelmsen and Forshage 2015
A. brevis (Thomson, 1862)	CAN	_	_	_	_	BC	_	_	_	ON	_	NB	_	_	_	_	_	Andrews 1978
A. castanea (Hartig, 1841) = A. auebeci Andrews, 1978	CAN	-	-	-	-	BC	-	-	-	ON	QC	-	-	-	-	-	-	
A. consobrina (Zetterstedt, 1838)	CAN	-	-	-	-	BC	-	-	-	ON	-	NB	-	-	-	-	-	
A filimentosus Andrews 1978	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	
A. fracticornis (Thomson, 1862)	CAN	_	_	_	_	-	_	_	_	ON	_	_	_	_	_	_	_	Ferrer-Suay et al.
A. fuscicornis (Hartig, 1841)	CAN	_	_	_	_	BC	_	_	_	ON	_	NB	_	_	_	_	_	2014
A. halterata (Thomson, 1862)	CAN	_	YT	_	-	_	-	_	_	_	_	_	_	_	_	_	-	Ratzlaff 2018
A. japonica (Ashmead, 1904)	_	AK	_	_	_	_	_	_	_	_	_	_	_	_	_	_	-	
A. lachni (Ashmead, 1885)	CAN	_	_	_	_	BC	_	_	MB	ON	_	_	_	_	_	_	_	Andrews 1978
A. macrophadna (Hartig, 1841) = A. alaskensis Ashmead, 1902	CAN	AK	-	NT	-	BC	-	-	MB	ON	QC	-	PE	-	-	NF	-	Ferrer-Suay et al. 2014
A. minuscula Andrews, 1978	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	
<i>A. obscurata</i> (Hartig, 1840) = <i>A. anthracina</i> Andrews, 1978	CAN	AK	ΥT	_	-	BC	AB	-	-	-	QC	-	-	-	-	-	-	Ratzlaff 2018; Andrews 1978; Ferrer-Suay et al.
	~										~ ~							2012
A. pallidicornis (Curtis, 1838) A. pilipennis (Hartig, 1840)	CAN <i>CAN</i>	АК <i>АК</i>	_	_	_	BC BC	АВ —	_	_	_	QC -	NB -	_	_	_	_	_	Ratzlaff 2018 Ferrer-Suay et al.
4	CAN		VT															2014 D1-# 2018
A. postica (Hartig. 1841) A. vandenboschi Andrews, 1978	CAN	– AK	×1	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	Ferrer-Suay et al.
4 winterie (Wenteren 1 1922)	CAN		vT			DC	AD		MD	ON	00	ND					CI	2013 Villedamore and
A. victrix (Westwood, 1833)	CAN	-	YI	-	-	BC	AB	-	мв	ON	QC	NB	-	-	-	-	GL	Forshage 2015
<i>A. xanthopsis</i> (Ashmead, 1896) Genus <i>Dilyta</i> Förster, 1869	CAN	AK	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	Andrews 1978
D. rathmanae Menke & Evenhuis,	CAN	-	ΥT	_	_	_	AB	_	_	_	QC	-	_	_	-	-	-	
D. subclavata Förster, 1869	CAN	AK	YT	_	_	_	_	_	_	_	_	NB	_	-	_	-	_	Paretas-Martínez
<b>Genus</b> <i>Lytoxysta</i> <b>Kieffer, 1909</b> Generic diagnosis – Menke and Evenhuis 1	1991.																	et al. 2011
L. brevipalpis Kieffer, 1909	CAN	AK	-	-	-	BC	AB	SK	MB	ON	-	-	-	-	-	-	-	Menke and Evenhuis 1991
<b>Genus</b> <i>Phaenoglyphis</i> <b>Förster</b> , <b>1869</b> World revision – Ferrer-Suay et al. 2019.																		
P. americana Baker, 1896	CAN	AK	-	-	-	BC	AB	-	MB	ON	QC	NB	-	NS	-	-	-	Menke and Evenhuis 1991
<i>P. falcata</i> Andrews, 1978	CAN	_	_	_	_	BC	AB	_	_	_	_	_	_	_	_	_	_	
P. gutierrezi Andrews, 1978	CAN	_	YT	_	_	BC	_	SK	_	_	_	_	_	_	_	_	_	Ratzlaff 2018
P. heterocera (Hartig, 1841)	CAN	_	_	_	_	_	AB	_	_	_	_	_	_	_	_	_	_	Ferrer-Suay et al.
Listed as Palaearctic only by Ferrer-Suay et al. 2019																		2014
P. laevis Andrews, 1978	CAN	-	-	_	-	BC	AB	_	_	_	_	_	_	_	_	_	-	
P. palmirae Pujade-Villar, 2018	-	AK	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Ferrer-Suay et al. 2019
P. pilosus Andrews, 1978	CAN	_	YT	_	_	BC	AB	_	-	-	_	_	_	-	_	_	_	Ratzlaff 2018
P. ruficornis Förster, 1869	CAN	-	ΥT	_	-	BC	-	SK	-	ON	QC	-	-	-	-	-	-	Ratzlaff 2018; Menke and Evenhuis 1991
P. stenos Andrews, 1978	-	AK	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	

<i>P. villosa</i> (Hartig, 1841) = <i>P. ambrosiae</i> (Ashmead, 1898)	CAN	-	ΥT	NT	-	BC	AB	-	MB	ON	-	NB	-	NS	-	-	_	YT-Ratzlaff 2018; NT,AB- Menke and Evenbuis 1991
SUBFAMILY EUCOILINAE																		Lveninus 1771
Key to major Holarctic genera – Forshage a	und Nord	llande	r 200	8; rev	ision	of Zai	iecolil	lini –	Buffi	ngton 2	2009;	revisio	n of	Diglyp	hose	matini	– Buf	ffington 2011;
Nearctic catalogue – Forshage et al. 2013; I	key to wo	orld tri	ibes a	nd lis	t of w	orld g	enera	– Buf	ffingto	on et al	. 2020	).						
Genus Banacuniculus Buffington, 20	010																	
Revision – Buffington 2010a.	CAN					DC	A D					NID		NIC				D
B. nunteri (Crawford, 1913)	CAN	-	-	_	-	ЪС	AD	-	-	-	_	IND	_	183	_	-	-	2010a
B. merickeli (Miller, 1989)	CAN	_	_	_	_	_	AB	_	_	_	_	_	_	_	_	_	_	
B. nigrimanus (Kieffer, 1907)	CAN	_	_	_	_	_	AB	_	_	_	_	_	_	_	_	_	_	
B. utilis (Beardsley, 1988)	CAN	-	-	-	-	-	AB	-	-	-	-	-	_	-	-	-	-	
Genus Cothonaspis Hartig, 1840																		
C. pentatomus Hartig, 1840	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	
Genus Eucoila Westwood, 1833																		
E. hirticornis Kieffer, 1910	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	
Genus Ganaspidium Weld, 1955																		
Revision – Buffington 2010b.	CAN					PC	٨D	ςν										
<i>C. hongamic</i> Buffington, 2010	CAN	-	-	-	-	ЪС	AB	31	-	-	_	_	-	-	-	-	_	
G tasillae Weld 1955	CAN	_	_	_	_	_	AB	_	_	_	_	_	_			_	_	
Genus Ganastis Förster 1869	0/11						nD											
Revision of <i>G. brasiliensis</i> species complex -	- Sosa-Ca	alvo et	: al. 2	024.														
<i>G. kimorum</i> Buffington, 2024	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	
Genus Hexacola Förster, 1869																		
Presence in Canada – Diamond et al. 2001																		
H. neoscatellae Beardsley, 1990	CAN	-	-	-	-	-	-	-	-	ON	_	-	-	-	-	-	_	
Genus Kleidotoma Westwood, 1833																		
K. psiloides Westwood, 1833	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	GL	Vilhelmsen and Forshage 2015
Genus <i>Leptopilina</i> Förster, 1869 Revision – Nordlander 1980; review includer of al 2026	ling key	to spe	cies o	f easte	ern US	5A – I	.ue et	al. 20	)16; N	Jearctic	c distri	butior	n as p	arasito	ids of	f Dros	ophila	<i>suzukii –</i> Gariepy
Leheterotoma (Thomson, 1862)	CAN	_	_	_	BC	_	_	_	_	ON	_	_	_	_	_	_	_	Gariepy et al.
2					20					011								2024
L. japonica Novkovic & Kimura, 2011	CAN	-	_	-	BC	-	-	_	_	ON	_	_	_	_	_	_	_	
L. leipsi Lue & Buffington, 2016	CAN	-	-	-	-	-	-	-	-	ON	_	-	-	-	-	-	_	Gariepy et al.
L. maia Lue & Buffington, 2016	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	2024 Gariepy et al.
Come Standard Buffmaders 2011																		2024
Description – Buffington 2011.																		
S. pacifica (Yoshimoto, 1962)	CAN	-	-	-	-	-	AB	-	-	-	-	-	-	-	-	-	-	
Genus Striatovertex Schick, Forshage	e & No	rdlan	ıder,	201	1													
Generic description and included species –	Schick e	t al. 2	011.															
S. erythropa (Ashmead, 1888)	CAN	-	-	-	-	-	-	SK	-	ON	_	NB	-	-	-	-	-	
S. impatiens (Say, 1856)	CAN	-	-	-	-	BC		-	-	ON		-	-	-	-	-	_	
S. rujocincia (Kieffer, 1907)	CAIN	-	-	-	-	DC	AD	-	-	UN	QC	_	_	_	_	-	-	
Review with generic diagnosis – Nordlande	er 1981.																	
T. clavatipalpis (Kieffer, 1907)	CAN	-	-	-	-	-	-	-	-	ON	_	-	-	-	-	-	-	CAS
T. cupilifera (Provancher, 1881)	CAN	-	-	-	-	-	-	-	-	-	QC	-	-	-	-	-	-	ULQC
T. diaphana (Hartig, 1841)	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	ULQC
= T. nigricornis (Provancher, 1888)																		
T. rapae (Westwood, 1835)	CAN	AK	-	_	-	BC	AB	SK	MB	ON	QC	NB	-	NS	-	NF	-	AK,QC,NB,NS- Forshage, unpublished
T. simulatrix (Ruthe, 1859)	_	AK	_	_	_	_	_	_	_	_	_	_	_	_	_	_	GL	
= Eucoela alaskensis Ashmead, 1902																		
T. stigmata (Say, 1836)	CAN	_	_	_	_	_	_	_	_	-	QC	-	_	-	_	_	-	ULQC
= T. macuilipennis (Provancher, 1881)																		
Genus Zaeucoila Ashmead, 1903				_														
World revision and senior status relative to	Agrostocy	mips I	Díaz –	Buff	ingtor	ı et al.	2017			<u></u>								
Z. robusta (Ashmead, 1894)	CAN	-	-	-	-	-	-	-	-	ON	-	_	-	-	-	_	_	

SUBFAMILY FIGITINAE																		
Key to genera with scutellar spine – Jiméne	z et al. 2	008b.																
Genus Amphithectus Hartig. 1840																		
Review with generic diagnosis – Forshage a	nd Nord	llande	r 201	8.														
A slassonge (Crawford, 1918), comb	CAN	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_		
nov	0.11								011									
= Melanits slossonae (Crawford, 1918)																		
Genus Neralsia Cameron 1883																		
Nearctic revision – Jiménez et al. 2008a																		
N achmandi Jiménez and Dujada	CAN									ON								
Villar 2008	Chiv	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	
N Invaliate annie (Ashmood 1997)	CAN									ON								
N. instruction (Astimetad, 1887)	CAN	-	_	-	-	-	-	_	-	ON	-	-	_	-	-	_	_	
Villar 2006	CAIN	-	-	-	-	BC	-	-	-	ON	QC	-	-	-	-	-	-	
	CAN									0.11								
IV. readae Jimenez and Pujade-Villar,	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	
2008	0.001									0.11	~~							
N. weldi Jiménez and Pujade-Villar,	CAN	-	-	-	-	-	-	-	-	ON	QC	-	-	-	-	-	-	
2008																		
Genus Xyalophora Kieffer, 1901																		
World revision – Jiménez et al. 2008b																		
X. clavata (Giraud, 1860)	CAN	-	-	-	-	-	AB	SK	-	-	QC	-	-	-	-	-	-	Jiménez et al.
																		2008Ь
X. singularis (Ashmead, 1896)	_	AK	_	-	-	-	-	-	-	-	-	-	-	-	-	-	-	Jiménez et al.
																		2008b
Genus Xyalophoroides Jiménez & Pujade-Villar, 2008 World revision – Jiménez et al. 2008																		
World revision – Jiménez et al. 2008b.																		
X. quinquelineata (Say, 1836)	CAN	-	-	-	-	BC	AB	SK	MB	ON	QC	-	-	NS	-	-	-	Jiménez et al.
																		2008b
FAMILY IBALIIDAE																		
Review and keys to genera and species – Li	u and N	ordlar	nder 1	994.														
Genus Ibalia Latreille, 1802																		
I. anceps Say, 1824	CAN	_	_	_	_	_	_	_	_	ON	QC	NB	_	NS	_	_	_	Liu and
																		Nordlander
																		1994
I. leucospoides (Hochenwarth, 1785)	CAN	_	_	NT	_	BC	AB	_	MB	ON	QC	NB	_	NS	_	_	_	Kerrich 1973
I. montana Cresson, 1879	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	
I. rufipes Cresson, 1879	CAN	_	_	_	_	_	_	_	_	_	QC	NB	_	NS	_	_	_	Liu and
51																		Nordlander
																		1992
FAMILY LIOPTERIDAE																		
Genus Paramblynotus Cameron, 190	8																	
Revision and key to species - Liu et al. 200	7.																	
P. virginianus Liu, Ronguist &	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	
Nordlander, 2007																		
SUPERFAMILY EVANIOIDEA																		
Key to families – Mason 1993.																		
FAMILY AULACIDAE																		
Key to Nearctic species – Townes 1950: ke	v to easte	rn Ne	arcti	- snecia		mith 1	9962											
Genus Aulacus Inrine, 1807	, to case		curcus	opeen			.,,,											
1 humania (Provenskan 1882)	CAN									ON	00			MC				Townee 1950
A. li in li T 1050	CAN	-	_	-	-	-	-	_	-	ON	QC	-	_	143	-	_	_	Iownes 1750
A. augutatus Townes, 1950	CAN	-	-	-	-	-	-	-	-	ON	QC	-	-	-	-	-	-	
A. lovei (Ashmead, 1901)	CAN	-	-	_	-	_	-	-	_	ON	QC	NB	-	NS	-	-	-	
A. pallipes Cresson, 1879	CAN	-	-	NT	-	BC	-	-	MB	ON	QC	NB	-	-	-	-	-	
Genus Pristaulacus Kieffer, 1900																		
P. bilobatus (Provancher, 1878)	CAN	_	-	-	_	-	_	_	-	ON	-	-	_	NS	_	-	_	
P. canadensis (Townes, 1950)	CAN	_	_	_	_	_	_	_	MB	ON	_	_	_	_	_	_	_	
P. editus (Cresson, 1880)	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	
P. flavicrurus (Bradley, 1901)	CAN	_	_	_	_		_	_	_	ON	_	_	_	_	_	_	_	
P forleei (Townes 1950)	CAN					BC	_	_			_	_	_	_	_	_		
D minon (Crossop 1990)	CAN	_	-	-	_	DC	_	_	_	_	00		_	_	_		_	
r. mutor (Cresson, 1880)	CAIN	-	-	-	-	DC	-	-	-	-	ųc	-	-	-	-	-	-	
P. montanus (Cresson, 1879)	CAN	-	-	-	-	вC	-	-	_	_	_	-	-	_	-	-	-	
P. niger (Shuckard, 1841)	CAN	-	-	-	-	-	-	-	MB	ON	QC	-	-	NS	-	-	-	Smith 2001
P. occidentalis (Cresson, 1879)	CAN	-	-	-	-	BC	AB	-	-	-	-	-	-	-	-	-	-	PMAE
P. pacificus (Cresson, 1879)	CAN	-	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	
P. resutorivorus (Westwood, 1851)	CAN	_	_	_	_	BC	AB	_	_	ON	QC	_	_	_	_	_	_	Townes 1950
P. rufitarsis (Cresson, 1864)	CAN	AK	ΥT	NT	_	BC	AB	SK	MB	ON	QC	NB	PE	NS	_	_	_	Carlson 1979b
-											~							

P. stigmaterus (Cresson, 1864)	CAN	_	_	_	_	_	_	_	_	ON	QC	_	_	_	_	_	_	
P. strangaliae Rohwer, 1917	CAN	_	_	_	_	_	_	_	MB	ON	QC	NB	PE	NS	_	_	_	
FAMILY EVANIIDAE																		
World catalog – Deans 2005, Deans et al. 2023; key to world genera – Deans and Huben 2003.																		
Genus <i>Evaniella</i> Bradley, 1905																		
E. semaeoda Bradley, 1908	CAN	_	_	_	_	_	_	_	_	ON	_	_	_	_	_	_	_	
Genus Hyptia Illiger, 1807																		
Key to Nearctic species - Townes 1949b.																		
H. harpyoides Bradley, 1908	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	
H. reticulata (Say, 1837)	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	
H. thoracica (Blanchard, 1840)	CAN	-	-	-	-	-	-	-	-	ON	QC	-	-	-	-	-	-	
FAMILY GASTERUPTIIDAE																		
Key to Nearctic species – Townes 1950; key	to easte	rn Ne	arctic	specie	es - Sr	nith 1	996b											
Genus Gasteruption Latreille, 1796																		
G. assectator (Linnaeus, 1758)	CAN	AK	-	-	-	BC	AB	-	MB	ON	QC	NB	-	NS	-	NF	-	Smith 1996b
G. barnstoni (Westwood, 1851)	CAN	AK	-	NT	-	BC	AB	SK	MB	ON	QC	NB	PE	NS	-	-	-	Townes 1950
G. floridanum (Bradley, 1908)	CAN	-	-	-	-	-	-	-	-	ON	QC	-	-	-	-	-	-	
G. kirbii (Westwood, 1851)	CAN	_	-	_	-	BC	-	SK		ON	QC	NB	PE	NS	-	-	-	
G. occidentale (Cresson, 1864)	CAN	_	-	_	-	BC	-	-	-	-	_	-	_	-	-	-	-	Townes 1950
G. septentrionale Schletterer, 1890	CAN	_	_	_	_	BC	AB	_	_	_	_	_	_	_	_	_	_	Bradley 1908
G. striatum (Townes, 1950)	CAN	_	_	_	_	BC	_	_	_	_	_	_	_	_	_	_	_	
G. tarsatorium (Say, 1824)	CAN	_	_	_	_	_	_	_	_	ON	QC	_	_	_	_	_	_	
SUPERFAMILY STEPHANOIDEA																		
FAMILY STEPHANIDAE																		
Revision and key to Nearctic species – Agu	iar and Jo	ohnsor	n 200	3; woi	rld ca	talog -	– Agu	iar 20	04.									
Genus Megischus Brullé, 1846																		
M. bicolor (Westwood, 1841)	CAN	_	-	_	-	_	-	-	_	ON	QC	-	_	-	-	-	-	QC-BugG
Genus Schlettererius Ashmead, 1900																		
S. cinctipes (Cresson, 1880)	CAN	-	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	
SUPERFAMILY TRIGONALYOIDE	E <b>A</b>																	
FAMILY TRIGONALYIDAE																		
Revision and key to Nearctic species – Tow	nes 1956	; phyl	ogene	etic rev	vision	, key t	o gen	era ar	nd and	l list o	f world	l speci	es – (	Carme	an an	d Kim	sey 1	998
SUBFAMILY ORTHOGONALYINA	E																	
Genus Orthogonalys Schulz, 1905																		
O. pulchella (Cresson, 1867)	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	
SUBFAMILY TRIGONALYINAE																		
Genus Bareogonalos Schulz, 1907																		
B. canadensis (Harrington, 1896)	CAN	-	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	
Genus Lycogaster Shuckard, 1841																		
L. pullata Shuckard, 1841	CAN	-	-	-	-	-	AB	SK	-	ON	QC	-	-	-	-	-	-	AB-PMAE,
																		SK-RSKM
Genus Taeniogonalos Schulz, 1906										_								011170.01
T. gundlachii (Cresson, 1865)	CAN	-	-	-	-	-	-	-	-	ON	QC	NB	-	NS	-	-	-	ON,NB-iNat; QC-LEMQ

Previously, Johnson and Musetti (2004) listed 122 described species (55 Ceraphronidae and 71 Megaspilidae) from North America north of Mexico. The earlier catalogue of the same region by Muesebeck (1979) recorded 109 species (48 Ceraphronidae and 61 Megaspilidae) of which 26 were recorded from Canada (13 of each family) with 1 species of Megaspilidae from Alaska. Masner et al. (1979) estimated that there were 70 species of Ceraphronoidea in Canada (35 in each family). Bennett et al. (2019) revised the number of described species of Ceraphronoidea recorded in Canada to 47 (26 Ceraphronidae and 21 Megaspilidae) meaning that the estimate of Masner et al. (1979) included some unrecorded or undescribed species. Furthermore, Bennett et al. (2019) estimated that there could be as many as 376 species of Ceraphronoidea in Canada (275 Ceraphronidae and 101 Megaspilidae) based on specimens sequenced in the University of Guelph Barcode of Life Datasystems (BOLD) DNA barcode da**Table 3.** Previously published, questionable records from Canada, Alaska and Greenland omitted from the checklist pending confirmation. See Methods for description of acronyms of regions and Figs 1–3 for their locations.

ORDER HYMENOPTERA SUPERFAMILY CERAPHRONOID FAMILY MEGASPILIDAE	EA																	
SUBFAMILY MEGASPILINAE																		
Genus Conostigmus Dahlbom, 1858																		
C. canadensis (Ashmead, 1888)	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	Trietsch et al. 2020
C. harringtoni (Ashmead, 1888)	CAN	-	-	-	-	-	_	-	-	ON	-	_	-	-	-	-	-	Trietsch et al. 2020
C. ottawensis (Ashmead, 1888)	CAN	-	-	-	-	-	_	-	-	ON	-	_	-	-	-	-	-	Trietsch et al. 2020
C. rufoniger (Provancher, 1888)	CAN	-	-	-	-	-	-	-	-	-	QC	-	-	-	-	-	-	Trietsch et al. 2020
SUPERFAMILY CYNIPOIDEA																		
FAMILI FIGITIDAE																		
Comer Accility Wellow 1925																		
Genus Aegurps walker, 1855	CAN																	D
A. aciculatus Provancher, 1881	CAIN	-	-	-	-	-	-	-	_	-	-	-	-	-	-	-	-	Asharand 1806
A. victoriae Ashmead, 1896	CAIV	-	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	Ashmead 1896
Genus Anacharis Dalman, 1823																		
A. levifrons Kieffer, 1907	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	Kieffer 1907
A. marginata Provancher, 1887	CAN	-	-	-	-	-	-	-	-	-	QC	-	-	-	-	-	-	Provancher 1887
A. mellipes (Provancher, 1888)	CAN	-	-	-	-	-	-	-	-	-	QC	-	-	-	-	-	-	Provancher 1888
A. pediculata (Provancher, 1887)	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	Provancher 1887
A. subcompressa (Provancher, 1881)	CAN	-	-	-	-	-	-	-	-	-	QC	-	-	-	-	-	-	Provancher 1881
SUBFAMILY ASPICERINAE																		
Genus Melanips Haliday, 1835																		
M. iowensis Ashmead, 1887	CAN	-	-	-	-	-	-	-	MB	-	-	-	-	-	-	-	-	Batulla and
Previous literature records may refer to other genera or species.																		Robinson 1983
SUBFAMILY CHARIPINAE																		
Genus Alloxysta Förster, 1869																		
<i>A. halli</i> Andrews, 1978	CAN	-	-	-	-	BC	AB	-	-	ON	-	-	-	-	-	-	-	Ferrer-Suay et al. 2013
SUBFAMILY EUCOILINAE																		
Genus Didyctium Riley. 1879																		
D ruficorne (Ashmend 1887)	CAN	_	_	_	_	_	_	_	_	_	00	_	_	_	_	_	_	Nordlander 1981
Genus Granatama Förster 1869	0.111										20							
Generic concept and species checklist – Buff	fington (	2011																
<i>C. canadancis</i> (Ashmed 1887)	C4N	2011.									00							Ashmend 1887
One variable species or species complex	C211 V	_	_	_	_	_	_	_	_	_	QC	_	_	_	_	_	_	Tommedia 1007
Cenus Heyacola Förster 1869																		
H minimum (Provenchar 1883)	CAN									ON								Burks 1979
comb nov	C/IIV	_	_	_	_	_	_	_	_	011	_	_	_	_	_	_	_	Durks 1979
= Kleidotoma minima Provancher 1883																		
Genus Kleidotoma Westwood, 1833																		
K alaskensis (Ashmead 1902)	_	AK	_	_	_	_	_	_	_	_	_	_	_	_	_	_	_	USNM
K americana Ashmood 1887	CAN	7111									00							USNM
SUBEAMILY ELCITINAE	C/IIV	_	-	-	-	_	_	_	_	-	QC	-	_	-	_	_	_	0011111
Conver Eigites Latroille 1962																		
E in amaia (Drayran ak 1997)	CAN										00							Drownshar 1997
<i>E. mermis</i> (Provancher, 1887)	CAIV	_	-	_	-	-	-	_	_	-	QC	-	_	-	_	-	-	riovaliciter 100/
Genus Loncmata Thomson, 1802	CIN										00							D
L. nirta (Provancher, 188/)	CAN	-	-	-	-	-	-	-	-	-	ŲĊ	-	-	-	-	-	-	rrovancner 1887
Genus Sarothrus Hartig, 1840	o																	10.00 1000
S. canadensis Kieffer, 1907	CAN	-	-	-	-	-	-	-	-	ON	-	-	-	-	-	-	-	Kieffer 1907
S. nasoni Ashmead, 1896	CAN	-	-	-	-	BC	-	-	-	-	-	-	-	-	-	-	-	Ratzlaff 2018
Genus Zygosis Förster, 1869																		
Z. laeviscutum (Provancher, 1887)	CAN	-	-	-	-	_	-	-	-	ON	QC	-	-	-	-	_	-	Provancher 1887



**Figure 2.** Map of Canada, Alaska and Greenland showing number of described, recorded Cynipoidea species and percentage of total species by region. Canada is comprised of all regions except for Alaska (AK), Greenland (GL) and St. Pierre and Miquelon (SPM). See Methods, Presentation of data section for all acronyms of regions treated in the checklist.

tabase. This implies that based on specimens in BOLD, there are  $7.8 \times as$  many species of Ceraphronoidea in Canada as there are currently recorded ( $10.2 \times for$  Ceraphronidae and 4.0 times for Megaspilidae). This was the second highest value for predicted species versus recorded species of any superfamily of Hymenoptera in Canada in Bennett et al. (2019), after Platygastroidea ( $14.3 \times$ ).

Relative to other parts of the Northern Hemisphere, the ceraphronoid fauna of northern North America is similarly speciose/studied versus other large-scale surveys. For example, the survey of the Hymenoptera of Russia (Belokobylskij et al. 2019) lists 77 species of Ceraphronoidea: 39 Ceraphronidae and 38 Megaspilidae (Alekseev 2019) which, given Russia's surface area (17.1 million km<sup>2</sup>) equals 4.5 species per million km<sup>2</sup>. The comparable number for northern North America (13.9 million km<sup>2</sup>) is 3.9 species per million km<sup>2</sup> and 4.9 species per million km<sup>2</sup> for Canada (9.98 million km<sup>2</sup>). Surveys of smaller regions/countries in the Northern Hemisphere are magnitudes of size greater, for example, the checklist of the Ceraphronoidea of British and Irish Ceraphronoidea (Broad and Livermore 2014b) lists 94 described species (28 Ceraphronidae and 64 Megaspilidae) which, given the surface area of Britain and Ireland (313,100 km<sup>2</sup>), equates to 300 species per mil-



**Figure 3.** Map of Canada, Alaska and Greenland showing number of described, recorded Evanioidea, Stephanoidea and Trigonalyoidea species. Canada is comprised of all regions except for Alaska (AK), Greenland (GL) and St. Pierre and Miquelon (SPM). Numbers under or beside regional acronyms indicate number of species of Evanioidea/ Stephanoidea/ Trigonalyoidea recorded in each political region. See Methods, Presentation of data section for acronyms of regions treated in the checklist.

lion km<sup>2</sup>. Similarly, there are 80 species of Ceraphronoidea recorded in Finland (43 Ceraphronidae and 37 Megaspilidae) (FinBIF 2023a) which equals 230.5 species per million km<sup>2</sup> within a surface area of 338,440 km<sup>2</sup>. The trend of higher numbers of species per unit area in smaller regions compared to larger regions is similar to surveys of other Hymenoptera groups (Goulet and Bennett 2021 for sawflies, Huber et al. 2021 for Chalcidoidea) and is a reflection of greater sampling and taxonomic effort in these well-studied countries.

In terms of new records (red records in Table 2), this checklist reported one new generic record for Canada: *Creator* Alekseev (Megaspilidae), although the status of this genus is currently being reviewed and future work may result in its synonymy. There are 13 new Canadian species records of Ceraphronoidea (7 Ceraphronidae and 6 Megaspilidae) (Table 1). No new generic or species records were reported for either Alaska or Greenland. With respect to species richness by distributional area, the political regions with the highest recorded number of species of Ceraphronoidea are Ontario (28 species of 55 total, 51.0%), Quebec (17 species, (30.9%) and British Columbia (15 species, 27.3%) (Fig. 1, Table 1). No other political region has



Figures 4–9. Ceraphronoidea adults 4, 5 Ceraphronidae 6–9 Megaspilidae 4 *Aphanogmus* sp., Canada 5 *Pteroceraphron mirabilipennis*, Canada 6 *Lagynodes* sp., Canada 7 *Conostigmus fasciatipennis* [probably], Niagara, ON 8 *Dendrocerus conwentziae*, Algoma, ON 9 *Megaspilus armatus*, Canada. Photos in Figs 7, 8 courtesy of S. Marshall.

more than six species recorded and several regions (YT, NT, NU, PE, LB and NF) have zero species. The lack of Ceraphronoidea recorded in some regions is almost certainly because of poor collecting effort. The fact that both Alaska and Greenland have recorded species indicates that northern Canadian regions (YT, NT, NU) likely

also have Ceraphronoidea species present. Similarly, Prince Edward Island, Labrador and the Island of Newfoundland should also have species based on records in nearby New Brunswick, Nova Scotia and Quebec.

# Cynipoidea

The current study records 205 described species of Cynipoidea in 58 genera in 5 families in northern North America (Tables 1, 2): 89 species of Cynipidae (in 28 genera), 24 Diplolepididae (all in Diplolepis) (Fig. 15), 87 Figitidae (in 27 genera), 4 Ibaliidae (all in Ibalia Latreille) (Figs 31, 32) and 1 Liopteridae: Paramblynotus virginianus Liu, Ronquist and Nordlander (Fig. 33 is likely P. virginianus). Canada is home to 196 described species of Cynipoidea (89 Cynipidae, 24 Diplolepididae, 78 Figitidae, 4 Ibaliidae and 1 Liopteridae) in the same 58 genera. Alaska has 22 described cynipoid species (1 Cynipidae, 2 Diplolepididae in 1 genus and 19 Figitidae in 9 genera), and Greenland has 5 species (all Figitidae in 4 genera). With respect to new distributional records of Cynipoidea, the current study reports six new Canadian generic records (all Figitidae): Amphithectus, Cothonaspis Hartig, Dilyta Förster, Eucoila Westwood, Sinatra Buffington and Striatovertex Schick, Forshage & Nordlander as well as 28 new Canadian species records (12 Cynipidae, 3 Diplolepididae and 13 Figitidae) (Tables 1, 2). In terms of taxonomy, two formal changes are proposed. Kleidotoma minima Provancher, 1883 (Figitidae: Eucoilinae) is moved from this genus to Hexacola Förster, 1869 to form H. minima (Provancher, 1883), comb. nov. and Amblynotus slossonae Crawford, 1917 is moved from Melanips Walker, 1835 (Figitidae: Aspicerinae) to Amphithectus Hartig, 1840 (Figitidae: Figitinae) forming A. slossonae (Crawford, 1917), comb. nov. In addition, we place the two species of Xanthoteras Ashmead (Cynipidae): X. pulchellum (Beutenmüller, 1911) and X. radicola Ashmead, 1897 in Xanthoteras as opposed to Trigonaspis Hartig. The taxonomy of Xanthoteras and Trigonaspis has been ambiguous and future study may result in changes to species placements.

Previous Nearctic surveys of Cynipoidea include Burks (1979) who reported 817 species in North America north of Mexico of which 72 were recorded from Canada: 39 Cynipidae, 11 Diplolepididae (*Diplolepis*), 19 Figitidae (including those species previously classified in Eucoilidae and Alloxystidae) and 3 Ibaliidae. The same survey recorded three species of Cynipoidea (Figitidae) from Alaska and one species of figitid, *Alloxysta victrix* (Westwood), from Greenland. Masner et al. (1979) stated that 150 species of Cynipoidea were present in Canada: 110 Cynipidae (including Diplolepididae), 40 Figitidae (including Eucoilidae and Alloxystidae) and 4 Ibaliidae. Relative to the current survey, these numbers imply that Masner et al. (1979) must have included some unrecorded or undescribed species of Cynipidae in their totals. Liopteridae was not recorded from Canada in Burks (1979) or Masner et al. (1979), but a single specimen of *Paramblynotus virginianus* (now lost) was collected near Hamilton in southern Ontario (Liu et al. 2007). Bennett et al. (2019) stated that there were 127 species of described, extant Cynipoidea recorded in Canada and the species in this checklist form the majority of these records. They estimated that there were 755 species of Cynipoidea in Canada in



Figures 10–15. Cynipidae and Diplolepididae adults 10–14 Cynipidae 15 Diplolepididae 10 *Amphibolips quercusostensackenii* 11 *Andricus quercuspetiolicola*, Fergus, ON 12 *Diastrophus nebulosus* 13 *Aulacidea subterminalis*, Rangiwahia, New Zealand (introduced) 14 *Ceroptres* sp., Cedar Creek, ON 15 *Diplolepis rosae*, Fergus, ON. Photos courtesy of S. Marshall.

the BOLD DNA barcode database which, if representative of the total number of species in the database, means that as of 2019, there could have been as many as 631 unrecorded species of Cynipoidea in Canada. The ratio of the total estimated species to described species in Bennett et al. (2019) was 5.9 which indicates that Cynipoidea was the third



Figures 16–21. Cynipidae and Diplolepididae galls 16–20 Cynipidae 21 Diplolepididae Cynipidae galls 16 *Amphibolips quercusostensackenii* 17 *Diastrophus nebulosus*, Elora, ON 18 *Callirhytis seminator*, Turkey Point, ON 19 *Kokkocynips imbricariae*, Manester, ON 20 *Zopheroteras guttatum*, Ojibway Provincial Park, ON 21 *Diplolepis rosae*, Inverhaugh, ON Photos courtesy of S. Marshall.

most poorly known superfamily in Canada, after Platygastroidea (14.3) and Ceraphronoidea (7.8). Specifically, Cynipidae (including Diplolepididae) had 133 estimated species compared to 62 described (2.1×), whereas there were only 2 species of Ibaliidae from Canada in the BOLD database and no Liopteridae sequences. In comparison, the DNA barcode data summarized by Bennett et al. (2019) highlights the great undocumented diversity of the family Figitidae in Canada with 620 putative species based on DNA barcodes relative to 60 described (10.3× as many estimated species to described).

Because of the level of uncertainty of species identifications in Figitidae, a subfamily and generic summary is given below to provide an overview of the figitid genera known in northern North America, even if we cannot definitively provide species names within some genera.

# Figitidae: Anacharitinae

Within Canada, Alaska and Greenland, four genera of Anacharitinae are known (Tables 2, 3) of eight worldwide (Restrepo-Ortiz and Pujade-Villar 2010). Within the Nearctic region, only Xyalaspis Hartig has been revised (Mata-Casanova et al. 2014). *Hexacharis* Kieffer is rare and presently all records of the genus belong to one species: H. flavipes Kieffer that is only recorded in the current survey from Alaska (Restrepo-Ortiz and Pujade-Villar 2010). Aegilips Walker has several species recorded in Canada; however, revisionary work that has been done remains unpublished and distributional records may change after species concepts are refined. Because of this, the two previously published Canadian species records (Provancher 1881; Ashmead 1896) are omitted from the checklist and included in the list of species of unknown status (Table 3). Anacharis Dalman (Fig. 22) also has several species present in northern North America including A. euchariodes (Dalman) from Greenland (Vilhelmsen and Forshage 2015) (Table 2), but an unpublished study includes changes to species concepts and new/ changed distributional records therefore the other four previous Canadian records are omitted from the checklist and placed in Table 3. Anacharis is often commonly collected and its distribution extends into high latitudes. All species of Anacharitinae for which the biology is known are associated with aphid-communities in trees, shrubs and herbs (perhaps most commonly in trees) where they parasitize aphid-hunting Hemerobiidae and Chrysopidae (Neuroptera) larvae (Ronquist 1999).

# Figitidae: Aspicerinae

Five genera of Aspicerinae of nine worldwide (Buffington et al. 2020) are known from Canada and Alaska (Tables 2, 3). The subfamily is well-studied relative to other figitid subfamilies. Ros-Farré and Pujade-Villar (2013) revised *Aspicera* Dahlbom although the revision was based on only a small number of specimens, therefore undescribed species may be present and/or species limits may be revised following further study. Ros-Farré and Pujade-Villar (2009a) revised *Callaspidia* Dahlbom (Fig. 23). The only species considered to be found in northern North America is the widespread, but relatively uncommon Holarctic *C. defonscolombei* Dahlbom (Table 2). *Melanips* Haliday has not been revised. Currently, all specimens from northern North America are considered to belong to *M. iowensis* Ashmead; however, it is unknown how many of these records actually belong to this species including the one published record from Canada (Manitoba) by Batulla and Robinson

(1983). Undescribed species and/or unrecorded Palaearctic species are likely present in the Nearctic. *Melanips* specimens are frequently confused with other cynipoid taxa that are matte from dense microsculpture including various Cynipidae and the figitine genus *Amphithectus* Hartig (see below). For these reasons, *Melanips iowensis* is not included in the main checklist (Table 2), but instead is included among the questionable previous records (Table 3), pending further study. Finally, revisions of both *Omalaspis* Giraud and *Paraspicera* Kieffer have been published (Ros-Farré and Pujade-Villar 2011a, 2011b) with two and three species, respectively recorded in northern North America. All species of Aspicerinae for which the biology is known are associated with aphid-communities on herbs, shrubs and trees (most commonly on herbs) where they parasitize aphid-hunting larvae of Brachycera (Diptera) (Ronquist 1999). Most genera are relatively uncommon, except for *Melanips* Haliday. Aspicerinae are more common in open habitats than forests and their distribution does not generally extend significantly into high latitudes.

# Figitidae: Charipinae

Charipinae is perhaps the best-studied major subfamily of Figitidae. Four genera of eight worldwide (Buffington et al. 2020) are present in Canada, Alaska and Greenland (Table 2). Alloxysta Förster (Fig. 24) is very common and species-rich in northern North America (19 species in Table 2). The genus has been revised in several parts (Andrews 1978; Menke and Evenhuis 1991; Ferrer-Suay et al. 2012, 2013) that in some cases contradict each other. Certainly, there are undescribed Nearctic species and taxonomic changes are also expected. Paretas-Martinez et al. (2011) revised the Holarctic species of Dilyta including two species from the Nearctic region, but only one (D. subclavata Förster) was recorded from northern North America (Alaska). The current study provides new records for both Nearctic species from Canada. The genus Lytoxysta Kieffer was diagnosed by Menke and Evenhuis (1991) and presently all records are considered to belong to L. brevipalpis Kieffer. Finally, Phaenoglyphis Förster (Fig. 25) is common and rather species-rich in Canada and Alaska (Table 2). It has been revised for the world (Ferrer-Suay et al. 2019); however, it is likely there are still undescribed species in the Nearctic region including the north. All species of Charipinae for which biology is known are hyperparasitoids of Braconidae and Chalcidoidea (Hymenoptera) that parasitize Aphididae and Psyllidae (Hemiptera: Sternorrhyncha) (Ronquist 1999; Buffington et al. 2020). Specimens are commonly collected with distributions extending into high latitudes and are perhaps more commonly found on herbs rather than trees and shrubs.

#### Figitidae: Emargininae

This monotypic subfamily consisting of *Thoreauella* Girault was previously thought to be found only in tropical regions as well as the eastern Palaearctic (Buffington et al. 2020). More recent collections have found specimens of *Thoreauella* as far north as New Hampshire, so it is possible that future collections will find emarginines in southern Canada.

# Figitidae: Euceroptrinae

The monotypic subfamily Euceroptrinae (*Euceroptres* Ashmead) is comprised of four Nearctic species (Buffington and Liljeblad 2008). No specimens have been collected in Canada or Alaska; however, specimens are known from Oregon in the west and Connecticut and Massachusetts in the east, therefore it is quite likely that the subfamily is present in southern Canada, but not yet recorded. Rearing records indicate that the group are parasitoids or inquilines of *Andricus* spp. (Cynipidae) that form galls on oaks (Buffington et al. 2020).

# Figitidae: Eucoilinae

As noted above, Eucoilinae is by far the most species-rich subfamily of Figitidae, as well as the most poorly known. There are 91 described genera worldwide (Buffington et al. 2020). Within northern North America, only 12 genera are considered to have described species recorded (Table 2). Banacuniculus Buffington was described and revised by Buffington (2010a) and includes four species in Canada, with three species known only in the west (Alberta) and one species with a range extending from British Columbia to Nova Scotia (Table 2). At least a few species of *Cothonaspis* are present in Canada but the lack of a revision of this genus makes it uncertain if these are mainly widespread/ synantropic Holarctic species or whether they are indigenous to northern North America and undescribed. Table 2 lists C. pentatomus Hartig as a new generic and species record for Canada (Ontario). Eucoila is an uncommon and species-poor genus in Canada but is known to the current authors from eastern Canada. Most or all of the Nearctic fauna is considered to belong to one species: E. hirticornis (Kieffer); however, most specimens in collections identified as Eucoila actually belong to Striatovertex which superficially resembles Eucoila but belongs to a different tribe (Schick et al. 2011). Ganaspidium Weld was revised by Buffington (2010b) following removal of some species that were placed in Banacuniculus. It is not common, but three species are present in western Canada (Table 2). Ganaspis Förster is a common and species-rich genus in Canada, but the Nearctic fauna is almost completely unrevised. However, the adventive biocontrol agent reported in the North American literature as G. brasiliensis (Ihering) (Abram et al. 2020) has recently been described as a distinct species: G. kimorum Buffington (Fig. 26) (Sosa-Calvo et al. 2024).

Both *Hexacola* Förster and *Kleidotoma* Westwood are common and species-rich in northern North America, but both remain completely unrevised in the Nearctic region and therefore most previously published Nearctic records for these genera are listed in Table 3 since they can very rarely be used with confidence and may change following revision. *Kleidotoma* is present in high latitudes including Greenland (Vilhelmsen and Forshage 2015). *Kleidotoma minima* Provancher, 1883 was described from Canada (Ontario) but the type has not been located. Ashmead (1885) made it a junior synonym of *Figites mellipes* Say, 1836 which he moved into *Eucoila*. Ashmead collaborated and exchanged specimens with Provancher so he is expected to have had a fairly good idea of Provancher's species, but we have no good reason why he would have known

the true identity of Say's species. The specimens that Ashmead identified as *Eucoila mellipes* in the USNM are *Hexacola* spp. Thus, we consider *F. mellipes* Say a *nomen dubium* rather than a senior synonym of *K. minima*, and we tentatively make the new combination *Hexacola minimum* (Provancher, 1883), comb. nov., placing it in Table 3 since it is not yet well-known enough to be recognisable at the species level.

Together with *Ganaspis*, *Leptopilina* Förster (Fig. 27) has recently become very important to biological control because of introduction to various parts of the world of the invasive pest, spotted wing Drosophila: *D. suzukii* (Matsumura) (Abram et al. 2020). *Leptopilina* is common and relatively species-rich in northern North America. Unlike *Ganaspis* that is not revised for the Nearctic and has very challenging taxonomy, *Leptopilina* is more well known including a revision (Nordlander 1980) and a more recent review of the species from the eastern United States that includes a species key for the area (Lue et al. 2016). Despite this, additional revisionary work is required for the region. Gariepy et al. (2024) report the presence of some species in Canada that were previously only recorded from the United States.

The monotypic Sinatra comprises S. pacifica (Yoshimoto) found previously throughout the mid and southwestern United States (as well as Hawaii, the south Pacific and Japan) (Buffington 2011), but is newly recorded from Alberta (Table 2). Museum specimens and previous species records of Sinatra are often under the genus name Disorygma Beardsley. As noted above, most Nearctic specimens identified as Eucoila are actually Striatovertex. Three species are newly recorded here from Canada based on identifications by Kathy Schick, but revisionary work has remained unpublished and distributional records may change as species concepts are refined. Trybliographa Förster (Fig. 28) is common and species-rich in Canada with some unpublished revisionary work. Some Holarctic species are present in Canada, but most of the Canadian species are undescribed. Trybliographa simulatrix (Ruthe) is recorded from both Alaska (current study) and Greenland (Vilhelmsen and Forshage 2015). By far, most of the larger-sized eucoilines in boreal habitats belong to Trybliographa and they are often common in collections, sometimes under the junior synonym Pseudeucoila Ashmead. Finally, Zaeucoila Ashmead is uncommon and species-poor in northern North America with all Canadian records currently considered to belong to Z. robusta (Ashmead) and known only from Ontario (Buffington et al. 2017). However, Buffington and Scheffer (2008), in their treatment of the junior synonym Agrostocynips Díaz noted that the genus was also known from British Columbia. This record was not included in the later revision of Zaeucoila by Buffington et al. (2017) and is not included in Table 2 since the species recorded in British Columbia was not noted.

Six additional genera of Eucoilinae are known from northern North America (*Didyctium* Riley, *Dieucoila* Ashmead, *Gronotoma* Förster, *Quasimodoana* Forshage, Nordlander & Ronquist, *Rhoptromeris* Förster and *Trichoplasta* Benoit), but such is the poor state of knowledge of the subfamily that these specimens remain unidentified at the species level because they represent undescribed species or in some cases, the species and/or generic concepts are unclear so that it is not possible to put names on them until taxa are revised. *Didyctium* Riley is common and species-rich in northern North America, but is completely unrevised, therefore most species are undescribed and the available names can very rarely been used with confidence, therefore the species



Figures 22–27. Figitidae adults 22 Anacharis sp., (Anacharitinae), Orton, ON 23 Callaspidia sp. (Aspicerinae), near Castlegar, BC 24 Alloxysta victrix (Charipinae), Tongapõrutu, New Zealand 25 Phaenoglyphis villosa, Makakahi, New Zealand 26 Ganaspis kimorum (Eucoilinae), BC 27 Leptopilina japonica (Eucoilinae), BC. Photos in Figs 22, 24–25 courtesy of S. Marshall; Fig. 23 courtesy of J. Dulisse; Figs 26–27 courtesy of W.H.L. Wong.

previously recorded in Canada: *D. ruficorne* (Ashmead) (Nordlander 1981) is only included among the questionable records (Table 3). *Dieucoila* is an uncommon genus which, as currently defined, has several undescribed species in Canada. The genus has a great range of morphological variation and its current circumscription actually

includes several undescribed genera. Gronotoma is uncommon in northern North America and completely unrevised. Because of this, it remains uncertain whether the single species-level name: G. canadensis (Ashmead) (Ashmead 1887) associated with Canadian records (Table 3), is a widespread and variable species or whether it may represent several species. In museum collections, Gronotoma specimens are sometimes curated under the junior synonym Eucoilidea Ashmead (Buffington 2002). Quasimodoana is rare and species-poor in Canada, but undescribed species are present from at least British Columbia and Quebec (Forshage et al. 2008). Rhoptromeris is common and relatively species-rich in Canada, but no Canadian records have been associated with a species-level name. Trichoplasta is present in Canada, but uncommon and completely unrevised for the region and the several known Nearctic species are all undescribed. All Eucoilinae host records are from cyclorrhaphous Diptera larvae in hidden substrates especially on saprophagous flies in ephemeral habitats (e.g., dung, carcasses, compost, rotting fruit) or phytophagous flies, especially leafminers (Buffington et al. 2020). Several genera are common in a variety of boreal habitats and the group extends into high latitudes.

# Figitidae: Figitinae

Figitinae is much less species-rich than Eucoilinae with the species classified in only 14 genera worldwide (Buffington et al. 2020) of which 4 have described species in northern North America: *Amphithectus* Hartig, *Neralsia* Cameron (Fig. 29), *Xyalophora* Kieffer and *Xyalophoroides* Jiménez and Pujade-Villar (Fig. 30). A further four genera are known to be present in northern North America (*Figites* Latreille, *Lonchidia* Thomson, *Sarothrus* Hartig and *Zygosis* Förster) (Table 3), but these genera either do not have described species recorded from the area or the species concepts are unclear making it uncertain how to apply the few available species-group names. All Figitinae are parasitoids of muscomorphan Diptera (Buffington et al. 2020). The majority of species for which the biology is known parasitize larvae in hidden substrates mostly on saprophagous hosts in ephemeral habitats (e.g., dung, carcasses, compost, rotting fruit) or in a few cases, phytophagous hosts. Most genera are rare and usually associated with open landscapes, especially agricultural. Only *Figites* and *Neralsia* can be common. The subfamily is not recorded from the high Arctic (Tables 2, 3).

Amphithectus Hartig is uncommon and species poor in northern North America with all Canadian records currently belonging to one species (Table 2). Some Amphithectus species superficially resemble Melanips due to the matte integument, but differ in many respects, belong to another subfamily, and are perhaps most easy to recognise by the large female metasoma. The type of Amblynotus slossonae in USNM is clearly an Amphithectus and corresponds to specimens reared from cones in Canada, therefore Amblynotus slossonae Crawford, 1918 is moved from Melanips to Amphithectus forming Amphithectus slossonae (Crawford, 1918), comb. nov. Amphithectus species parasitize Anthomyiidae flies including seed cone pests such as Strobilomyia Michelsen (Forshage and Nordlander 2018) and in this respect, they
have been considered as biocontrol agents. *Neralsia* is common in northern North America and relatively species-rich and a Nearctic revision has been published (Jiménez et al. 2008a) with five species recorded in the area (Table 2). *Neralsia* parasitize calyptrate flies in dung and carcasses. Similarly, *Xyalophora* Kieffer and *Xyalophoroides* Jiménez and Pujade-Villar have been revised on a world level (Jiménez et al. 2008b), although circumscription of the species is still somewhat problematic. Two species of *Xyalophora* are recorded from northern North America and the single species of *Xyalophoroides* is also recorded from the area (Table 2). Hosts of both genera are calyptrate flies in dung and carcasses.

With respect to the figitine genera with problemetic species identifications and limits, Figites is seemingly species-rich in northern North America, but remains completely unrevised and it is uncertain how to apply the few available Nearctic species-level names, e.g., F. inermis (Provancher) recorded from Quebec (Burks 1979) (Table 3). The genus parasitizes calyptrate flies in dung and carcasses. Lonchidia Thomson is uncommonly collected in northern North America and likely has only a few species present. Similar to Figites, it is completely unrevised in the Nearctic and therefore it is not clear how to apply the few available Nearctic species-level names, e.g., L. hirta Provancher recorded from Quebec (Burks 1979) (Table 3). A revision is required in order to determine to what extent present species are widespread/ Holarctic or endemic to the Nearctic and indeed, very few Canadian records have been associated with a species-level identification. Sarothrus Hartig is another genus of figitine that remains completely unrevised for the Nearctic region. Historically, three Nearctic species have been recorded: S. canadensis Kieffer from Ontario (Burks 1979), S. nasoni Ashmead from Illinois (Burks 1979) and British Columbia (Ratzlaff 2018) (Table 3) and S. californicus Kieffer from California (Burks 1979). Similar to Figites and Lonchidia, a revision is required in order to determine how to apply available species-level names to Nearctic specimens. Lastly with respect to Figitinae, Zygosis Förster is another genus that is completely unrevised and therefore it is unclear how to apply the few available Nearctic species-level names, e.g., Z. laeviscutum (Provancher) recorded from Ontario and Quebec (Provancher 1887) (Table 3).

### Figitidae: Thrasorinae

The final Nearctic subfamily of Figitidae is Thrasorinae which is known only from the southern Nearctic region (two species of *Myrtopsen* Rübsaamen from Arizona) (Ros-Farré and Pujade-Villar 2009b). It is not expected that this group will be recorded from northern North America.

# Comparison to Palaearctic Cynipoidea surveys

Relative to surveys of Palaearctic Cynipoidea, the northern Nearctic has less described species recorded. Forshage et al. (2017) listed 220 species of Cynipoidea from Britain and Ireland: 91 Cynipidae (including 5 Diplolepididae), 127 Figitidae and 2 Ibaliidae.

The checklist of the species of Finland lists 205 described species of Cynipoidea: 53 Cynipidae (including 5 Diplolepididae), 149 Figitidae and 3 Ibaliidae (FinBIF 2023b). Sweden has 271 species of Cynipoidea: 66 Cynipidae, 5 Diplolepididae, 198 Figitidae and 2 Ibaliidae (Forshage unpublished). Melika (2019) catalogued the Cynipoidea of Russia, listing 291 described species: 127 Cynipidae (including 9 Diplolepididae), 160 Figitidae, 2 Ibaliidae and 1 Liopteridae. The fact that all four of these surveys include a higher number of Figitidae than Cynipidae corroborates the DNA barcode data of Bennett et al. (2019) that the Figitidae of northern North America are understudied relative to the Palaearctic region.

#### Cynipoidea distributional summary

The highest species diversity of Cynipoidea is Ontario with 58.0% of the total species (119 of 205) comprised of 57 species of Cynipidae, 18 Diplolepididae, 41 Figitidae, 2 Ibaliidae and 1 Liopteridae. British Columbia is the second most diverse (79 species: 38.5%) and then Alberta (59: 28.8%). In general, Cynipidae is restricted to more southern regions, with no species recorded from the Northwest Territories, Nunavut or Greenland, whereas some species of Figitidae do occur in the Northwest Territories and Greenland (but not yet recorded from Nunavut). Interestingly, one species of Ibaliidae: *Ibalia leucospoides* (Hochenwarth) (Fig. 32) has a range that extends to the Northwest Territories, but otherwise, this family is mostly found in southern Canada. As noted previously, the range of the single species of Liopteridae found in Canada is limited to southern Ontario.

#### Evanioidea

This checklist includes 30 described species of Evanioidea in Canada, Alaska and Greenland: 18 Aulacidae (in 2 genera), 4 Evaniidae (in 2 genera) and 8 Gasteruptiidae (in 1 genus) (Table 2). All 30 species are present in Canada. Alaska currently has only three species of Evanioidea recorded: *Pristaulacus rufitarsis* (Cresson) (Aulacidae) and *Gasteruption assectator* (Linnaeus) (Fig. 38) and *G. barnstoni* (Westwood) (Gasteruptiidae). There are no Evanioidea known from Greenland.

With respect to previous surveys of Evanioidea in the Nearctic region, the catalogue of Carlson (1979b) listed 54 species of which 24 were recorded from Canada: 16 Aulacidae including 3 *Aulacus* spp. and 13 *Pristaulacus* spp., 1 species of Evaniidae, *Hyptia thoracica* (Blanchard), and 7 species of Gasteruptiidae (all in *Gasteruption*). There was one species of Aulacidae and two species of Gasteruptiidae recorded from Alaska, all of which were also recorded from Canada. Masner et al. (1979) stated that there were 31 species of Evanioidea in Canada (17 Aulacidae, 4 Evaniidae and 10 Gasteruptiidae) but this study did not list species.

In terms of the total number of species of Evanioidea that may occur in Canada, Alaska and Greenland, it is not expected that there will be a great deal more species discovered, but there will likely be some. Bennett et al. (2019) reported that there were



Figures 28–33. Cynipoidea adults 28–30 Figitidae 31, 32 Ibaliidae 33 Liopteridae 28 *Trybliographa* sp. (Eucoilinae) 29 *Neralsia ashmeadi* (Figitinae), Constance Bay, ON 30 *Xyalophoroides quinquelineata* (Figitinae) 31 *Ibalia anceps*, ON 32 *Ibalia leucospoides*, ON 33 *Paramblynotus* sp., White Plains, NY, USA. Photos in Figs 28, 30 courtesy of S. Marshall; Figs 31, 32 courtesy of H. Goulet; Fig. 33 courtesy of C. Holmes.

only 16 Evanioidea DNA barcodes from Canada in the Barcode of Life Datasystems database (6 Aulacidae, 2 Evaniidae and 8 Gasteruptiidae) which indicates that more sampling of Aulacidae and Evaniidae (at least) is required. Carlson (1979b) reported ranges for several evanioid species from northern states bordering Canada, for example,

*Pristaulacus fasciatus* (Say) is found in Michigan and *P. melleus* (Cresson) is known from Washington state. Both of these species remain unknown in Canada at present. With respect to Gasteruptiidae, *Gasteruption pattersonae* Melander and Brues may be present in British Columbia since it is recorded from Washington state and Idaho. Finally, in terms of Evaniidae, it is possible that one or two widespread species that prey on invasive cockroaches may be present in urban areas of Canada. *Evania appendigaster* (Linnaeus) is known from New York state and Massachusetts and is associated with the American cockroach, *Periplaneta americana* (Linnaeus). *Prosovania fuscipes* (Illiger) is also associated with the American cockroach as well as the Oriental cockroach *Blatta orientalis* Linnaeus and is recorded from Massachusetts (Carlson 1979b).

Comparing the diversity of the evanioid fauna in northern North America to other parts of the Northern Hemisphere reveals a similarly depauperate fauna in Europe and Asia relative to more southern latitudes. Broad and Livermore (2014a) reported only eight species of Evanioidea from Britain and Ireland (one species of Aulacidae, two Evaniidae and five Gasteruptiidae). The inventory of the Evanioidea of Finland (FinBIF 2023c) lists 11 species: 1 aulacid, 1 evaniid and 9 gasteruptiids and the survey of the Hymenoptera of Russia recorded 44 species: 12 Aulacidae (Sundukov and Lelej 2019), 3 Evaniidae (Belokobylskij 2019b) and 29 Gasteruptiidae (van Achterberg 2019).

The current study reports one new generic record of Evanioidea for Canada (*Evaniella* Bradley) (Evaniidae) and two new species records: *Evaniella semaeoda* Bradley (Fig. 36) is recorded from Ontario, previously known from Rhode Island west to southern Michigan (Carlson 1979b). *Hyptia reticulata* (Say) is also reported from Ontario having previously been known from Massachusetts west to mid Michigan. There were no new records of Evanioidea for Alaska.

#### Stephanoidea

In terms of species richness, Stephanoidea is one of the smallest superfamilies in northern North America with only two species recorded: Megischus bicolor (Westwood) (Fig. 40) from Ontario and a new record from Quebec and Schlettererius cinctipes (Cresson) (Fig. 41) from British Columbia (Table 2). Previous surveys of Stephanidae from northern North America also only recorded these two species (Carlson 1979a; Masner et al. 1979; Aguiar 2004). No species of Stephanidae are known from Alaska or Greenland. Historically, it appeared as if the two Canadian species were separated geographically with one in the west and one in the east (Carlson 1979a), but more recently, S. cinctipes has been collected in the eastern United States: Virginia (Smith 1997), Kentucky (Johansen et al. 2010) and Maryland (Deczynski 2016). The latter study suggested that movement of wood by humans was the reason for the recent range extension of S. cinctipes and its Siricidae hosts which raises the possibility that S. cinctipes could become established in eastern Canada in the future by similar means. Bennett et al. (2019) reported that there were no Canadian DNA barcodes of Stephanidae in the BOLD DNA barcode database which illustrates the rarity of Stephanidae in Canada despite the large specimen size.



Figures 34–39. Evanioidea adults 34–36 Aulacidae 37 Evaniidae 38, 39 Gasteruptiidae 34 Aulacus lovei, Fergus, ON 35 Pristaulacus strangaliae, Rondeau Provincial Park, ON 36 Evaniella semaeoda, Marriottsville, MD, USA 37 Hyptia harpyoides, Rondeau Provincial Park, ON 38 Gasteruption sp., [either *G. assectator* or *G. kirbii*], ON 39 Gasteruption tarsatorium, Little Current, ON. Photos in Figs 34–35, 37, 39 courtesy of S. Marshall; Fig. 36 courtesy of Z. Dankowicz; Fig. 38 courtesy of H. Goulet.

There are eight species of Stephanidae recorded from North America north of Mexico: seven species of *Megischus* and *S. cinctipes* (Aguiar and Johnson 2003). It is unlikely that any more than two species are present in Canada because none of

the other six species of *Megischus* are recorded in any states bordering Canada – the next most northerly species is *M. californicus* Townes known from southern Oregon (Aguiar and Johnson 2003). Similarly, it is unlikely that *S. cinctipes* will be found in Alaska as the most northerly records for this species are all from southern British Columbia (Townes 1949a).

Stephanidae are much more diverse in southern latitudes compared to northern. There are no species of Stephanidae in Britain and Ireland (Broad 2014) or Finland (FinBIF 2023d). The whole of Europe has only two species of Stephanidae with the farthest north records from Germany and France (Ceccolini 2021). Similar to northern North America, Russia has two species of Stephanidae recorded (Belokobylskij 2019a).

#### Trigonalyoidea

There are four species of Trigonalyoidea (Trigonalyidae) recorded from northern North America classified into four genera: Orthogonalys pulchella (Cresson) (Fig. 42) from Ontario, Bareogonalos canadensis (Harrington) from British Columbia, Lycogaster pullata from Alberta, Saskatchewan, Ontario and Quebec, and Taeniogonalos gundlachii (Cresson) (Fig. 43) from Ontario, Quebec, New Brunswick and Nova Scotia (Table 2). No Trigonalyidae are recorded from Alaska or Greenland. In terms of previous surveys, Masner et al. (1979) and Bennett et al. (2019) reported four species from Canada, but these papers did not list the species. The revision of Carmean and Kimsey (1998) confirmed that these four species were present in Canada, but only listed country distributions, not provinces. The only published provincial record of a Canadian trigonalyid that we could find is for Bareogonalos canadensis from BC (Harrington 1896; Townes 1956; Carlson 1979c). The records of ON for Orthogonalys pulchella, ON and QC for Lycogaster pullata and ON, QC, NB and NS for T. gundlachii may have been known previously, but we have considered them as new in order to emphasize the current distributions. The finding that *L. pullata* is present in western Canada (AB and SK) is almost certainly new, as this species was previously only known to us from eastern Canada (based on specimens in the CNC).

With respect to North America, five species of Trigonalyidae are known (Smith and Stocks 2005). The fifth species, *O. bella* Smith and Stocks, is only recorded from the southeast of the United States (Tennessee) and is not expected to occur in northern North America. Four distinct Trigonalyidae DNA barcodes from Canada are present in the BOLD DNA barcode database (Bennett et al. 2019) which corroborates the number of species in Canada. It is unlikely that *B. canadensis* is present in Alaska because in Canada it is only known from coastal regions of southern British Columbia (Harrington 1896; Townes 1956). However, the new records of *L. pullata* from AB and SK demonstrate that this species is more widespread than previously thought and therefore it could possibly be present in Alaska.

Similar to Evanioidea and Stephanoidea, Trigonalyoidea are more abundant in southern latitudes compared to northern. With respect to Palaearctic surveys, there is



Figures 40–43. Stephanoidea and Trigonalyoidea adults 40, 41 Stephanidae 42, 43 Trigonalyidae 40 *Megischus bicolor*, MI, USA 41 *Schlettererius cinctipes*, WA, USA 42 *Orthogonalys pulchella*, Canton, GA, USA 43 *Taeniogonalos gundlachii*, AZ, USA. Photos in Figs 40, 41 courtesy of N. Schiff; Fig. 42 courtesy of C. Butler; Fig. 43 courtesy of S. Marshall.

only one species of Trigonalyidae recorded in Britain and Ireland: *Pseudogonalos hahnii* (Spinola, 1840) (Broad 2014) and this is the same as in Finland (FinBIF 2023e). There are eight species of Trigonalyidae recorded in Russia (Lelej 2019).

### Summary

This paper lists the described species of Ceraphronoidea, Cynipoidea, Evanioidea, Stephanoidea and Trigonalyoidea and their distributions in Canada, Alaska and Greenland (Table 2). The Introduction to the checklist series (Bennett 2021) stated that the species in these five superfamilies totalled 237 species (52 Ceraphronoidea, 149 Cynipoidea, 30 Evanioidea, 2 Stephanoidea and 4 Trigonalyoidea) which comprised 2.6% of the total (9250) species. The current total is 296 (55 Ceraphronoidea, 205 Cynipoidea, 30 Evanioidea, 2 Stephanoidea and 4 Trigonalyoidea). The differences in the totals for Ceraphronoidea arise from the following: the revision of Conostigmus by Trietsch et al. (2020) that was not included in the totals in Bennett (2021) as well as re-assessment of the validity of several records of Aphanogmus Thomson and Ceraphron Jurine (Ceraphronidae) as well as the new record for Creator. The remainder of the differences between the numbers in Bennett (2021) and the current study belong to Cynipoidea. These arose because of publication of the catalogue of rose and herb gall wasps (Cynipidae and Diplolepididae) by Nastasi and Deans (2021), several other collaborative papers by these authors, a paper on distributions of *Diplolepis* (Diplolepididae) (Zhang et al. 2019), two papers by Earley (2024, in press), several confirmed records on iNaturalist (see acknowledgements) and recent personal collecting by GM. In addition, two papers by David Evans on cynipid galls on Garry oak: Quercus garryana Douglas in BC (Evans 1972, 1985) were not considered by Bennett (2021) resulting in the addition of several more species to the Canadian list. Because Evans (1985) was published as an unsubstantiated list of species, only records that could be confirmed by examination of specimens were included and therefore, the following remain unsubstantiated, but possibly correct records for Canada and BC: Ceroptres montensis Weld, 1957; Feron pattersonae (Fullaway, 1911), Loxaulus atrior (Kinsey, 1922) and Synergus oneratus (Harris, 1841). Differences in the numbers of Figitidae reported between Bennett (2021) and the current study was mostly due to addition of new records and careful assessment of published records by MF, the latter process resulting in removal of some previous records to Table 3. No differences occurred in Ibaliidae, Liopteridae (or Stephanoidea or Trigonalyoidea). All species and distributions in the current paper will be added to the online checklist of the Hymenoptera of Canada, Alaska and Greenland (Bennett 2024).

The percentage of records of Ceraphronoidea and Cynipoidea that are new to Canada highlights the poor state of knowledge of these two superfamilies in northern North America: 26.5% (13 of 49) of Ceraphronoidea species are new to Canada and 14.3% (28 of 196) of Cynipoidea (Table 1). This is also demonstrated by the presence of unverifiable previously published records in Table 3 (4 Megaspilidae and 19 Figitidae). Distributional surveys of some groups have not been made since the Catalog of Hymenoptera of America north of Mexico in 1979, especially almost all genera in Eucoilinae (Figitidae) and all Ceraphronidae. Based

on the findings of this paper and the DNA barcode results of Bennett et al. (2019) it is clear that much more work is required in these groups (and others) in order to document their taxonomic composition and distributions within northern North America. In addition, the startlingly low number of species recorded from Alaska (only 31 species) and other northern and central areas (e.g., Saskatchewan) highlights the need for much greater sampling in these regions. Nevertheless, this checklist adds greatly to our knowledge and provides baseline data on which future surveys can be built.

#### Acknowledgements

We gratefully acknowledge the curators of the collections in which examined specimens are deposited. This study would not have been possible without the work of many summer students who surveyed the CNC and the literature for relevant records. D. Barnes now retired from Agriculture and Agri-food Canada (AAFC) in Ottawa helped compile the list of species present in the CNC and the literature. A. Bass (AAFC Ottawa) helped format references and take photographs of specimens. E. Maw (AAFC Ottawa, retired) wrote scripts to help produce the checklists from the CNC inventory files. P. Abram (AAFC Agassiz, BC) and T. Gariepy (AAFC London, ON) discussed current biocontrol work using Eucoilinae to help control spotted wing Drosophila in Canada. J. Huber (Canadian Forest Service, Ottawa, retired) was instrumental in providing advice and guidance to AMRB during the very long preparation of this checklist and also for hosting MF during visits to the CNC. Several people are greatly thanked for permission to include photos as attributed in the Figure headings: S. Marshall (University of Guelph, ON, retired; H. Goulet (AAFC Ottawa, ON, retired); N. Schiff (US Department of Agriculture Stoneville, MS, USA); W. Wong (University of British Columbia, Vancouver, BC); J. Dulisse (BC, Canada); C. Holmes (NY, USA); Z. Dankowicz (Potomac, MD, USA); C. Butler (GA, USA). The NF record of Phanacis taraxaci was provided by Adam Kalab (Sudbury, ON). The ON record of Taeniogonalos gundlachii was provided by M. King (Brampton, ON) and the NB record by S. Tingley (Cocagne, NB). The QC record of Megischus bicolor was provided by J. Brodeur (Granby, QC). The AB records of Pristaulacus occidentalis and Lycogaster pullata were provided by M. Buck (Royal Alberta Museum, Canada). The SK record of L. pullata was provided by C. Sheffield (Royal Saskatchewan Museum, Canada). N. Earley (University of Victoria, BC) is thanked for checking material and records of Cynipidae reared from Garry oak in British Columbia. I. Lobato-Vila (Museu de Ciències Naturals de Barcelona, Spain), S. van Noort (Iziko Museums of Cape Town, South Africa) and an anonymous reviewer are thanked for their reviews and suggestions to the manuscript. Finally, YM Zhang (University of Edinburgh, Scotland) is greatly thanked for acting as associate editor for the Journal of Hymenoptera Research and his many suggestions and additions to the checklist.

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# Life history of two new species of Prorops (Hymenoptera, Bethylidae) ectoparasitic on adult Hypothenemus eruditus beetles (Curculionidae, Scolytinae) in Hawai'i

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Academic editor: Michael Ohl | Received 29 September 2024 | Accepted 4 November 2024 | Published 25 November 2024

https://zoobank.org/F8C7D787-8DC8-4B57-9FF4-4111F8957D47

**Citation:** Honsberger DN, Magnacca KN, Lorenzo-Elarco JH, Wright MG (2024) Life history of two new species of *Prorops* (Hymenoptera, Bethylidae) ectoparasitic on adult *Hypothenemus eruditus* beetles (Curculionidae, Scolytinae) in Hawai'i. Journal of Hymenoptera Research 97: 1221–1256. https://doi.org/10.3897/jhr.97.138113

#### Abstract

Aspects of the life history and biology of two *Prorops* spp. are explored, *Prorops maya* **sp. nov.** and *Prorops umiehu* **sp. nov.** Aspects of their behavior are deduced through dissection of plant material and through the use of "phloem sandwich" style observation chambers. Both were found to be ectoparasitoids of adult *Hypothenemus eruditus* beetles. They thus show a novel feeding behavior as, along with a *Plastanoxus* sp., the only bethylids known to parasitize the adult stage of their hosts, and the only known ectoparasitoids of adult scolytids. Searching, stinging, host feeding, and oviposition behaviors are reported and illustrated with photographs and video. Oviposition occurs on the ventral side of the membraneous region between the pro- and mesothorax of the beetle, and larvae feed through this location. The projection on the frons, a defining character of the genus *Prorops*, is observed to function as a tongue and groove mechanism with which the adult female pushes on the edge of the prothoracic sclerite of the host beetle while maintaining use of its mandibles to chew on the membrane underneath for host feeding and in preparation for oviposition. Defensive action of a *Hypothenemus* sp. against the wasp's sting by clamping down on the intruding ovipositor between its pro- and mesothorax is also reported, though this behavior was only observed once and thus its generality is uncertain.

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#### **Keywords**

Functional morphology, host defense, macadamia, parasitoid Hymenoptera, Scolytinae

### Introduction

There are currently eleven known species in the genus *Prorops* (Hymenoptera: Bethylidae), including the two described here. Members of this genus can be distinguished from other members of Scleroderminae by having a distinct snout, a projection of the anterior part of the frons that is either a singular projection with a median groove, or is separated into two distinct projections on either side (Azevedo et al. 2018). A list of previously described species is provided below. Location records were obtained through reports in published literature, so there may be specimens collected from other places that are not noted here:

### Prorops impotens Waichert & Azevedo, 2012

Known from Madagascar. No recorded hosts.

### Prorops mandibularis Lim & Lee, 2011

Known from Central Cardamom, Cambodia. No recorded hosts.

### Prorops nasuta Waterson, 1923

A parasitoid of Hypothenemus hampei (Ferrari, 1867), the coffee berry borer. Prorops *nasuta* has been imported from its native range in Africa to much of the coffee growing world as a biological control agent. It enters coffee berries, host feeds on all immature stages, stings and paralyzes the adult stage, and is an ectoparasitoid on the pupal and late instar larval stages (Infante et al. 2005). It is thought to be native to parts of Central and East Africa including Uganda, the adjacent northwest part of Tanzania, the DRC, and parts of West Africa (Le Pelley 1968). It has been released as a biocontrol agent in South and Central America, southern Asia, and Indonesia (Vega et al. 2015). In addition to the coffee berry borer, this species was also recorded emerging from Hypothenemus seriatus (Eichhoff, 1872) in Jamaica (Evans 1977), and is reported to attack and develop on Caulophilus oryzae (Gyllenhal, 1838) (Col: Curculionidae) when presented with their larvae in an artificial laboratory setting (Pérez-Lachaud and Hardy 2001). Terayama (2006) also recorded it from the mountains in Aichi Prefecture on the island of Honshu in Japan, where very little or no coffee is grown or occurs and the coffee berry borer is not known to be present. This raises the question as to what it uses as a host there, or if this record was possibly a misidentification.

### Prorops obsoleta Evans, 1977

Known from Trinidad island, Trinidad and Tobago. No recorded hosts.

#### Prorops petila Evans, 1977

Known from Louisiana, USA; and Guanabara, Brazil. It has been found associated with loblolly pine (*Pinus taeda* L.) (Pinaceae) in Louisiana where it is possibly a parasitoid of *Dendroctonus frontalis* Zimmerman, 1868.

#### Prorops rakan Terayama, 2006

Known from Aichi Prefecture, Japan. No recorded hosts.

#### Prorops sparsa Waichert & Azevedo, 2012

Known from Madagascar. No recorded hosts.

In addition to the validly described species above, in an unpublished PhD dissertation Vargas (2017) provided descriptions of three additional species, *Prorops* "sp. 23" from Thailand, *Prorops* "sp. 24" from Vietnam, and *Prorops* "sp. 25" from the United Arab Emirates. No hosts are recorded. The last appears to be the same as the taxon described here as *Prorops uniehu* sp. nov., but we have not been able to examine the UAE specimens to confirm. Mention of these manuscript names and their characters in the key below are not nomenclatural acts (International Commission on Zoological Nomenclature 2012, Art. 8.2).

Both species explored in the present study and described herein were found attacking Hypothenemus eruditus Westwood, 1836 (Curculionidae: Scolytinae). This is currently the only known host for both of the species. Hypothenemus eruditus is regarded as a supergeneralist, found inhabiting dead wood of a wide variety of tree species over a large taxonomic range, and has even been recorded from fungi (Beaver 1976; Browne 1961; Wood 2007; see Atkinson (2016) for the most comprehensive host list). The type specimens were found boring into the cover of a book, which gave rise to the species name (Westwood 1836). Wood (2007) proposed this species to be the most "widely distributed and abundant" member of Scolytinae in the world. Despite its prevalence, H. eruditus rarely achieves high densities and is thought to usually enter only dead wood, and is thus not regarded as a pest species in many environments where it occurs (Kambestad et al. 2017; Tuncer et al. 2017). There are, however, reports of it attacking and damaging a variety of fruit trees including Malus domestica Borkh. (apple), Morus L. (mulberry), Ficus carica L. (fig), Mangifera indica L. (mango), Sesbania sesban (L.) Merr. (sesban) (Batt 2019, and studies cited therein), Theobroma cacao L. (cacao) seedlings (Browne 1961), mature and stored seeds (Wood 1977; Mitchell and Maddox 2010), and stunting the growth of Dryobalanops aromatica Gaertn.f. (Malay camphor tree) transplants (Browne 1961), and it thus has in fact been suggested to act as a significant pest of agricultural systems and forest environments in some circumstances. There is known to be wide morphological and genetic variation in this species, even between individuals found in the same plant or gallery, and it is possible that H. eruditus is in fact better thought of as a species complex (Kambestad et al. 2017). Cephalonomia hyalinipennis Ashmead, 1893 is the only other parasitoid known to attack H.

*eruditus* in nature (Bushing 1965, cited within). *Phymastichus coffea* LaSalle, 1990, a parasitoid of the coffee berry borer, was found to attack and develop in *H. eruditus* in a laboratory setting in glass vials (Castillo et al. 2004) but has not been observed to do so in nature. Interestingly, in testing using similar methods but beetles from Hawai'i, *P. coffea* was found not to parasitize *H. eruditus* (Yousuf et al. 2020), possibly because of genetic dissimilarity between the populations of *H. eruditus*.

# Methods

### Species description

Specimens collected from wood and other plant parts were examined and photographed using a Leica MZ16 stereomicroscope or Macropod Pro imaging system. Specimens were also dissected, examined, and photographed using an Olympus CX31 compound microscope. Terminology relating to morphological characters follows Azevedo et al. (2018) and Lanes et al. (2020).

Morphometrics of the head were measured as in Fig. 1, all in full face view. Acronyms in Fig. 1 and descriptions of the measurements are as follows:

T T T	
LH	Length of head; longitudinal line even with posterior of vertex to tip of shout.
LH\S	Length of head not including snout; longitudinal line even with posterior of
	vertex to base of mandible.
VOL	Vertex-ocular line: longitudinal line even with posterior of vertex to even
VOL	with posterior margin of wa
	with posterior margin of eye.
LE	Length of eye; posterior margin to anterior margin of compound eye.
LHAE	Length of head above bottom of eye; longitudinal line even with posterior of
	vertex to even with anterior margin of compound eye.
LHBE	Length of head below bottom of eye; longitudinal line even with anterior
	margin of compound eye to tip of snout.
WH	Width of head; maximum width of head including eyes.
WF	Width of frons; minimum distance between compound eyes on frons.
BEM	Bottom of eye to mandible; longitudinal line from even with anterior margin
	of compound eve to base of mandible.
WOT	Width of ocellar triangles distance between the outer margins of the
wOI	width of ocenar thangle; distance between the outer margins of the
~ ~ -	posterior ocelli.
OOL	Ocellar-ocular line; shortest distance from margin of posterior ocellus to margin of compound eve
101	Lateral application of
AOL	anterior ocellus
POL	Posterior ocellar line: shortest distance between inner margins of
101	posterior celli
AOT	Angle between lines joining middle of anterior ocellus and middle of each
	posterior ocellus.

- **LPD** Length of metapectal-propodeal disc; distance along median line from anterior margin of metapectal-propodeal complex to declivity, measured in plane perpendicular to overall surface of disc.
- **WPD** Width of metapectal-propodeal disc; greatest transverse distance between lateral marginal carinae or lateral edges of disc, posterior of propodeal spiracles; measured in plane perpendicular to overall surface of disc.

Ratios and measurements were among those typically used in Bethylidae and the genus *Prorops*, with the addition of LHBE : LHAE, which gives a sense of the relative length of the snout and may be useful in the genus *Prorops*. Body length was obtained by adding the length of the head from the apex of the snout to the occipital foramen, the occipital foramen to the anterior of the tegula, the anterior of the tegula to the petiole, and the petiole to the apex of the abdomen, to give the full body length if the body including the head were outstretched. Measurements were made on dried, point mounted specimens. Ranges of coloration reported cover that observed for live individuals and fresh or air dried specimens, and may be outside this range depending on preservation method.



Figure 1. *Prorops umiehu* sp. nov. head (paratype) showing morphometric measurements. Acronyms explained in text. Scale bar (upper left):  $100 \mu m$ .

# Biology and behavior

## Observations of behavior in field-collected plant material

Wood and other plant parts containing Scolytinae were collected in forest, agricultural, and urban environments, and returned to a laboratory for dissection under a microscope.

### Observation chambers in a laboratory setting

Behavior was also observed using "phloem-sandwich" style observation chambers, consisting of thin sheets of plant material compressed between a sheet of plexiglass and a sheet of aluminum, the same apparatus used and described in Honsberger (2024) (Fig. 11a). Such observation chambers were made using either *Trema orienta-lis* (L.) Blume wood or *Delonix regia* (Boj. ex Hook.) Raf. seed pods. For *T. orientalis*, bark was peeled off branches to the xylem layer and tunnels were cut into the inner surface of the bark with a knife. For *D. regia* seed pods, sections of plant material containing *H. eruditus* tunnels were cut into small pieces and used as they were, or tunnels were cut into uninfested sections of seed pods with a knife. These sections of wood were then placed into the observation chambers, and *H. eruditus* larvae, pupae, and adults, and occasionally other co-occurring beetles collected from *D. regia* pods were placed into the tunnels. Sections of plant material with beetles were sprinkled with debris from the tunnels where the beetles were collected, the plexiglass lid was attached, the boxes were sealed, and female wasps were entered into the boxes through the small holes drilled in the plexiglass.

### Genetic analysis

DNA was extracted from adult wasps using the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Inc., Valencia, Ca, USA), and the CO1 gene was amplified using the primers in Folmer et al. (1994). This was done for two adults of *P. maya* sp. nov., collected from fallen *T. orientalis* branches in the upper reaches of Mānoa Valley, Oʻahu, Hawaiʻi, and described subsequently. The resulting sequences were identical and are reported in GenBank Accession # PP498809.

### Repositories

Specimens are deposited in the following museums:

- UHIM University of Hawai'i Insect Museum, Honolulu, Hawai'i, USA
- BPBM Bernice Pauahi Bishop Museum, Honolulu, Hawai'i, USA
- **CNC** Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Ontario, Canada

#### Prorops maya Honsberger, Lorenzo-Elarco & Magnacca, sp. nov.

https://zoobank.org/4B7A22E2-5D18-4049-93BA-C4C65F76B6ED Figs 2, 3

**Diagnosis.** Females can be distinguished from other described *Prorops* spp. by the dark colored head and metasoma contrasting with the orange mesosoma; snout apically bifid and with mesal sulcus; head including snout approximately 1.1 times as long as wide; fore wing with vein 2r-rs+Rs distinct; metapectal-propodeal disc longer than wide in dorsal view, and with lateral carina. Males can be distinguished by the same set of characters except the coloration which is less pronounced than in the females, the head and metasoma brown and the mesosoma lighter yellow-brown.

**Differential diagnosis.** *Prorops maya* females and males can be differentiated from the other species known from Hawai'i, *Prorops umiehu* sp. nov., by the fore wing with vein 2r-rs+Rs distinct (fore wing with 2r-rs+Rs absent in *P. umiehu*); female head only slightly longer than wide (head substantially longer than wide in females of *P. umiehu*); metanotum continuous posterior to mesoscutellum in dorsal view (mesoscutellum covers metanotum medially in *P. umiehu*); mandible more narrow and bidentate (mandible wider and tridentate in *P. umiehu*); clypeus with dorsal and ventral margins more acutely rounded (clypeus dorsal margin more broadly rounded and ventral margin less curved in *P. umiehu*); metapectal-propodeal complex with lateral marginal carina (lateral marginal carina weaker or absent in *P. umiehu*); females by the more distinct coloration, with the mesosoma orange and the head and metasoma dark brown (head and mesosoma of similar reddish-brown color, sometimes mesosoma lighter but only slightly, in *P. umiehu* females).

Female (Figs 2a-d, 3). Length range: 1.10-1.23 mm (n = 6), Holotype 1.23 mm

Head (Figs 2b, c, 3c, e). Frons, gena, vertex, and occiput dark brown and shiny with sparse setae. Very anterior of head, including snout, basal antennomeres, mandible, clypeus, and mouthparts lighter in color, often orange, of similar color to mesosoma. Frons and gena with lightly reticulate texture, density of reticulations increasing towards snout, snout itself with bumpy texture. Compound eye with short, sparse setae between ommatidia. Vertex incurved. Head with sides more or less parallel and only slightly outcurved, eye projecting slightly so widest part of head is across eyes. Snout bifid apically, but indistinctly in face view, ending in two lobes apically curved dorsally to form two small teeth; with dorsal median groove extending from where lobes meet to even with anterior of compound eye, sometimes continuing more weakly to approximately even with middle of eye. Torulus located ventral to lateral margins of snout at approximately half its length, visible in dorsal view. Clypeus in anterior view extending laterally past torulus, tapers laterad; medially with dorsal margin somewhat acutely arched against snout and torulus, ventral margin strongly incurved; overall appearing as handlebar mustache turned dorsad at its lateral corners. Antenna with scape curved ventrally and widened apically, its apical surface forming cavity. Pedicel slightly rounded subquadrate, with somewhat nodose basal section connected to dorsal portion of cavity at apex of scape.



**Figure 2.** *Prorops maya* sp. nov. holotype  $\stackrel{\frown}{=}$  (**a**-**d**) and allotype  $\stackrel{\frown}{\circ}$  (**e**-**h**) **a**, **e** side view **b**, **g** anterior view of head **c**, **f** head **d**, **h** dorsal view. Scale bars: 500 µm (**a**, **c**-**h**); 100 µm (**b**).

Ten flagellomeres, 1<sup>st</sup> smallest and cone shaped, 2<sup>nd</sup> through 9<sup>th</sup> shaped like apically truncated spheres, and similar in size, shape, and structure. Terminal flagellomere ovate. Setae of similar length and density on all flagellomeres, less dense on scape and pedicel. Antenna yellow-orange to orange at least basally, apical flagellomeres darker. Mandible with two apical teeth; ventral tooth longer, two thick setae on mandible just dorsad of

teeth. Anterior region of head, including snout, clypeus, and mandible, distinctly more densely setose than rest of head. *Morphometrics* (range, n = 3 for all measurements): LH : WH = 1.06–1.11; LH : LE = 2.65–2.78; LH : VOL = 2.51–2.58; LHBE : LHAE = 0.29–0.34; VOL : LE = 1.05–1.08; WF : LE = 1.60–1.70; LE : BEM = 5.70–7.42; WOT : OOL = 0.46–0.50; POL : AOL = 1.13–1.28; AOT = 70°–75°; LH\S : WH = 0.89–0.93. Antennal ratio approximately Scape : Pedicel : F1 : F2 : F3 : F4 : F5 : F6 : F7 : F8 : F9 : F10 = 3.3 : 2.1: 1.0 : 1.3 : 1.3 : 1.4 : 1.4 : 1.5 : 1.6 : 1.6 : 2.4.

Mesosoma (Figs 2a, d, 3d). Mesosoma bright orange, contrasting with brown head and metasoma. Pronotum shiny and with light reticulate texture posterior to pronotal flange; pronotal flange conspicuous, shiny with faintly coriaceous texture; other thoracic nota and metapectal-propodeal complex smooth and shiny with only very light reticulate texture, difficult to see except under high magnification and with the right lighting, anteromesoscutum and posterior region of metapectal-propodeal disc especially smooth and glassy. Pronotum with sparse setae, longer setae at posterior margin. Anteromesoscutum with scattered short mesal pointing setae; mesoscutellum with pair of short setae on its lateral margin approximately even with posterior margin of axillae, another pair of longer mesally pointing setae at its posterior; axillae with sparse, short setae; tegula with few setae, denser than on surrounding sclerites; metanotum with pair of setae near its posterior margin, approximately in line with lateral margin of mesoscutellum; metapectal-propodeal disc without setae, declivity with few setae just mesal of lateral carina. Transscutal suture such that posterior margin of anteromesoscutum is slightly outcurved. Anterior boundary of anteromesoscutum somewhat visible under translucent pronotum. Mesosoma relatively flat along dorsomedian line. Notaulus somewhat visible as dark streak but does not manifest on cuticle surface. Parapsidal signum present but very light. Metanotum continuous and visible posterior to mesoscutellum, thin and slightly elevated medially, wider laterally. Length of mesoscutellum approximately 2.5 times length of metanotum on medial line. Mesopleuron projects from side of mesosoma, flattened subcylindrical in shape, though tapering slightly near connection with mesocoxa, and with few setae only on its ventral side. Mesopleural pit somewhat centrally located. Metapectal-propodeal disc approximately 1.2 times as long as wide; flat medially, vaguely outcurved towards lateral edges mesal of lateral marginal carina; lateral marginal carina often distinct but somewhat weak in some individuals, becoming less distinct on declivity before reaching petiole; shape of declivity subtriangular when viewed perpendicular to its surface. Lateral surface of metapectalpropodeal complex flat or slightly convex, inclined past vertical.

*Legs* (Fig. 3f–h). Legs of similar color to rest of mesosoma, sometimes a bit lighter. All tibiae with scythe shaped apical spur with comb-like setae on inner edge. Mesotibia with apical spines more numerous and stronger than in pro- and metatibiae, and with additional row of strong spines over its length on side opposite tibial spur; pro- and metatibia lacking this row of spines. First tarsomere longest in each leg, most notably so in pro- and metalegs where it is only slightly shorter than 2<sup>nd</sup> through 4<sup>th</sup> tarsomeres combined. 2<sup>nd</sup> through 4<sup>th</sup> tarsomeres subequal in length in proleg, sequentially decrease in length in meso- and metaleg. Length of 5<sup>th</sup> tarsomere not including claw subequal to combined length of 2<sup>nd</sup> and 3<sup>rd</sup> tarsomeres in proleg, and subequal to 2<sup>nd</sup> segment alone in meso- and metalegs.



**Figure 3.** *Prorops maya* sp. nov. **a** fore wing  $\bigcirc$  **b** hind wing  $\bigcirc$  **c** anterior view of head  $\bigcirc$  (paratype) **d** dorsal view  $\bigcirc$  (paratype, wings removed) **e** antenna  $\bigcirc$  **f** proleg  $\bigcirc$  **g** mesoleg  $\bigcirc$  **h** metaleg  $\bigcirc$  **i** male genitalia, ventral view. Scale bars: 100 µm (**c**); 500 µm (**d**).

*Fore wing* (Fig. 3a). Sc+R vein, prestigmal abcissa of radial 1, pterostigma, and 2rrs+Rs vein strong. Rs+M, M+Cu, and A veins lightly indicated. Sc+R vein with three setae. 2r-rs+Rs vein extending from pterostigma to approximately 0.7× full length of wing. Prestigmal abcissa of radial 1 inset from wing margin, pterostigma borders margin. Prestigmal flexion line present as hyaline stripe separating prestigmal abcissa of radial 1 and pterostigma; thickness of hyaline stripe and shape of prestigmal abcissa of radial 1 and pterostigma somewhat variable among individuals, though prestigmal abcissa of radial 1 usually longer than pterostigma and neither wider than approximately twice width of basal part of 2r-rs+Rs vein. Wing membrane subhyaline, with the following additional flexion lines visible as hyaline stripes. Cubital flexion line emerges just posterior to where indications of M+Cu and A veins meet, bounded by small setae and pointing towards middle of retinaculum, fading before reaching wing margin. Longer, somewhat wavy median flexion line emerges just posterior of prestigmal abcissa of radial 1, generally pointing apicad of trailing edge of wing and reaching approximately even with end of 2r-rs+Rs vein, also marked by trail of short setae. Wing membrane posterior and basal to median flexion line with few setae other than those bounding cubital flexion line and indications of Rs+M, M+Cu, and A veins in basal region of wing. Small hyaline spot projects into wing membrane on its posterior margin just apical of retinaculum. Marginal setae present from prestigmal abcissa of radial 1 around to apex of retinaculum. *Hind wing* (Fig. 3b). Wing membrane subhyaline with short setae of approximately equal length and density over its surface. Marginal setae short on leading edge, longest around apical margin and on apical half of trailing edge where their length is about half maximum width of wing, gradually decreasing basad towards basal trailing margin. Leading edge with slight projection culminating in dark spot with three hamuli at about half wing length.

*Metasoma* (Figs 2a, d, 3d). Petiole and metasoma dark brown to black, in distinct contrast with orange mesosoma. First tergite constricted anteriorly to form distinct petiole, segment as a whole somewhat wider than long; constricted petiolar region of subequal length and width, with fine bumpy texture and shallow median dorsal groove extending its length. Remainder of metasoma shiny dark brown to black with smooth texture and sparse setae over most of its length. Very few setae present dorsally in anterior half; setae steadily increase in density in posterior third both dorsally and laterally, ring of setae present at apex of metasoma where sting emerges. In dorsal view, petiole and 2<sup>nd</sup> metasomal segment subequal in length on median line, 3<sup>rd</sup> and 4<sup>th</sup> also subequal but shorter than 1<sup>st</sup> and 2<sup>nd</sup>. Metasoma widest near posterior margin of 4<sup>th</sup> segment. Sting often visible projecting slightly from apex of abdomen in dried or alcohol preserved specimens.

**Male** (Fig. 2e–h). *Length range:* 0.75–0.97 mm (n = 2), Allotype 0.97 mm. As in female but with the following differences. Coloration dull, head and metasoma brown, mesosoma yellowish brown.  $2^{nd}$  through  $9^{ch}$  antennal flagellomeres of more cylindrical shape, longer than wide, and antenna overall longer than in female relative to body size. Morphometrics of head similar to that of female, but with eye larger and more bulging relative to face than female; exact ratios could not be obtained because faces of the two known specimens were somewhat collapsed. *Genitalia:* See Fig. 3i. Small relative to body size. Genital capsule narrow, gonostipites and harpes combined about twice as long as wide; harpe elongate, about 2/3 as long as gonostipes, broadly rounded distally. Penis valvae much shorter than volsella, mostly concealed in ventral view.

**Materials examined.** *Holotype* (Fig. 2a–d):  $\bigcirc$ ; Hawaiian Islands, Oʻahu, Mānoa Valley; 21.3288°N, 157.7930°W, 154 m; 12.ii.2020; ex *Hypothenemus eruditus* tunnel in *Trema orientalis* branch; D. Honsberger (UHIM).

*Allotype* (Fig. 2e–h):  $\mathcal{J}$ ; same data as holotype; (UHIM).

*Paratypes*:  $7 \Leftrightarrow 1 \circlearrowleft$ ; all with same data as holotype ( $2 \Leftrightarrow UHIM$ , 1 individual with wings removed;  $3 \Leftrightarrow 1 \circlearrowright BPBM$ ;  $2 \Leftrightarrow CNC$ ).

**Etymology.** This beautiful wasp is named after Maya Honsberger, a wonderful and beautiful human being. It has also been elusive for us to find, all individuals found on only one occasion, as with Maya, for whom it is also rare to find as wonderful a wife as her. The name is to be treated as a noun in apposition.

For the Hawaiian common name, mai'apala (lit., *ripe banana*) was selected. Mai'a (general term for banana) is similar in sound and spelling to the species name *maya* and also one of the favorite foods of Maya Honsberger, combined with the similarity of the yellow and brown coloration of the wasp to a ripe (pala) banana.

**Known distribution.** This species is known from the island of O'ahu in Hawai'i, where it is likely adventive. Based on its limited abundance and distribution, it is probably a recent arrival.

Known hosts. Hypothenemus eruditus (Coleoptera: Scolytinae); see Biology section.

#### Prorops umiehu Honsberger, Lorenzo-Elarco & Magnacca, sp. nov.

https://zoobank.org/31D3C969-F035-4AE8-A31A-A5401A8B800F Figs 4, 5

**Diagnosis.** Females can be distinguished from other described *Prorops* spp. by the combination of: head and mesosoma orangish-brown to reddish-brown; fore wing without vein 2r-rs+Rs; snout bifid and with mesal sulcus; head including snout approximately 1.3 times as long as wide; metapectal-propodeal disc approximately 1.2 times longer than wide in dorsal view, and without distinct lateral carina. Males can be distinguished by the same set of characters as the females except for coloration and morphometrics of the head: body darker in color, brownish; head including snout approximately 1.1 times as long as wide.

**Differential diagnosis.** Prorops umiehu can be differentiated from Prorops maya by lack of vein 2r-rs+Rs in the fore wing (2r-rs+Rs distinct in *P. maya*); metapectal-propodeal complex and mesoscutellum overlapping medially, dividing metanotum in dorsal view (metanotum continuously visible posterior to mesoscutellum in *P. maya*); female head 1.3 times as long as wide, male head 1.1 times as long as wide (head 1.1 times as long as wide in both sexes of *P. maya*); mandible wide and tridentate, though dorsal tooth small and inconspicuous (mandible more narrow and bidentate in *P. maya*); clypeus with anterior margin broadly rounded, posterior margin slightly emarginate (anterior margin acutely rounded, posterior margin sinusoidal in *P. maya*); metapectal-propodeal complex without distinct lateral marginal carina (lateral marginal carina more distinctly conspicuous in *P. maya*); female with head and mesosoma of similar orange-red-brown color (dark brown head and metasoma contrasting with orange mesosoma in *P. maya* female).

**Female** (Figs 1, 4a–d, 5). *Length range:* 1.18–1.41 mm (n = 11); Holotype: 1.38 mm. *Head* (Figs 1, 4a–c, 5c, e). Face, gena, vertex, and occiput orange to red-brown


**Figure 4.** *Prorops umiehu* sp. nov. holotype  $\bigcirc$  (**a-d**) and allotype  $\bigcirc$  (**e-g**) **a**, **e** side view **b**, **f** head **c**, **g** anterior view of head **d** dorsal view. Scale bars: 500 µm (**a**, **b**, **d**, **e**); 250 µm (**c**, **f**, **g**).

in color. Snout slightly lighter orange-brown, antenna yellow-brown basally, fading to brown apically. Frons and gena with lightly reticulate texture, density of reticulations increasing towards snout, snout itself with bumpy texture. Compound eye with short, sparse setae between ommatidia. Vertex incurved medially. Head with sides more or



**Figure 5.** *Prorops uniehu* sp. nov. **a** fore wing  $\bigcirc$  **b** hind wing  $\bigcirc$  **c** anterior view of head  $\bigcirc$  (paratype) **d** dorsal view  $\bigcirc$  (paratype) **e** antenna  $\bigcirc$  **f** proleg  $\bigcirc$  **g** mesoleg  $\bigcirc$  **h** metaleg  $\bigcirc$  **i** male genitalia, ventral view. Scale bars: 250 µm (**c**); 500 µm (**d**).

less parallel and only slightly outcurved, eye protruding slightly so widest part of head is across eyes and about half-way along VOL. Snout clearly bifid apically, ending in two distinct lobes apically curved dorsally to form two small teeth, and with dorsal median groove extending from where lobes meet to approximately even with middle of eye. Torulus located ventral to lateral margins of snout at approximately half its length, visible in dorsal view. Clypeus in anterior view extending laterally past torulus, tapers laterad; medially with dorsal margin broadly arched against snout and torulus, ventral margin shallowly incurved; overall appearing as handlebar mustache not, or only slightly, turned dorsad at its lateral corners. Antenna with scape curved ventrally and widened apically, apical surface forming cavity; pedicel subovate. Ten flagellomeres, 1<sup>st</sup> smallest and cone shaped, 2<sup>nd</sup> through 9<sup>th</sup> shaped like apically truncated spheres, and similar in size, shape, and structure. Terminal flagellomere ovate. Setae of similar length and density on all flagellomeres, less dense on scape and pedicel. Mandible wide, ventral margin thickened with blunt ventral knob at about half its length; apically tridentate, ventral tooth largest, middle tooth smaller, dorsal tooth small and inconspicuous. Anterior region of head, including snout, clypeus, and mandible, distinctly more densely setose than rest of head. *Morphometrics* (range, n = 7 for all measurements): LH : WH = 1.24-1.31; LH : LE = 3.26-3.64; LH : VOL = 2.19-2.34; LHBE : LHAE = 0.35–0.38; VOL : LE = 1.41–1.66; WF : LE = 1.70–1.87; LE : BEM = 5.71– 7.30; WOT : OOL = 0.40-0.45; POL : AOL = 1.10-1.54; AOT = 66°-75°; LH\S : WH = 0.97–1.03. Antennal ratio approximately Scape : Pedicel : F1 : F2 : F3 : F4 : F5 : F6 : F7 : F8 : F9 : F10 = 4.0 : 2.6 : 1.0 : 0.9 : 1.2 : 1.2 : 1.4 : 1.4 : 1.5 : 1.6 : 1.6 : 2.9.

Mesosoma (Figs 4a, d, 5d). Pronotum and metapectal-propodeal complex yellow to reddish-brown; mesothorax slightly darker in some individuals; legs apical of femora yellow-brown. Nota shiny with very light reticulate texture, difficult to see except under high magnification with the right lighting. Texture on dorsal surfaces slightly strongest on pronotal flange and metapectal-propodeal disc. Pronotal flange conspicuous; pronotum with sparse setae, longer setae at posterior margin. Anteromesoscutum with scattered short setae; mesoscutellum with pair of short setae on its lateral margin approximately even with posterior of axillae, another pair of longer mesally pointing setae at its posterior; tegula with few setae, denser than on surrounding sclerites; metapectalpropodeal disc without setae, declivity with few setae just mesal of transition to lateral surface of metapectal-propodeal complex. Transscutal suture such that posterior margin of anteromesoscutum is straight mesal of axillae. Anterior margin of anteromesoscutum somewhat visible under translucent pronotum. Mesosoma relatively flat along dorsomedian line. Neither notaulus nor parapsidal signum manifest on cuticle surface. Mesocutellum reaches metapectal-propodeal complex medially, metanotum very thin or not visible medially in dorsal view, distinct laterally. Mesopleuron projects from side of mesosoma, flattened subcylindrical in shape, and with few setae only on its ventral side. Mesopleural pit somewhat centrally located. Metapectal-propodeal disc approximately 1.25 times as long as wide; lateral marginal carina indistinct or absent, transition from disc to lateral surface rounded, though cuticle may appear thickened in dorsal view at this transition; disc somewhat outcurved transversely. Declivity when viewed perpendicular to its surface has vaguely subtriangular raised region, but appears overall subrectangular: posterior margin of metapectal-propodeal complex straight except for small bump above petiolar foramen. Lateral surface of metapectal-propodeal complex flat or slightly convex.

*Legs* (Fig. 5f-h). All tibiae with scythe shaped apical spur with comb-like setae on inner edge. Mesotibia with apical spines more numerous and stronger than in pro- and

metatibiae, and with additional row of strong spines over its length on side opposite tibial spur; pro- and metatibiae lacking this row of spines. First tarsomere longest in each leg, most notably so in pro- and metaleg where it is subequal to  $2^{nd}$  through  $4^{th}$  tarsomeres combined.  $2^{nd}$  through  $4^{th}$  tarsomeres subequal in length in proleg, and sequentially decrease in length in meso- and metalegs. Length of  $5^{th}$  tarsomere not including claw subequal to combined length of  $2^{nd}$  and  $3^{rd}$  tarsomeres in proleg, and subequal to  $2^{nd}$  segment alone in meso- and metalegs.

Fore wing (Fig. 5a). Sc+R vein, prestigmal abcissa of radial 1, and pterostigma present; 2r-rs+Rs absent, reduced to fold. Rs+M, M+Cu, and A veins lightly indicated. Sc+R vein with 1-3 setae. Prestigmal abcissa of radial 1 slightly inset from wing margin, pterostigma borders margin. Prestigmal flexion line present as hyaline stripe that separates prestigmal abcissa of radial 1 and pterostigma; thickness of this hyaline stripe and shape and size of prestigmal abcissa of radial 1 and pterostigma somewhat variable among individuals, though prestigmal abcissa of radial 1 and pterostigma typically subequal in size. Wing membrane overall subhyaline, slightly infuscate basal of prestigmal abcissa of radial 1 and apical of imaginary line between pterostigma and apex of retinaculum. Cubital and median flexion lines not visibly present; small hyaline spot projects into wing membrane on posterior margin at apex of retinaculum. Marginal setae present from prestigmal abcissa of radial 1 around wing apex, abruptly ending at beginning of straight trailing margin of wing. *Hind wing* (Fig. 5b). Wing membrane subhyaline, slightly infuscate apical of hamuli. Marginal setae absent on leading edge, present around apical margin and on trailing edge where length is about half maximum width of wing. Leading edge with slight projection culminating in dark spot with three hamuli at about half wing length.

*Metasoma* (Figs 4a, b, 5d). Petiole and gaster dark brown to black, distinctly darker than orangish-brown mesosoma. First tergite constricted anteriorly to form distinct petiole, segment as a whole somewhat wider than long; constricted petiolar region of subequal length and width, with fine bumpy texture and shallow median dorsal groove extending its length. Remainder of metasoma shiny dark brown to black with smooth texture, each segment dorsally with sparse setae in a somewhat transverse row, these setae increasing slightly in length on posterior segments, last segment before sting with many setae on dorsal and lateral surfaces. In dorsal view, 1<sup>st</sup> and 2<sup>nd</sup> gastral segments subequal in length on median line, 3<sup>rd</sup> and 4<sup>th</sup> also subequal but shorter than 1<sup>st</sup> and 2<sup>nd</sup>. Metasoma widest at approximately 4<sup>th</sup> segment. Sting often visible projecting slightly from apex of abdomen in dried or alcohol preserved specimens.

**Male** (Figs 4e–g, 5i). *Length range*: 0.87–1.38 mm (n = 3); Allotype: 1.38 mm

As in female but with the following differences: Head more square than in female, length to width ratio approximately 1.1; eye larger and more bulging; ocelli more widely placed; vertex only weakly concave;  $2^{nd}$  through  $9^{th}$  antennal flagellomeres longer and more cylindrical; coloration typically darker with head and metasoma brown, mesosoma slightly lighter brown. *Genitalia*: See Fig. 5i. Small relative to body size. Genital capsule broad, gonostipites and harpes combined only slightly longer than wide; harpe short, quadrate, truncate distally, shallowly concave medially. Penis valvae equal to or slightly exceeding volsella, distinct in ventral view. *Morphometrics* (range, n = 3 for all measurements):LH : WH = 1.07–1.12; LH : LE = 2.48–2.63; LH : VOL = 2.71–3.11;

LHBE :LHAE = 0.33–0.38; VOL : LE = 0.80–0.96; WF : LE = 1.42–1.58; LE : BEM = 6.34–7.72; WOT : OOL = 0.63–0.74; POL : AOL = 1.35–1.68; AOT = 75°–82°; LH\S : WH = 0.87–0.88

**Materials examined.** *Holotype* (Fig. 4a–d): ♀; Hawaiian Islands, Oʻahu, Kahana Bay; 21.5573°N, 157.8781°W, 15 m; 27.viii.2021; ex *Trema orientalis* branches; D. Honsberger (UHIM).

*Allotype* (Figs 4e–g, 9): ♂; Hawaiian Islands, Oʻahu, Mānoa Valley; 21.3288°N, 157.7930°W, 154 m; 12.ii.2020; ex *H. eruditus* tunnel in *T. orientalis* branch; D. Honsberger (UHIM).

Paratypes: 18 9, 5 8. Hawaiian Islands, Oʻahu, Kahana Bay; 21.5573°N, 157.8781°W, 15 m; 27.viii.2021; ex Trema orientalis branches; D. Honsberger (1 ♀, 1 ♂ BPBM) • Hawaiian Islands, Oʻahu, Mānoa; 21.3009°N, 157.8196°W, 39 m; 20.v.2021; ex *Delonix regia* seed pod; D. Honsberger (1 ♀ BPBM) • same data as previous except 13.iv.2021 (1  $\bigcirc$  UHIM; 1  $\bigcirc$  BPBM; 1  $\bigcirc$  CNC) • Hawaiian Islands, Oʻahu, Mānoa; 21.3009°N, 157.8196°W, 39 m; 23.iv.2021; reared from Hypothenemus eruditus adult in Delonix regia seed pod; D. Honsberger (1  $\bigcirc$ CNC) • Hawaiian Islands, Oʻahu, Waimānalo; 21.3341°N, 157.7113°W, 28 m; 19.ii.2021; reared from *Hypothenemus seriatus* adult in *Macadamia integrifolia* husk; D. Honsberger (1 2 UHIM) • Hawaiian Islands, Oʻahu, Wahiawā; 21.5151°N, 158.0423°W, 296 m; 11.i.2020; ex Hypothenemus eruditus tunnel in Spathodea campanulata branch; D. Honsberger (1 d CNC) • Hawaiian Islands, O'ahu, Wahiawā; 21.5143°N, 158.0419°W, 301 m; 1.iii.2019; ex Spathodea campanulata branches; D. Honsberger (1  $\bigcirc$  CNC) • Hawaiian Islands, O'ahu, Pearl Harbor; vi.1954 (1  $\bigcirc$ BPBM) • Hawaiian Islands, Oʻahu, Waipiʻo; ix.1957; light trap; J.W. Beardsley (1 S BPBM) • Hawaiian Islands, Oʻahu, Waipiʻo; ii.1960; light trap; J.W. Beardsley  $(1 \bigcirc BPBM)$  • Hawaiian Islands, O'ahu, Pearl Harbor, West Loch, el. 3 ft; 13–24. vi.1998; yellow sticky board trap; W.D. Perreira (2 9 BPBM) • Hawaiian Islands, Moloka'i, Kamalō Bridge, 3 ft.; 19.viii–2.ix.1994; yellow sticky board trap; W.D. Perreira (1  $\bigcirc$  BPBM) • Hawaiian Islands, Moloka'i, Kualapu'u in coffee field, el. 750 ft.; 27.x-10.xi.1995; yellow sticky board trap; J.W. Beardsley and W.D. Perreira (1 ♀ BPBM) • Hawaiian Islands, Maui, Kahului Airport; 4.x.1999; Malaise trap site #1, wet spot nr. bike path, nr. water amongst kiawe & palm trees; F.G. Howarth, D.J. Preston, & J. Dockall (1 2 BPBM) • Hawaiian Islands, Maui, Kahului Airport; 20°54'22"N, 156°25'42"W; 3–16.xii.1999; Malaise trap site #2; F.G. Howarth, D.J. Preston, F. Starr, & K. Martz (1 🖉 BPBM) • Hawaiian Islands, Maui, Kahului Airport; 20°54'22"N, 156°25'56"W; 1.ii.2000; Malaise trap site #1; F.G. Howarth, D.J. Preston, J.E. Dockall, F. Starr, & K. Martz (1 3 BPBM) • Hawaiian Islands, Hawai'i, Honomalino; iv.1987; carob fruits; HY 87–14; G. Shaner (3  $\stackrel{\circ}{\downarrow}$  BPBM) • Hawaiian Islands, Hawai'i, MacFarms; 9.iii.1995 (2 ♀ BPBM).

**Etymology.** The species name is Hawaiian, 'umi'ehu (lit., *blonde mustache*). When the head is viewed anteriorly (Fig. 5c), the clypeus appears as a blonde ('ehu) handlebar mustache ('umi'umi) between its snout and mouth. This small, cryptoparasitic wasp also appears like a mist ('ehu) in the environment, often faintly perceptible and then evaporates from view. The name is to be treated as a noun in apposition.

**Known distribution.** This species is known from the islands of O'ahu, Moloka'i, Maui, and Hawai'i in the Hawaiian Islands, where it is likely adventive, and from the United Arab Emirates near Al Ajban, Emirate of Abu Dhabi (Vargas 2017). It has long been present in the islands, with the earliest Hawai'i specimen dating back to 1954. This suggests it may have arrived from the southwest Pacific during World War II or shortly afterward.

**Known hosts.** *Hypothenemus eruditus* and *Hypothenemus seriatus* (Coleoptera: Scolytinae); see Biology section.

### Key to the known world species of Prorops

Note that males of *P. rakan*, *P. mandibularis*, *P.* "sp. 23", and *P.* "sp. 24" are currently unknown.

1	Fore wing without vein 2r-rs+Rs, or 2r-rs+Rs vein very faint, reduced to
	fold2
_	Fore wing with distinct vein 2r-rs+Rs emanating from pterostigma4
2	Snout with median groove but not clearly bifid, instead rounded or trifid api-
	cally; notauli present <i>P. obsoleta</i> ( $\bigcirc$ $\bigcirc$ )
-	Snout clearly bifid apically (ends in two distinct lobes); notauli absent3
3	LH subequal to WH; metapectal-propodeal disc wider than long, LPD:WPD
	$\approx$ 0.9 (both sexes); AND if female, vertex slightly incurved in face view; if
	male, vertex nearly straight in face view <i>P. impotens</i> $(\stackrel{\bigcirc}{+}\stackrel{\bigcirc}{\wedge})$
-	Metapectal-propodeal disc longer than wide, LPD:WPD $\approx$ 1.25; vertex dis-
	tinctly incurved in face view (both sexes); AND if female, LH:WH $\approx$ 1.3; if
	male, LH:WH $\approx 1.1$
4	Snout divided into two widely separated arms not contiguous basally or api-
	cally
-	Snout divided or with median groove, but contiguous at least basally5
5	Snout with median groove but rounded apically, not clearly bifid6
_	Snout clearly bifid apically (ends in two distinct lobes7
6	LH:WH $\approx$ 1.6, and LH\S also distinctly greater than WH; LHAE:LHBE
	$\approx$ 2.9; mandible tridentate; lengths of first four antennomeres with ratio of
	10:3:1:2; head with vertex somewhat straight <i>P. petila</i> ( $\bigcirc$ $\bigcirc$ )
-	LH:WH $\approx$ 1.3, and LH\S subequal to WH; snout long, LHAE:LHBE $\approx$ 1.3;
	mandible bidentate; first four antennomeres in ratio of 3.5:1.6:1.1:1.0; head
	with vertex incurved medially <i>P. mandibularis</i> $(\bigcirc$ +)
7	LH:WH $\approx$ 1.4, first four antennomeres in ratio of 5:2:1:1; mandible triden-
	tate <i>P. rakan</i> ( <sup>○</sup> <sub>+</sub> )
-	LH subequal to WH8
8	In females, mesosoma, mandible, snout, and basal region of antenna bright
	orange to reddish brown, in distinct contrast with metasoma and remainder
	of head almost black; in males, head and metasoma brown, mesosoma light

brown. In both sexes, LPD distinctly greater than WPD, disc shiny with lateral carina, declivity also smooth and shiny with lateral carina at least anteriorly; mesonotum with only a few setae, usually just 2 on each side of median line of mesoscutellum; metanotum visible as continuous narrow band posterior to mesoscutellum in dorsal view; LH:WH ≈ 1.1; LHAE:LBHE ≈ Coloration entirely dark brown to black; WPD subequal to or greater than LPD, disc without lateral marginal carina; mesonotum with few to many setae on both anteromesoscutum and mesoscutellum; mesoscutellum covers metanotum medially......9 9 Head widest across eyes, narrowing between eye posterior margin and vertex; WPD slightly greater than 1.5 times LPD; LH:LE  $\approx$  2.4; LHAE:LHBE  $\approx$  2.5; mesonotum setose, including medially; mesoscutum with slightly rough texture, metapectal-propodeal disc smooth and glassy; head with vertex strongly Width of head just anterior to vertex subequal to or slightly greater than width across eyes; WPD distinctly less than 1.5 times LPD; LH:LE > 2.5; Vertex only somewhat incurved, such that anterior ocellus slightly pos-10terior to top of compound eye in full face view; WH:LE ≈ 2.5; LH:LE ≈ 2.9; LHAE:LHBE  $\approx$  1.9; WH:LHBE  $\approx$  1.4; metapectal-propodeal disc only slightly wider than long, WPD:LPD  $\approx$  1.1, disc with rough texture; mesoscutum and scutellum setose, including medially ...... *P. nasuta* (Q Z) Vertex strongly incurved, such that anterior ocellus slightly anterior to top of compound eye in full face view; eyes smaller, so that WH:LE  $\approx$  3.3; LH:LE  $\approx$ 2.4; LHAE:LHBE ≈ 1.3; WH:LHBE ≈ 1.7; metapectal-propodeal disc substantially wider than long, WPD:LPD ≈ 1.3, disc smooth and glassy; mesoscutum less setose, with few or no setae medially on mesoscutum ..... 

## Biology

### Known hosts

*Prorops maya* has been found parasitizing *H. eruditus* adults in *Trema orientalis* (gunpowder tree) branches in Mānoa Valley at the foot of the Koʻolau Mountains on Oʻahu island (21.3288°N, 157.7930°W, 154 m) (Fig. 6).

Prorops umiehu has been found parasitizing H. eruditus in T. orientalis branches and D. regia seed pods in Mānoa, Oʻahu island, and Hypothenemus seriatus in macadamia nut husks in Waimānalo, Oʻahu (Figs 6, 7). It has been found emerging from Spathodea campanulata P.Beauv (African tulip) branches near Wahiawā, Oʻahu and Ceratonia siliqua L. (carob) pods in South Kona, Hawaiʻi, but its development was not observed. While we cannot confirm the host relationship in these S. campanulata



**Figure 6.** *Hypothenemus eruditus* beetles paralyzed and parasitized by *P. maya* or *P. umiehu* in *T. orientalis* branches. All photographs are of naturally occurring situations, taken while peeling bark from branches found in a forested region of Mānoa Valley on Oʻahu (21.3288°N, 157.7930°W, 154 m). Some beetles, such as each of the three in (**a**), are clearly parasitized with a *P. maya* or *P. umiehu* larva feeding through the membranous region of the beetle ventrally between the pro- and mesothorax, the posterior of the larva wrapped around the beetle. All larvae of *P. maya* and *P. umiehu* found in this study were observed to feed in this way. *Prorops* pupae, empty pupal cocoons, and more developing larvae are also visible in (**b**,**c**,**d**). Eggs of a thrips species that may scavenge on the remains can also be seen placed on top of beetles in (**d**). All beetles in these pictures were not moving, either paralyzed or killed presumably by *P. maya* or *P. umiehu*. Note that, in contrast to Fig. 8, these photographs are all of *H. eruditus* beetles in unconfined, wide chambers, and thus the development and construction of a pupal cocoon by wasp prepupae does not typically split the beetle into two pieces, and parasitoid pupae are located adjacent to or near the host beetle. It is unknown which of the developing parasitoids in these photographs correspond to which species of *Prorops*, as immatures collected from these branches yielded both *P. maya* and *P. umiehu*.

branches, we presume it also to be attacking *H. eruditus* because this was the only Scolytinae found to be present in the collections from which *P. umiehu* also emerged. Thus there seems to be overlap in host tree and host beetle use between these two species.



Figure 7. Prorops umiehu developing immatures. Photographs are of naturally occuring situations, taken while dissecting plant material collected from field environments **a** *P. umiehu* larva on *H. eruditus* from *D. regia* pods collected from the campus of UH Mānoa **b** pupating *P. umiehu* having completed its larval stage on H. *eruditus* in *D. regia* pods from UH Mānoa **c, d** *P. umiehu* larvae on *H. eruditus* from *D. regia* from UH Mānoa **e** macadamia husk from Waimānalo, O'ahu with its inner layer peeled, showing pupating *P. umiehu* having developed on the *H. seriatus* adults next to them.

Notably, *P. umiehu* has not been found parasitizing the related *Hypothenemus* spp. which commonly co-occur with *H. eruditus* in *D. regia* seed pods. Since *H. eruditus* uses many more trees than the three listed above as hosts in Hawai'i, it seems reasonable to assume that both species are associated with more trees than the few listed here.

## Life cycle

Development of *P. maya* and *P. umiehu* immature stages has been observed to occur on *H. eruditus* adult beetles in chambers and galleries the beetles excavate below the surface of the plant material (Figs 6–8). Both species follow a similar pattern. Eggs are laid on the adult beetle on the ventral side of the membranous region of articulation between the prothorax and mesothorax, and the emerging larvae feed on the beetle through the same location. As the developing larva feeds and grows, much of the larva remains outside the beetle and wraps around it, as if the beetle were wearing a necklace, and the anterior of the wasp's body extends further inside the beetle. When feeding by the wasp larva on its host has completed, the larva disconnects from the remains of the beetle and spins an off-white ovoid pupal cocoon in which it pupates.



**Figure 8.** Typical placement of pupae when development occurs in a narrow tunnel environment. The parasitoid larva feeds on the adult beetle through the ventral membranous region between the pro- and the mesothorax. The growth of the larva and its subsequent construction of a pupal chamber forces these two sections of the beetle apart, and pupating larvae are typically found concealed between them. In these pictures, the white material near or around the parasitoid immature is what remains of the pupal cocoon it had constructed after the tunnel was broken open by peeling apart the plant material. Photographs are of naturally occurring situations, taken of plant material collected outdoors **a**, **b** *Prorops sp.* prepupa (**a**) and pupa (**b**) between two halves of an *H. eruditus* beetle in an *H. eruditus* tunnel in a *T. orientalis* branch collected from Mānoa Valley on Oʻahu; **c:** *Prorops umiehu* pupa in a *D. regia* pod from a tree on the campus of the University of Hawaiʻi at Mānoa. Note the position of the pupal cocoon relative to the beetle in (**c**), not the larva itself which was moved as the pod was peeled apart. Such placement was more common in *T. orientalis* branches where scolytid tunnel systems were often more linear, but atypical in *D. regia* pods possibly due to the less linear and more confused organization of beetle feeding in these pods, but in (**c**) developed in this way due to the topography in the certain section where the beetle was parasitized.

The growth of the larva, positioned as it is, forces the two halves of the beetle apart. If development occurs in a tunnel, there is nowhere for this extra volume to go except to expand along the length of the tunnel. Thus between the growth of the wasp larva, the increased brittleness of the beetle after having been desiccated by the feeding of the larva, and the activity involved in creation of a pupation area by the wasp prepupa, the beetle splits apart and pupating wasps are often found in-between the two parts of the beetle, with the beetle's head and prothorax on one side of the pupating larva and the rest of the beetle on the other (Fig. 8).

Field collections have indicated that oviposition and larval development occurs exclusively on the adult stage of the beetle, and the laboratory tests subsequently described that present *P. maya* and *P. umiehu* adult females with a variety of life stages of *H. eruditus* have resulted in parasitism of only adult beetles. Larval development of laboratory reared *P. umiehu* from egg to adult eclosion is pictured in Fig. 9.

### Behavior observed in field collected plant material

When parasitized beetles were found in *T. orientalis* branches, nearly all the beetles in the gallery were either paralyzed or parasitized (see Fig. 6b–d for examples). In such circumstances, parasitoids on the beetles were close to the same stage of development, and most of

the beetles were dead or paralyzed but not obviously parasitized. This was observed for gallerv systems containing developing larvae that yielded *P. maya* (n = 5) and *P. umiehu* (n = 1). Because the density of beetles in these galleries was in the range of that typically observed for surrounding, unaffected gallery systems, this suggests that *P. maya* often attacks nearly all beetles in a host patch. The proportion of adult individuals that were clearly parasitized in a gallery versus dead or paralyzed was recorded on four occasions, with 5/19, 5/6, 3/6, and 5/6 beetles parasitized. Adults of the two Prorops spp. were only sometimes found in the galleries with parasitized beetles, implying that adult females of these species do not necessarily remain with their young as do some other bethylids [see for example Sclerodermus harmandi (Hu et al. 2012), and Goniozus nephantidis (Hardy and Blackburn 1991)]. In the T. orientalis branches found to contain these Prorops spp., there were often many distinct, unconnected beetle gallery systems in a branch. Wasps or paralyzed beetles were found in very few of these galleries, with the vast majority of galleries inhabited by healthy beetles. This implies that while P. maya tends to use nearly the whole host patch within a beetle gallery, most galleries were not utilized by these wasps, and the resulting overall percent parasitism and host mortality in this particular environment was low.

In *D. regia* pods, the pattern of patch use within a gallery system seems to be different. It seems to be much more sparse than in the *T. orientalis* branches, with only a small proportion of individuals in a gallery section either paralyzed or parasitized. This was observed only for *P. umiehu* (n > 15); *P. maya* has thus far only been found in *T. orientalis* branches. While this could be a result of differences in behavior between the two species, it appears more likely that this could be because the geometry of *H. eruditus* gallery systems tends to be different in these two plants. In *T. orientalis* branches, *H. eruditus* use only the thin phloem layer, and tend to construct a somewhat round chamber that extends in two dimensions under the bark, though this chamber eventually branches into a network of tunnels as the second and subsequent generations of beetles develop in the wood. Thus, at least in the earlier stages of beetle activity in the wood, their population tends to be somewhat localized in an uncomplex shape. In D. regia pods, the tissue the beetles use as a food source is thick enough relative to the size of the beetles to accommodate movement in three dimensions. Instead of forming a chamber, the beetle galleries take on a topologically more complex pattern, eventually creating a sponge-like network of tunnels spread through the material. The population of beetles inhabiting these tunnels tends to be more spread out within this maze of tunnels. Such variability in the gallery system created by H. eruditus among different host plants has been previously reported by Wood (1982) and Browne (1961). The geometry of the host's tunnels may contribute to this difference in patch use patterns, possibly due to the wasps' ability to locate their hosts within them.

### Observation chambers in a laboratory setting

Observed behaviors were largely similar between *P. maya* and *P. umiehu*. While differences in behavior presumably exist, none of the general aspects of behavior and observations recorded here were distinct enough to be clearly associated with one species or the other. Typical observed behavior was as follows, and unless noted otherwise, the below observations apply similarly to both species.



**Figure 9.** Development of *P. umiehu* on *H. eruditus*. The beetle was parasitized by a *P. umiehu* adult female entered into the observation chamber described in the text containing *H. eruditus* beetles on a piece of *D. re-gia* pod with channels cut into it with a knife. The parasitized beetle was then moved into a small hole carved into a wood substrate and covered with a piece of glass slide cover to mediate humidity and to create an enclosed environment to facilitate construction of a pupal cocoon by the prepupa. Time elapsed after presence of an egg was first observed on the beetle are noted in the photographs. The emerged adult is the allotype.

*General searching behavior* (Video 1: https://vimeo.com/688211081, Video 2: https://vimeo.com/691136279): The wasps quickly moved through the tunnels in the wood, holding their antennae straight, vibrating and feathering them over the surfaces. This position of the antennae is in contrast to *Allobethylus ewa* (Bridwell, 1920), another bethylid observed in separate studies using the same apparatus, which holds its antennae curved while antennating the surface of a wood substrate or beetles within it, which may function to increase the contact area of the antenna against surfaces with

pits or other irregular texture (D. Honsberger, pers. obs.). The *Prorops* spp. showed clear interest upon finding a beetle, and when immature and adult beetles were present together, the wasps seemed to take preferential interest in the adults, and subsequent stinging, malaxation, chewing, and host feeding behaviors were initially focused on them.

Upon encountering an active *H. eruditus* adult beetle, a female wasp was observed to typically examine and antennate it, often climbing somewhat on top of the beetle in doing so. This was most often followed by an attempt at stinging the beetle, or more rarely, the wasp would either move away and explore elsewhere or repeatedly bite the beetle with its mandibles seemingly with the objective of attempting to move it. Stinging was typically followed by a quick exploration of the beetle and the area around it, and then often by a chewing behavior and host feeding, these actions covered in more detail below. The beetle was typically then abandoned and the wasp moved through the arena and was arrested by the presence of additional beetles on which it performed similar behaviors. Beetles that had previously been stung and paralyzed were often re-encountered by the wasps, who would examine them, occasionally sting them again, and often perform additional chewing or host feeding. *Prorops umiehu*, if taking interest in a larva or pupa, was observed to exhibit a similar progression of stinging and host feeding as with an adult.

The wasps were observed to adeptly turn themselves around in the tight space of a tunnel. Similar behavior has been observed in other parasitoids living in concealed tunnel environments using the same apparatus, such as *Acerocephala hanuuanamu* (Honsberger et al. 2024). As in that species, this maneuver seems to be made possible by the flat shape of the head and the long, articulating prothorax, presumably evolutionary adaptations to moving in tunnel environments. In this maneuver, the wasp ducks its head under its thorax, and follows it with the prothorax, the rest of the mesosoma, and then the flexible abdomen, smoothly sliding over its own body to switch the position of its head and metasoma (Fig. 10e, Video 1: https://vimeo.com/688211081).

**Stinging** (Figs 10a, b, 11b, c, Video 1: https://vimeo.com/688211081, Video 2: https://vimeo.com/691136279): Initial exploration of an active adult beetle was most often followed by an attempt to sting the beetle, in which the wasp would climb fully on top of the beetle, grip the beetle's elytra or abdomen with its legs, and elongate and arch its metasoma around the beetle and search with its ovipositor for a location on the beetle susceptible to its sting. Crevices in the beetle's morphology encountered by the apex of the abdomen seemed to draw the focus of the exploration, though whether the wasp was able to contact an acceptable part of the beetle with its stinger often seemed more a matter of luck than of planning. A particular preference for aiming at the junction between the pro- and mesothorax was observed, especially evident for *P. umiehu* for which the number of observed stinging events was higher, but attempts were also observed to be made at stinging the ventral side of the abdomen, between the elytra, or the apex of the abdomen for both species. An attempt at stinging was either over quickly and often repeated more than once (though it was unclear if these attempts were successful), or in other cases the behavior persisted for a longer period of up to



**Figure 10.** Aspects of the behavior of *P. maya* in laboratory observation chambers. The apparatus is the same as in Fig. 11a except using bark peeled from *T. orientalis* branches with channels cut into it with a knife. Beetles are all *H. eruditus*. **a**, **b** stinging **c** chewing behavior on adult beetle, it was unclear if (**c**) was host feeding or the eventually abandoned preparation of an oviposition site or both **d** host feeding on a larva **e** turning around, reversing the orientation of its body in the tight space of a tunnel. These actions are also shown in Video 1: https://vimeo.com/688211081.

5 minutes. *Hypothenemus eruditus* larvae and pupae were also similarly explored and occasionally stung by both species.

An adult or immature beetle that was successfully stung slowed down over the next few minutes before becoming more or less motionless, making only marginal twitchy movements. After a few days, such subtle twitching movements were still observed, including in beetles having been oviposited on. This implies that the chemicals injected by the wasp are paralytic and do not necessarily kill the beetle. This may maintain the integrity of the nutrition and water content of the beetle as its young develops on it (Vinson and Iwantsch 1980), while preventing the host from dislodging the egg or larva through its movements (Quicke 2015).

*Chewing, oviposition, host feeding, and function of the snout* (Figs 10c, d, 11e, f, 12; Video 1: https://vimeo.com/688211081, Video 2: https://vimeo.com/691136279,



**Figure 11.** Stinging and chewing behavior of *P. umiehu* in laboratory observation chambers **a** the observation chamber used in this study with a piece of *D. regia* pod tissue having been naturally infested by *H. eruditus* sandwiched between the aluminum and plexiglass **b**, **c** *P. umiehu* stinging *H. eruditus* adult females **d** profile view of a *P. umiehu* female next to *H. eruditus*, showing the groove formed between the snout dorsally and the mandibles ventrally which acts as a mechanism for holding the edge of the prothoracic sclerite of its host **e** the wasp grasps the abdomen of the beetle with its legs and pushes forward on the sclerite with this structure to expose the membranous region between the pro- and mesothorax of the beetle, while maintaining use of the mandibles for chewing on the stretched membrane. This was observed, as in (**e**), for the purposes of host feeding on adults having previously been stung and paralyzed, and was also observed during preparation for oviposition (shown in Fig. 12) **f** host feeding on an *H. eruditus* pupa previously stung and paralyzed. These actions are also shown in Video 2: https://vimeo.com/691136279.

Video 3: https://vimeo.com/688588477): Stinging was often followed by the wasp climbing on top of the lateral or ventral side of the beetle and chewing on the membraneous region between the pro- and mesothorax. This behavior was either abandoned quickly or persisted for extended periods of time, typically in the vicinity of 5 minutes but occasionally as long as 15 minutes. While performing the chewing behavior, the wasp gripped the beetle's abdomen with its legs and pushed the prothorax of the beetle forward using its head, widening the separation between the pro- and mesothoracic sclerites and opening up the membranous region of articulation. The chewing was performed on the stretched membrane at a position as anteriorly advanced as the wasp was able to achieve. In this maneuver, the wasp was able to push on the prothorax by locking the groove formed between the projecting snout and mandibles with the edge of the prothoracic sclerite of the beetle, and in doing so was able to push the sclerite



**Figure 12.** Oviposition by *P. umiehu* on *H. eruditus* in a laboratory observation chamber. The apparatus in which this occurred is the same as that pictured in Fig. 11a **a** *H. eruditus* beetle approximately 30 minutes subsequent to oviposition, showing the newly laid egg between the beetle's pro-and mesothorax **b**, **c** use of the groove between the snout and mandibles in *P. umiehu* to push forward on the prothoracic sclerite of the beetle while chewing on the exposed and tensioned membrane, in preparation for oviposition **d** the wasp then placed the apex of its metasoma between the pro- and mesothorax, into the crevice that remained open as a result of the chewing as in (**b**) and (**c**), and maintained that position for approximately 10 minutes **e** the wasp slowly draws her metasoma across the crevice while the egg exits **f** the host, wasp, and egg subsequent to completion of oviposition. These actions are also shown in Video 3: https://vimeo.com/688588477.

forward without it sliding over the wasp's face while maintaining use of its large mandibles for chewing. This chewing action functioned as the method of host feeding on adult beetles and was also performed in preparation for oviposition.

All eggs observed both in the laboratory observation chambers and field collected wood from both species were placed at the same location on the adult beetles: transversely oriented on the ventral side of the membraneous region of articulation between the pro- and mesothorax. Thus one use of the chewing behavior was apparently to prepare the host for oviposition, though its exact function was not clear: it could possibly be to cut the membrane so that the gap between the pro- and mesothorax would remain open and present an accessible area for oviposition and egg development; to cut open the tissue so that the emerging larva would be able to penetrate the membrane and feed; to cut the ventral nerve cord; for the adult to taste the beetle's hemolymph to assess its quality as a host; or alternatively, simply for the adult to host feed on the beetle. Adult *Sclerodermus harmandi* (Buysson, 1903) (Hym.: Bethylidae) have been observed to chew holes through the cuticle of their host larvae through which their offspring feed as larvae (Hu et al. 2012)

The act of oviposition (Video 3: https://vimeo.com/688588477) was only observed once, for *P. umiehu*. An *H. eruditus* adult previously stung, paralyzed, and likely chewed on as evidenced by the separation between the pro- and mesothorax greater than normal for a beetle that had simply been stung, was approached by the wasp and its actions were observed for the 2.5 hours leading up to oviposition. In this time, the wasp initially explored the beetle and the surrounding area, focusing much of its attention near the junction of the pro- and mesothorax, and attempted to subtly manipulate the beetle's position in the tunnel by grabbing the body of the beetle with its mandibles. The wasp then remained motionless in the tunnel, its body oriented opposite that of the beetle, the two touching head to head. This was followed by a short chewing interval, after which the wasp reassumed its position motionless in the tunnel with the beetle for approximately 1.5 hours. The wasp then resumed its exploration of the beetle, short chewing intervals, and subtle manipulations of the beetle's position, followed by an extended chewing event on the membrane along the midline of the beetle. It then explored the area and the beetle, repeating short but vigorous chewing intervals. The wasp then after a few attempts grabbed the beetle and repositioned it approximately a body length away in a slightly wider section of the tunnel. This was followed by one more vigorous chewing event, after which the wasp turned around and reached the apex of her metasoma into the gap between the pro- and mesothorax. The wasp remained in this position for about 10 minutes, her metasoma pulsating slightly. Then, over about 30 seconds, the wasp slowly moved the apex of her metasoma transversely across the crevice and the egg was visible emerging. The wasp slowly withdrew and became active again, exploring the vicinity for a few minutes and then left the area. The next day, the wasp was observed again in the tunnel in the same position as that in which it had remained motionless for extended intervals prior to oviposition, this time for at least 30 minutes as if host guarding, but did not maintain that position.

The chewing behavior was commonly observed on paralyzed adult beetles for both *Prorops* spp., and in the vast majority of observed instances were not followed by oviposition. Many of these interactions seemed to be for the purpose of host feeding, but it was unclear if some also were for the purpose of oviposition but on a host that was eventually rejected. Chewing by both species was also observed to occur on immature stages that had previously been stung. Since no eggs or developing larvae were ever observed on an immature stage, chewing on pupae and larvae was presumably not for the purpose of oviposition, but instead for host feeding.

*Intraspecific interactions* were also observed. When encountering each other in open space, the wasps typically ignored each other. Females in the action of stinging or chewing were typically not interrupted by passing conspecifics, which might explore the beetle with their antennae. They were observed to be somewhat affected, though not to show any overt aggression, if both were exploring the same beetle adult or immature: if the wasps came in contact with each other, they would move slightly apart.

Defense against stinging by a Hypothenemus sp. (Fig. 13, Video 4: https://vimeo. com/688212175): An unidentified Hypothenemus sp. male, not H. eruditus but similar in size to H. eruditus females, was placed in the observation chamber along with H. eruditus beetles. In a behavior not observed in *H. eruditus* beetles under the same circumstances, when a *P. umiehu* adult female attempted to sting the *Hypothenemus* sp. adult dorsally between the pro- and mesothorax, the beetle clamped down at this junction on the apex of the wasp's abdomen as soon as it made contact. The wasp did not seem to become agitated, but when appearing to attempt to withdraw after 1.5 minutes, a time in the range of a normal stinging interval, seemed to struggle and was unable to extract its metasoma from the grasp of the beetle until it relaxed 3.5 minutes later. The beetle seemed to be unaffected by the stinging attempt and remained active through the next day. It was unclear if the beetle was not paralyzed because P. umiehu is not physiologically able to paralyze this species, or was a result of this behavior which resulted in an unsuccessful stinging attempt. This behavior was only observed once. The wasps for the most part showed little interest in this species when they were placed in the arena and focused their attention on H. eruditus. Aside from this observation, neither this Hypothenemus sp. nor H. eruditus were observed to present other active forms of defense, such as running away or biting, against the wasps.

**Patch use:** Almost all beetles entered into the observation chambers with *P. maya* or *P. umiehu* females were motionless within 12 hours (n = 3 for *P. maya*, n = 3 for *P. umiehu*), helping to confirm the observation in field collected wood that *P. maya*, and potentially *P. umiehu* as well, typically attacks more or less the whole



**Figure 13.** Defense by *Hypothenemus* sp. male against a stinging attempt by *P. umiehu*. The identity of the beetle is unknown, but is not *H. eruditus* **a** position immediately prior to contact of stinger. Note that the beetle is in a relaxed state, with the gap between the pro- and mesothorax slightly open **b** The beetle quickly clamps down after contact, trapping the apex of the metasoma of *P. umiehu*, and maintains that position for approximately 3.5 minutes, during which time the wasp was not visibly agitated but was unable to extricate itself. The beetle appeared to remain healthy and active in the subsequent hours, seemingly unaffected by the stinging attempt. These actions are also shown in Video 4: https://vimeo.com/688212175.

host patch at least in geometrically simple environments such as those with which they were presented. In one instance where the details were more precisely recorded, five *H. eruditus* and the one unidentified *Hypothenemus* sp. male which showed the defensive behavior were inserted into the observation chamber in naturally bored *H. eruditus* galleries in *D. regia* pods with two *P. umiehu* adult females. All five *H. eruditus* were stung and paralyzed within two hours.

## Interest in Hypothenemus hampei, the coffee berry borer?

Given that the congeneric *Prorops nasuta* is a parasitoid of the coffee berry borer *H. hampei*, and of the known species of *Prorops* it seems close at least morphologically to *P. maya* females, and *H. eruditus* and *H. hampei* are also congenerics, we investigated whether *P. maya* would take any interest in the coffee berry borer. To test this, wasps were released into the same apparatus described above that successfully resulted in stinging, chewing, host feeding, and parasitism of *H. eruditus*, with *H. eruditus* adults and immatures switched out with *H. hampei* adults and immatures (Video 5: https://vimeo. com/691136424). No interest was observed, and the wasps even seemed to show slight repulsion, upon encounter briefly antennating the beetles and then quickly moving on. No stinging, chewing, host feeding, or parasitism was observed. Given this lack of interest, no further tests were done.

# Discussion

*Prorops maya* and *P. umiehu* are ectoparasitoids of adult *H. eruditus* beetles living below the surface of wood. Both species enter tunnels bored by the scolytid in the plant material, and sting, paralyze, oviposit, and develop as an ectoparasitoid on the adults. *Prorops maya* and *P. umiehu* are, as far as we are aware, along with a *Plastanoxus* sp. found to parasitize *Euwallacea fornicatus* by Husein et al. (2023), the only bethylids known to parasitize the adult stage of their host, and the only known ectoparasitoids of the adult stage of a scolytid.

## Notes on the life history and morphology of P. maya and P. umiehu

The vast majority of parasitoids of Scolytinae whose biology are known reproduce only on immature host stages (Kenis et al. 2007). Intuitively, this makes sense because larvae and pupae are much less mobile and sclerotized than adults, and often found at the end of a one-way tunnel. So why might a parasitoid attack the adult stage? It may be advantageous as an escape from competition with other parasitoids or predators; it may be because adult scolytids might be present in gallery systems more consistently than immature stages if their reproduction occurs only intermittently; or because of accessibility to adults for a cryptoparasitoid given their location within galleries, at entrances or in larger diameter tunnels. Development as an endoparasitoid inside the sclerotized adult stage may also offer protection from predators or hyperparasitoids, though endoparasitic development often also comes at the expense of having to defend against the host's immune system (Godfray 1994). *Prorops maya* and *P. umiehu* develop as ectoparasitoids on *H. eruditus* adults, but seem to have evolved a way of still using their host to protect themselves, at least when developing in a tunnel system. In such environments, *P. maya* and *P. umiehu* were observed to pupate between the prothorax and posterior of the beetle, having forced the two halves of the beetle apart during its growth and subsequent construction of a pupation chamber. This may be an adaptation to use the sclerotized body of its host to protect itself as best as it can given the potential evolutionary constraint of being an ectoparasitoid characteristic of Bethylidae, and maintaining the advantage of reduced exposure to the host's immune system inherent in being an ectoparasitoid.

Because *P. maya* and *P. umiehu* were found parasitizing nonnative beetles in nonnative trees, the host beetles in a tribe with no native species, and *Prorops* is not otherwise known in Hawai'i, Hawai'i is not likely part of the native range of either species. It may also be unlikely the native host of these species is *H. eruditus*: their pattern of host use was not observed to be efficient and *H. eruditus* showed a lack of defensive behavior against attack, while potentially effective defensive behavior was shown in another *Hypothenemus* sp.

While *P. maya* seemed to parasitize or paralyze nearly every *H. eruditus* beetle in a gallery system in *T. orientalis* branches, most unconnected active beetle gallery systems in a contiguous piece of wood appeared untouched, containing healthy populations of beetles. Because the environment where we have observed this species is likely not its native environment, to which it is presumably best adapted, such sparse host use could potentially result from inefficient searching behavior due to lack of adaptation to the exact host or environmental cues present. Or, possibly, this sparse and spatially disparate use of galleries could result from adaptation to an environment where its natural enemies tend to search in a spatially contiguous manner, *e.g.* by walking along a branch. Observed sporadic gallery use could also be related to low population density of the parasitoids, and restricting oviposition to a single gallery system and incapacitating all other occupants could also be related to brood guarding, though such behavior was not convincingly observed for these species.

Finally, we make a note about morphology. *Prorops* is the only genus in Scleroderminae with a projection on its frons, a synapomorphy that can be used to identify the genus. This, in combination with the large mandibles, has previously been suggested to possibly function as a means of digging through hard substrate (Waichert and Azevedo 2012). Of the three species in *Prorops* for which the biology is known, *P. maya* and *P. umiehu* are parasitoids of the adult stage of beetles, and *P. nasuta* is a parasitoid of the larval and pupal stages. Thus it may be that parasitism of the adult stage is more representative of the genus as a whole than parasitism of immature stages. For many ectoparasitoids of larvae and pupae, which have a cuticle almost entirely soft and easy to penetrate by an emerging parasitoid larva, the exact location of placement of the egg on a paralyzed host does not matter greatly. The location of egg placement on the host may matter more for parasitoids of adult beetles, which are sclerotized and have a cuticle not as easily penetrated. All eggs observed in this study were placed in the same location on the beetle, on the membraneous region of articulation between the pro- and mesothorax on the ventral side of the beetle. In preparation for oviposition, and in host feeding, P. maya and P. umiehu were observed to widen the separation between the pro- and mesothorax of the beetle by grasping the host beetle's abdomen with its legs and pushing the pronotal sclerite forward with its head. This was accomplished by fitting the edge of the pronotal sclerite into the groove formed between the mandibles ventrally and the snout dorsally, using this structure as a locking mechanism to hold the sclerite and push it forward while maintaining use of the mandibles for chewing on the exposed and tensioned membrane. Among possible other functions, this chewing presumably cuts the stretched membrane and results in the space between the pro- and mesothorax remaining open upon cessation of pushing by the wasp. For oviposition, the female wasp subsequently inserts the apex of its metasoma into this widened gap and lays an egg into it. The cut membrane may presumably also provide an opening through which the emerging larva is able to feed, and allows the wasp to host feed on the beetle. Alternatively, the snout could have evolved for host feeding on adults even if parasitism occurred only on immature stages. Given its variety of forms within the genus and apical dorsad curvature in both species considered here, which would appear possibly as a prying or positioning mechanism, the snout structure in *Prorops* may have additional uses as well that were not observed during this study. But the conferred ability to hold the prothorax of an adult host beetle and push on it, for the purpose of host feeding and in preparation for oviposition, represents one function.

## Data availability

Additional video materials: Video 1: Searching, stinging, chewing, and host feeding behavior by *Prorops maya* on *Hypothenemus eruditus*: https://vimeo.com/688211081; Video 2: Searching, stinging, chewing, and host feeding behavior by *P. umiehu* on *H. eruditus*: https://vimeo.com/691136279; Video 3: Oviposition by *P. umiehu* on *H. eruditus*: https://vimeo.com/688588477; Video 4: Defense by *Hypothenemus* sp. male against a stinging attempt by *P. umiehu*: https://vimeo.com/688212175; Video 5: Response of *P. maya* to the coffee berry borer, *H. hampei*: https://vimeo.com/691136424.

## Acknowledgments

These studies were helped immensely by Maya Honsberger, who made this project very enjoyable and contributed observations, insights, and support. We thank our coworkers Abdulla Ali, Michelle Au, Conrad Gillett, Mitchell Logan, Ali Miarkiani, Robert Sakuda, Vanessa Goodman, and Laura Doucette for their support. We acknowledge that this research took place on the mokupuni (island) of Oʻahu in the ahupuaʻa (land division) of Waikīkī in the moku (district) of Kona, Kamananui in the moku of Waialua (now Wahiawā), Kahana in the moku of Koʻolauloa, and Waimānalo in the moku of Koʻolaupoko, the ancestral and traditional land of Native Hawaiian people. We are very grateful to USDA, HDoA and Hatch project HAW09041-H, administered by CTAHR, for their funding.

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RESEARCH ARTICLE



# Discovery of the subfamily Microleptinae (Hymenoptera, Ichneumonidae) from India and Thailand with the description of five new species

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Academic editor: Tamara Spasojevic | Received 11 July 2024 | Accepted 25 October 2024 | Published 26 November 2024

https://zoobank.org/60FBA642-B425-40B8-8718-614C4751CAF4

**Citation:** Ranjith AP, Humala AE, Priyadarsanan DR, Butcher BA (2024) Discovery of the subfamily Microleptinae (Hymenoptera, Ichneumonidae) from India and Thailand with the description of five new species. Journal of Hymenoptera Research 97: 1257–1284. https://doi.org/10.3897/jhr.97.131822

### Abstract

The ichneumonid subfamily Microleptinae is reported from India and Thailand for the first time. We describe four new species from India (*Microleptes chiani* Ranjith & Humala, **sp. nov.**, *M. gowrishankari* Ranjith & Humala, **sp. nov.**, *M. sandeshkaduri* Ranjith & Humala, **sp. nov.**, *M. tehriensis* Ranjith & Humala, **sp. nov.**) and one new species from Thailand (*M. depressus* Ranjith & Humala, **sp. nov.**), and for the first time, we report the Chinese species, *M. xinbinensis* Sheng & Sun, from India and describe the hitherto unknown female. An identification key to the extant species of *Microleptes* is provided.

### **Keywords**

India, key, Microleptes, New distribution, Oriental region, taxonomy, Thailand

# Introduction

Microleptinae is one of the smallest subfamilies of Ichneumonidae, having a single genus *Microleptes* Gravenhorst, 1829 with 14 known species (Yu et al. 2016). The subfamily is distributed in the Palaearctic, Nearctic and Oriental regions with

most species reported from the Palaearctic region (Yu et al. 2016). Only one species, Microleptes malaisei Kasparyan, 1998, is known from the Oriental region (Kasparyan 1998). Henry Townes-one of the leading ichneumonid systematists of 20<sup>th</sup> century, whose classification of ichneumonids was widely recognized-placed several genera with unclear systematic position in the subfamily Microleptinae and called it a "waste-basket" (Townes 1971). These primarily included the genera Microleptes, Hyperacmus Holmgren, 1858, Cylloceria Schiødte, 1838, Tatogaster Townes, 1971 and Oxytorus Förster, 1969, which were subsequently excluded therefrom. In a revision of the family-group names in Ichneumonidae by Fitton and Gauld (1976) the valid name Oxytorinae Thomson, 1883 with the type genus Oxytorus was adopted for Microleptinae sensu Townes according to the International Code of Zoological Nomenclature. Its classification has undergone major changes as a result of the study of head capsules in larvae of some representatives of the subfamily by D. Wahl. He excluded the genus Microleptes from subfamily Oxytorinae and placed it in a separate monotypic subfamily Microleptinae, though its position relative to the other ichneumonid subfamilies remained unclear for a long time (Wahl 1986, 1990; Wahl and Gauld 1998). He also proposed to separate two more genera Cylloceria and Allomacrus Förster, 1969 from this group into independent subfamily Cylloceriinae and Tatogaster into Tatogasterinae; while the other genera, except for Oxytorus, assigned to a separate subfamily, should be merged with orthocentrines in an expanded Orthocentrinae (Wahl 1990), where they are currently considered (Yu et al. 2016).

Quicke et al. (2009) commented on the contradicting phylogenetic position of the subfamily Microleptinae within Darwin wasps based on 28S rRNA (within or related to Ichneumoniformes), morphological (within Ophioniformes) and combined analysis (within Ophioniformes). Based on some superficial similarities in appearance, the genus *Hyperacmus* Holmgren, 1858 was included in the subfamily Microleptinae (Dasch 1992; Humala 2003), but later *Hyperacmus* was excluded from Microleptinae and transferred to the Cylloceriinae (Broad 2004; Humala 2007; Quicke et al. 2009).

Even though some species of *Microleptes* have been reared from stratiomyids (Wahl 1986; Schwarz 1991) the genus does not share any larval synapomorphies with the groups having a similar biology (parasitoids of Diptera) (Wahl 1986). Broad et al. (2018) assigned Microleptinae to unplaced subfamilies, although it was suggested that this group possibly related to the Ichneumoniformes. Santos (2017) included Microleptinae among ichneumoniformes groups of subfamilies and Bennett et al. (2019) supported this view and placed Microleptinae at the base of Ichneumoniformes s.l.

Species of *Microleptes* can be recognized by a combination of characters: antennal sockets protruding anteriorly, head ventrally with angular corners, mandible with blunt teeth, often fused, inner side of hind tibia with a fringe of dense long setae apically, first metasomal tergite with spiracle at or just in front of midpoint and first metasomal sternite extending beyond the spiracle (Broad et al. 2018). Sexual dimorphism is evident within *Microleptes* though only few species are known from both sexes.

The aim of this work is to study material of *Microleptes* from India and Thailand, describe new species, and provide new faunistic records and a key to the world species.

## Materials and methods

Specimens were collected by Malaise traps and sweep nets in different parts of India (south and north-east of the country) and Thailand. The holotypes of the Indian species are deposited in the National Zoological Collections of the Zoological Survey of India, Western Ghat Regional Centre, Kozhikode (**ZSIK**) whereas the type specimen of the Thai species is deposited at the Queen Sirikit Botanic Garden, Chiang Mai, Thailand (**QSBG**). Paratype specimens of Indian species are deposited at the ATREE Insect Museum, Bangalore (**AIMB**). Images of Indian species and *M. xinbinensis* were taken with a Keyence VHX-6000 digital microscope and images of *M. depressus* sp. nov. were taken with a Leica M205 C stereomicroscope with a DMC5400 Camera, stacked in LASX (ver. 3.7.4.23463). Morphological terminology follows Broad et al. (2018). For cuticular sculpture we follow Harris (1979). The measurements of morphological structures were taken at longest and broadest points in appropriate view. Abbreviations used in the text: **OOL** – ocular-ocellar line, **POL** – postocellar line.

### Results

### Taxonomy

Order Hymenoptera Linnaeus, 1758 Superfamily Ichneumonoidea Latreille, 1802 Family Ichneumonidae Latreille, 1802 Subfamily Microleptinae Townes, 1958

### Microleptes Gravenhorst, 1829

- *Microleptes* Gravenhorst, 1829. Type species: *Microleptes splendidulus* Gravenhorst. Monobasic.
- *Miomeris* Förster, 1868. Type species: *Miomeris aquisgranensis* Förster. Designated by Förster (1871).
- *Gnathoniella* Schmiedeknecht, 1924. Type species: *Gnathoniella egregia* Schmiedeknecht (= *Miomeris rectangulus* Thomson). Monobasic.

**Diagnosis.** Body robust, in many species somewhat dorsoventrally depressed (Figs 1A, 3A, 5A, 7A, 9A, 11A). Head mostly wider than long (Figs 1B, 3B, 5B, 7B, 9B) rarely as long as wide (Fig. 11B). Face anteriorly usually protruding below antennal sockets (Figs 1D, 3A, E, 7A). Clypeus transverse, weakly separated from face (Figs 1B, 3B, 5B, 7B, 9B). Subocular sulcus present (Figs 1B, 3B, 5B, 7B, 9B). Mandible mostly with undivided single broad tooth, if divided lower tooth smaller than upper tooth (Figs 1B, 3B, C, 5B, 7B, 9B). Temple long (Figs 1C, D, 3A, D, E, 5C, 7C, 9C, D, 11C, D). Occipital carina complete (Figs 1C, 3D, 9C, 11C). Scape subcylindrical (Figs 1D, 3A, E). Antennae with 14–18 flagellomeres. Flagellomeres from longer than wide (Figs 9A,

11A) to distinctly transverse (Figs 1A, 3A, E, 7A, C). Male flagellum with tyloids present on flagellomeres 1-2, 1-3 or 5-9 in the form of longitudinal ridges. Epomia absent (Figs 1F, 4A, 5F, 7E, 9F, 11D). Mesoscutum with lateral longitudinal groove (Figs 1E, 4B, 5D, 7D, 9E, 11E). Notauli only impressed anteriorly (Figs 1E, 4B, 5D, 7D, 9E, 11E). Scuto-scutellar groove smooth, undivided, lateral carina of the mesoscutum not crossing scuto-scutellar groove (Figs 1E, 4B, 5D, 7D, 9E, 11E). Epicnemial carina present, extending to subtegular ridge, mostly with a deep groove (Figs 1F, 4A, 5E, 7E, 9F, 11D). Propodeum smooth or sculptured with distinct carination associated with wrinkles or rugosity (Figs 4C, 5F, 6A, 7F, 10A, 11F). Anterior transverse carina (costula) present or absent (Figs 4C, 5F, 6A, 7F, 10A, 11F). Area basalis and area superomedia confluent (Figs 4C, 5F, 6A, 7F, 10A, 11F). Posterior transverse carina usually complete (Figs 4C, 5F, 6A, 7F, 10A, 11F). Hind femur mostly robust (Figs 1A, 2C, 3A, 5A, 6A). Hind tibia with apical fringe of dense long setae on inner side. Claw simple, without basal lobe. Fore wing without areolet (vein 3rs-m absent) (Figs 2B, 4F, 6D, 8D, 10F, 12D); vein 2m-cu with one bulla (Figs 2B, 4F, 6D, 8D, 10F, 12D); vein M&RS strongly curved (Figs 2B, 4F, 6D, 8D, 10F, 12D); vein 1cu-a interstitial to postfurcal (Figs 2B, 4F, 6D, 8D, 10F, 12D). First metasomal tergite without glymma, spiracle situated near mid-length of tergite (Figs 2C, 4D, 6A, 8A, 10C). First metasomal sternite extending to mid-length of segment, fused with tergite (Figs 2C, 4D, 6A, 8A, 10C). Second metasomal tergite with thyridium (Figs 2D, 4E, 6B, 8B, 10D, 12B). Ovipositor shorter than apical height of metasoma, ovipositor sheath setose (Figs 2C, 4D, 6A, 8A, 12A).

**Distribution.** Holarctic and Oriental regions.

**Biology.** Two species have been reared from Stratiomyidae (Diptera) (Wahl 1986; Schwarz 1991).

# Key to Microleptes species

1	All flagellomeres elongate in both sexes; first flagellomere $3.6-4.8 \times as$ long as
	apical width (Fig. 11A); apical edge of clypeus clearly protruding, forming small
	tooth or tubercle in the middle (Fig. 11B); male antenna with tyloids on flagel-
	lomeres 5–7
_	Female flagellomeres, except for a few basal ones, usually transverse or subquad-
	rate; first flagellomere less than 3.0 × as long as apical width (Figs 1A, 3A, E, 5A,
	7A); apical edge of clypeus straight or slightly convex, without median tooth or
	tubercle (Figs 1B, 3B, C, 5B, 7B, 9B); male antenna with tyloids on flagellom-
	eres 1–2
2	Head in front view clearly tapered downwards, genae converging; mouth notch
	narrower than face width; head in dorsal view $0.7 \times$ as long as wide; flagellomere
	5 about $3.0 \times$ as along as wide; male antenna with tyloids on flagellomeres 5–8
	[Palaearctic]
_	Head in front view nearly rectangular, genae subparallel; mouth notch wid-
	er than face width (Fig. 11B); head in dorsal view 0.8-0.9 × as long as wide
	(Fig. 11C); flagellomere 5 shorter, 1.8-2.1 × as along as wide; male antenna
	with tyloids on flagellomeres 5–7

3	Fore wing vein 1cu-a strongly postfurcal; hind coxa nearly smooth, yellow, slightly infuscate anteriorly [Oriental (Myanmar)]
_	Fore wing vein 1cu-a nearly interstitial; hind coxa coriaceous with punctures, yellowish brown, strongly infuscate in anterior half [East Palaearctic (China) and Oriental regions (India)]
4	Males (unknown for <i>M. chiani</i> sp. nov., <i>M. depressus</i> sp. nov., <i>M. gowrishankari</i> sp. nov., <i>M. minor</i> , <i>M. sandeshkaduri</i> sp. nov., <i>M. spasskii</i> , <i>M. tibialis</i> )
5	Females (unknown for <i>M. belokobylskii</i> , <i>M. grandis</i> , <i>M. tehriensis</i> sp. nov.)
_	Propodeum, metasomal tergites and hind coxa matt, if weakly polished, then propodeal carination sometimes reduced and costula absent
6	Iemples slightly narrowed posteriorly in dorsal view [West Palaearctic]
_	Temples subparallel in dorsal view
7	Mesoscutum sparsely setose; fore wing with marginal cell longer than deep; flagel- lomeres 1 and 2 laterally concave; tyloids on flagellomeres 1–2; hind femur more robust, $3.7-4.3 \times as$ long as wide; OOL $1.5-1.6 \times diameter$ of lateral ocellus [Hol- arctic]
	<i>M. splendidulus</i> Gravenhorst. 1829 (= <i>Miomeris glabriventris</i> Thomson, 1888)
_	Mesoscutum densely setose; fore wing with marginal cell short, deeper than long; flagellomeres 1 and 2 slender and parallel-sided; tyloids on flagellomeres 1–3; hind femur slenderer, $4.8-5.1 \times as$ long as wide; OOL 1.0 × diameter of lateral ocellus [Nearctic]
8	First flagellomere as long as second flagellomere; propodeum without costula; posterior margin of apical sternite with a median process [Palaearctic]
_	First flagellomere shorter than the second; propodeum with distinct costula; posterior margin of apical sternite not protruding (except <i>M. aquisgranen-</i>
9	Antenna with 18 flagellomeres; comparatively large species, with body length about 7.5 mm and fore wing length 5.3 mm [first flagellomere $1.6 \times as$ long as wide posteriorly, second flagellomere $1.5 \times as$ long as first flagellomere; tyloids on flagellomeres 1–2; first tergite coriaceous, with longitudinal striation; first sternite reaches 0.4, spiracles 0.4 of segment length; hind coxa yellow] [East Palaearctic]
_	Antenna with 16–17 flagellomeres; smaller species, with body length less than
	5.0 mm and fore wing length not exceeding 4.0 mm 10
10	Flagellomeres 1–2 with tyloids
_ 11	Antenna as long as hind wing, with 16 flagellomeres; flagellomere 2 with tyloid in basal $0.5-0.6$ ; malar space short, less than half as long as basal width of man- dible; hind femur $4.7 \times$ as long as wide, dorsal surface slightly convex; posterior

margin of apical sternite with a median process [East Palaearctic]..... Antenna as long as fore wing, with 17 flagellomeres (Fig. 9A); flagellomere 2 with tyloid in basal 0.7; malar space as long as basal width of mandible (Fig. 9B, D); hind femur  $5.6 \times as$  long as wide, dorsal surface somewhat concave (Fig. 10C); posterior margin of apical sternite without process [Oriental] ..... Malar space half as long as basal width of mandible; hind leg stouter, hind femur 12  $4.0 \times$  as long as wide; propodeum with distinct lateral portions of anterior transverse carina; posterior margin of apical sternite angularly protruding medially Malar space as long as basal width of mandible; hind leg slenderer; propodeum roughly sculptured, only posterior transverse carina present; posterior margin of api-Hind femur stout,  $2.7-3.7 \times$  as long as wide; median flagellomeres quadrate 13 or transverse; second and following metasomal tergites and hind coxa mostly Hind femur slender,  $4.1-5.1 \times as$  long as wide; median flagellomeres distinctly elongate; second and following metasomal tergites and hind coxa mostly matt, Antenna nearly as long as mesosoma. First flagellomere as long as second flagel-14 lomere, twice as long as wide; hind tibia strongly swollen, 1.1 × as wide as hind Antenna much longer than mesosoma. First flagellomere distinctly longer than second flagellomere, hind tibia not swollen, narrower than hind femur; thy-Head  $1.1 \times as$  wide as long dorsally (Fig. 3D); temple long,  $1.1 \times as$  long as eye 15 in dorsal view (Fig. 3D) [Oriental]......*M. depressus* sp. nov. Head  $1.3-1.4 \times$  as wide as long dorsally; temple  $0.6-0.7 \times$  as long as eye in Fore wing vein 2rs-m 0.6-0.9 × as long as 2m-cu (Figs 2B, 6D); first flagel-16 lomere  $1.3 \times as$  long as wide (Figs 1D, 5B); hind femur  $2.5-2.8 \times as$  long as wide (Figs 2C, 6B) ..... 17 Fore wing vein 2rs-m half as long as 2m-cu; first flagellomere more than 1.5 × Face with trapezoidal protrusion and without longitudinal depression (Fig. 5B); 17 pronotum transversely striate medio-anteriorly (Fig. 5D); mesopleuron without sternaulus; costula absent (Fig. 5F); vein 2rs-m 0.6 × as long as 2m-cu; third tergite Face without such protrusion and with longitudinal median depression (Fig. 1B); pronotum punctate medio-anteriorly (Fig. 1E); mesopleuron with distinct sternaulus; costula present (Fig. 2A); vein 2rs-m 0.9 × as long as 2m-cu (Fig. 2B); 

18	Median flagellomeres quadrate or slightly transverse; first flagellomere slightly and evenly widened apically; temples widened posteriorly in dorsal view [West
	Palaearctic] M. obenbergeri Gregor, 1938
_	Median flagellomeres distinctly transverse; first flagellomere sharply widened apically; temples shorter, subparallel in dorsal view
19	Hind femur more robust, $3.0-3.3 \times as$ long as wide; POL longer than OOL; OOL
	1./5–2.0 × diameter of lateral ocellus; marginal cell elongate [Palaearctic]
	M. splendidulus Gravenhorst, 1829 (= Miomeris glabriventris Thomson, 1888)
_	Hind femur 3.8 × as long as wide (Fig. 8A); POL shorter than OOL; OOL 1.6 × diameter of lateral ocellus (Fig. 7C); marginal cell short (Fig. 8D) [Orien-
	tal]
20	First flagellomere longer than second flagellomere 21
20	First flagellomere distinctly shorter than second flagellomere 22
21	First flagellomere 2.2–2.4 x as long as wide posteriorly: malar space shorter.
- 1	0.5-0.6 x as long as basal width of mandible: face at level of antennal sockets
	with a strong rectangular protrusion, hordered below by a carina down-curved
	laterally: propodeum wrinkled, weakly shining, costula lacking [Palaearctic]
	<i>M</i> salishumansis Schwarz 1991
_	First flagellomere 1.9 x as long as wide posteriorly: malar space as long as basal
	width of mandible: face at level of antennal sockets with V-shaped protrusion
	not hordered by carina: propodeum coriaceous all carinae developed excluding
	anterior transverse carina [Fast Palaearctic] <i>M stassbii</i> Humala 2003
22	Face with V-shaped protrusion below antennal sockets not bordered below by ca-
	rina: propodeum roughly sculptured all carinae reduced excluding posterior trans-
	verse carina: hind cova brown [Palaearctic] <i>M aquisgrammis</i> (Förster 1871)
_	Face with V-shaped protrucion below antennal sockets with irregular sculpture
	bordered below by carina: propodeum coriaceous all carinae well developed
	evoluting anterior transverse carina: hind cova mostly vellow 23
23	Antenna slender first flagellomere 4.0 x as long as wide: second flagellomere 4.7 x
25	as long as wide: propodeum polished [Nearctic] <i>M rallus</i> Dasch 1992
	Antenna stouter, first flagellomere 2.1. 2.2 × as long as wide posteriorly: second
_	fagellomere 3.0. $3/4 \times as \log as wide posteriorly 1.3, 1.5 \times as \log as first flag.$
	ellomere: propodeum coriaceous
2/1	Malar space $0.7 \times as long as basal width of mandible: first flagellomere evenly$
24	widened 2.2 x as long as wide: second flagellomere 1.5 x as long as first flag.
	ellomere: first sternite reaching $0.5 \times$ tergite length; hind tibia with subbasal
	inflation evenly widened to apey Larger species fore wing 3.8 mm [Fast Palae.
	arctic] <i>M orientalio</i> Humala 2003
	Malar space 1.2 x as long as basal width of mandible: first flagellomera 2.1 x as
-	long as wide: second flagellomere 1.3 x as long as first flagellomere: first stormite
	reaching $0.6 \times$ terraite length; hind tibia comewhat constricted between subhasal
	inflation and apex. Smaller species fore wing 2.9 mm [Fast Palaearctic]
	M minar Humala 2002

### Microleptes chiani Ranjith & Humala, sp. nov.

https://zoobank.org/C9D273CA-6CF5-45BF-8E86-3EB1634BF6DB Figs 1, 2

**Material examined.** *Holotype* • female, INDIA: Tamil Nadu, Kalakad Mundanthurai Tiger Reserve (KMTR), tropical wet evergreen forest, understorey, Malaise trap, 5.x.2008, coll. Priyadarsanan, D.R. (ZSIK) Regd. No. ZSI/WGRC/IR/INV.27406.

**Description. Holotype, female.** Body length 6.2 mm, fore wing length 3.7 mm. *Head.* Head 1.6 × as wide as long in anterior view (Fig. 1B) and 1.4 × as wide as long in dorsal view (Fig. 1C); face flat, punctate, elevated anteriorly below antennal sockets, setose,  $1.7 \times as$  wide as long (Fig. 1A, B, D); clypeus strongly transverse, smooth, with lower margin slightly convex (Fig. 1B); tentorial pits transverse (Fig. 1B); malar space strongly reduced,  $0.3 \times basal$  width of mandible (Fig. 1B, C); mandible broad with single broad tooth (Fig. 1B); temple smooth, setose (Fig. 1D); frons and vertex smooth and sparsely setose (Fig. 1C); eye glabrous,  $1.5 \times as$  long as temple in dorsal view (Fig. 1B–D); OOL : diameter of lateral ocellus : POL = 1.4 : 1.0 : 1.2; antenna with 14 flagellomeres; scape subcylindrical, pedicel bulb-shaped (Fig. 1B, D); medial flagellomeres strongly transverse (Fig. 1A); first flagellomere  $2.0 \times as$  long as second flagellomere,  $1.3 \times as$  long as wide; second flagellomere  $0.6 \times as$  long as wide.

*Mesosoma*. Mesosoma 1.8 × as long as high (Fig. 1F); dorsal part of pronotum rugose-punctate medially, transversely wrinkled posteriorly (Fig. 1E), pronotum laterally smooth and polished (Fig. 1F); mesoscutum flat in lateral view, punctate, setose with a pair of elongate pits postero-laterally (Fig. 1F); notaulus present anteriorly (Fig. 1E); scuto-scutellar groove smooth without wrinkles (Fig. 1E); scutellum smooth, setose (Fig. 1E); mesopleural furrow widely crenulated (Fig. 1F); epicnemial carina present, joining with subtegular ridge and forming a smooth continuous groove anteriorly (Fig. 1F); metapleuron entirely rugulose, sparsely setose, sternaulus absent (Fig. 1F); propodeum rugulose, area superomedia smooth medially, faintly crenulated postero-laterally, slightly narrowing anteriorly, parallel-sided posteriorly; costula present (Fig. 2A); posterior transverse carina present, area dentipara slightly longer than wide, smooth medially; rest rugulose; pleural carina complete (Fig. 2A).

*Legs.* Femora slender (Fig. 1A); hind coxa smooth (Figs 1A, 2C); hind femur 2.5 × as long as wide; hind tibia 3.3 × as long as wide; hind basitarsus 3.8 × as long as wide.

*Wings.* Wings hyaline (Fig. 2B); pterostigma 2.8 × as long as wide; fore wing vein 2r&RS joining to pterostigma before its middle, 1.1 × as long as 2rs-m; vein 2rs-m 2.5 × as long as M between 2rs-m and 2m-cu; and 0.9 × as long as 2mc-u; vein 1cu-a slightly postfurcal (Fig. 2B); hind wing with nervellus (vein CU) intercepted in middle.

**Metasoma.** First tergite faintly sculptured medially, setose with indistinct dorsal carina,  $2.3 \times as$  long as its maximum width, spiracle situated at middle of tergite (Fig. 2C, D); second tergite with distinct thyridium, smooth, setose,  $1.1 \times as$  long as wide posteriorly (Fig. 2D); third tergite smooth, setose, as long as wide posteriorly (Fig. 2D); tergites 4–7 smooth, setose (Fig. 2D); hypopygium straight posteriorly; ovipositor hardly exposed, sheath apically setose,  $0.1 \times as$  long as hind tibia (Fig. 2C).



**Figure I.** *Microleptes chiani* Ranjith & Humala, sp. nov., holotype, female **A** habitus, lateral view **B** head, anterior view **C** head, dorsal view **D** head, lateral view **E** mesosoma, dorsal view **F** mesosoma, lateral view.

**Colour.** Body predominantly black; antenna, mandible, tegula; pterostigma, wing veins, coxae and metasoma dark brown; maxillary and labial palps, legs (except coxae) yellow.

Male. Unknown.

Distribution. India.

**Etymology.** The new species is named after our field assistant Mr. Thamilselvan, whom we fondly call 'Chian', who contributed much in establishing insect collection from the difficult terrain of KMTR.



**Figure 2.** *Microleptes chiani* Ranjith & Humala, sp. nov., holotype, female **A** propodeum, dorsal view **B** fore wing **C** metasoma, lateral view **D** metasoma, dorsal view.

**Comparative diagnosis.** Apart from the differences given in the key, the new species differs from *M. gowrishankari* sp. nov. by the following characters: head  $1.6 \times as$  wide as long in anterior view ( $1.3 \times in M.$  gowrishankari sp. nov.), face  $1.7 \times as$  wide as long ( $2.4 \times in M.$  gowrishankari sp. nov.), epicnemial area with complete groove behind epicnemial carina (incomplete in *M. gowrishankari* sp. nov.) and area dentipara of propodeum longer than wide (wider than long in *M. gowrishankari* sp. nov.).

### *Microleptes depressus* Ranjith & Humala, sp. nov. https://zoobank.org/F50738F1-7A48-4DC1-8BAB-4228128DA703 Figs 3, 4

**Material examined.** *Holotype* • female, THAILAND: Kamphaeng Phet, Malaise trap, 3–10.ix.2007, coll. Chumpol Piluk & Aram Inpuang (QSBG).

Description. Holotype, female. Body length 6.5 mm, fore wing length 4.0 mm.

*Head.* Head 1.5 × as wide as long in anterior view (Fig. 3B) and 1.1 × as wide as long in dorsal view (Fig. 3D); face flat, sparsely punctate, elevated anteriorly below antennal sockets, setose, 2.7 × as wide as long (Fig. 3A, B, C, E); clypeus strongly transverse, smooth, lower margin weakly convex (Fig. 3B, C); tentorial pits rounded (Fig. 3B); malar space short, 0.5 × basal width of mandible; mandible broad with two teeth, upper tooth longer and wider than lower tooth (Fig. 3B, C); vertex and temple strongly enlarged, temple 1.1 × as long as eye in dorsal view, sparsely punctate laterally, with sparse setae (Fig. 3D, E); frons and vertex polished, sparsely punctate and setose (Fig. 3D); eye glabrous (Fig. 3); OOL : diameter of lateral ocellus : POL = 1.8 : 1.0 : 1.1; antenna with 14 flagellomeres; scape subcylindrical, pedicel bulb-shaped (Fig. 3A, E); medial flagellomere and 1.3 × as long as wide; second flagellomere 0.9 × as long as wide.

*Mesosoma*. Mesosoma elongate, 2.8 × as long as high (Figs 3A, 4A); dorsal part of pronotum crenulated medially (Fig. 4B), pronotum laterally smooth and polished, crenulated medially (Fig. 4A); mesoscutum flat in lateral view (Fig. 4A), smooth, setose only medially (Fig. 4B); notaulus present anteriorly (Fig. 4B); scuto-scutellar groove smooth without wrinkles (Fig. 4B); scutellum smooth, setose laterally and posteriorly (Fig. 4B); mesopleuron coriaceous, setose (Fig. 4A); mesopleural furrow indistinct (Fig. 4A); epicnemial carina present, joining with subtegular ridge (Fig. 4A); metapleuron rugose with transverse wrinkles medially, sparsely setose (Fig. 4A); propodeum punctate in anterior half, transversely striate-rugose in posterior half, combined area basalis+superomedia narrowed in anterior 0.3, with irregular transverse wrinkles, costula absent, posterior transverse carina present; pleural carina complete (Fig. 4C).

*Legs.* Femora robust (Fig. 1A); hind coxa smooth (Fig. 4D); hind femur 2.9  $\times$  as long as wide (Fig. 4A, D); hind tibia 3.3  $\times$  as long as wide; hind basitarsus 4.7  $\times$  as long as wide (Fig. 4D).

*Wings.* Wings hyaline (Fig. 4F); pterostigma 3.2 × as long as wide; fore wing vein 2r&RS joining to pterostigma before its middle, 2.3 × as long as 2rs-m (Fig. 4F); vein 2rs-m 1.7 × as long as M between 2rs-m and 2m-cu; vein 1cu-a distinctly postfurcal (Fig. 4F); hind wing vein with nervellus (CU) intercepted in middle.

*Metasoma*. First metasomal tergite strongly convex in lateral view (Fig. 4D), sparsely punctate, setose with pair of weak dorsal carinae, twice as long as its maximum width; spiracle situated at middle of tergite (Fig. 4D–F); second tergite polished with distinct thyridium, sparsely punctate, setose,  $1.1 \times$  as long as wide (Fig. 4E, F); third tergite polished, as long as wide (Fig. 4E, F); tergites 4–7 polished, scarcely setose





**Figure 3.** *Microleptes depressus* Ranjith & Humala, sp. nov., holotype, female **A** habitus, lateral view **B** head, anterior view **C** head, antero-ventral view **D** head, dorsal view **E** antenna and head, lateral view.

laterally; hypopygium straight posteriorly; ovipositor hardly exposed; sheath setose,  $0.2 \times as$  long as hind tibia (Fig. 4D, E).

**Colour.** Body predominantly black; antenna, mandible, tegula, fore leg (excluding tibia and tarsus), hind leg (except tarsus) and tergites 3–7 reddish brown; flagellomeres 1–4, fore tibia and tarsus, mid leg, hind tarsus, posterior margin of hypopygium and ovipositor sheath yellow.

Male. Unknown.


Figure 4. *Microleptes depressus* Ranjith & Humala, sp. nov., holotype, female A mesosoma, lateral view B mesosoma, dorsal view C propodeum, dorsal view D metasoma, lateral view E metasoma, dorsal view F fore wing.

**Distribution.** Thailand.

Etymology. The new species is named after the distinctly depressed body.

**Comparative diagnosis.** The new species is similar to *M. tibialis*, but differs from this species by antenna as long as mesosoma length  $(1.4 \times \text{as long as mesosoma in } M. tibialis)$ , first flagellomere longer than second flagellomere (as long as second flagellomere in *M. tibialis*), temple  $1.1 \times \text{as long as eye in dorsal view, hind tibia not swollen, not wider than hind femur (hind tibia strongly swollen, <math>1.1 \times \text{as wide as hind femur in } M. tibialis$ ), distinct thyridium (lacking in *M. tibialis*).

#### Microleptes gowrishankari Ranjith & Humala, sp. nov.

https://zoobank.org/B9A56B80-AF79-4B68-A10A-E2FC1558BE4C Figs 5, 6

**Material examined.** *Holotype* • female, INDIA: Karnataka, Chamarajanagar, Biligiri Ranganathaswamy Temple Tiger Reserve, Gombekallu, 11°54.363'N, 77°11.235'E, evergreen forest, Malaise trap, 3.iv–16.v.2006, coll. Priyadarsanan, D.R. (ZSIK) Regd. No. ZSI/WGRC/IR/INV.27407. Paratype, 1 female with same data as holotype (AIMB).

Description. Holotype, female. Body length 5.6 mm, fore wing length 3.6 mm.

*Head.* Head  $1.3 \times as$  wide as long in frontal and dorsal views (Fig. 5B, C); face flat, punctate, elevated anteriorly below antennal sockets, setose,  $2.4 \times as$  wide as long,  $0.6 \times as$  wide as head (Fig. 5B); clypeus strongly transverse, smooth with lower margin convex (Fig. 5B); tentorial pits transverse (Fig. 5B); malar space strongly reduced,  $0.3 \times as$  basal width of mandible (Fig. 5B); mandible broad with single broad tooth (Fig. 5B); temple smooth, sparsely setose (Fig. 5A); frons and vertex smooth and sparsely setose (Fig. 5C); eye glabrous,  $1.2 \times as$  long as temple in dorsal view (Fig. 5A–C); OOL : diameter of lateral ocellus : POL = 2.0 : 1.0 : 1.4; antenna with 14 flagellomeres, scape subcylindrical, pedicel bulb-shaped (Fig. 5A, B); medial flagellomeres strongly transverse; first flagellomere  $1.8 \times as$  long as second flagellomere,  $1.3 \times as$  long as wide apically; second flagellomere  $0.6 \times as$  long as wide.

*Mesosoma*. Mesosoma 2.1 × as long as high (Fig. 5E); dorsal part of pronotum transversely striate medially (Fig. 5D), pronotum laterally smooth and polished (Fig. 5E); mesoscutum flat in lateral view (Fig. 5E), smooth with setiferous punctures, and a pair of elongate pits postero-laterally (Fig. 5D); notaulus present anteriorly (Fig. 5D); scuto-scutellar groove smooth without wrinkles (Fig. 5D); scutellum smooth, setose (Fig. 5D); mesopleuron smooth, setose (Fig. 5E); mesopleural furrow narrowly crenulated (Fig. 5E); epicnemial carina present, joining with subtegular ridge and forming an interrupted, faintly crenulated groove anteriorly (Fig. 5E); metapleuron smooth with transverse wrinkles medially, sparsely setose (Fig. 5E); propodeum smooth basally, irregularly punctate laterally, rugose in posterior half; area superomedia parallel-sided, smooth in anterior half, irregularly transversely striate posteriorly; costula lacking; posterior transverse carina present, pleural carina complete (Fig. 5F).

*Legs.* Femora robust (Fig. 5A); hind coxa smooth; hind femur  $2.8 \times as$  long as wide; hind tibia  $3.4 \times as$  long as wide; hind basitarsus  $3.8 \times as$  long as wide.

*Wings.* Wings hyaline (Fig. 6D); pterostigma  $2.6 \times$  as long as wide; fore wing vein 2r&RS joining to middle of pterostigma,  $1.6 \times$  as long as 2rs-m; vein 2rs-m  $2.0 \times$  as long as portion of M between 2rs-m and 2m-cu, and  $0.6 \times$  as long as 2mc-u; vein 1cu-a distinctly postfurcal (Fig. 6D); hind wing with nervellus (vein CU) intercepted in middle.

**Metasoma.** First tergite faintly sculptured medially, setose, with indistinct dorsal carina,  $1.7 \times as$  long as its maximum width; spiracle situated at middle of tergite (Fig. 6A, B); second tergite with distinct thyridium, smooth, setose,  $0.9 \times as$  long as wide posteriorly (Fig. 6B); third tergite smooth, setose,  $0.75 \times as$  long as wide



**Figure 5.** *Microleptes gowrishankari* Ranjith & Humala, sp. nov., holotype, female **A** habitus, lateral view **B** head, anterior view **C** head, dorsal view **D** mesosoma, dorsal view **E** mesosoma, lateral view **F** propodeum, dorsal view.

posteriorly (Fig. 6B); tergites 4–7 smooth, setose (Fig. 6B); hypopygium straight posteriorly, with long setae (Fig. 6C); ovipositor hardly exposed, its sheath setose,  $0.2 \times as$  long as hind tibia (Fig. 6A–C).

**Colour.** Body predominantly black; antenna, mandible, tegula; pterostigma, wing veins, coxae, metasoma dark brown; maxillary and labial palps and legs (except coxae) yellow.



**Figure 6.** *Microleptes gowrishankari* Ranjith & Humala, sp. nov., holotype, female **A** metasoma, lateral view **B** metasoma, dorsal view **C** apex of metasoma, ventral view **D** fore wing.

Male. Unknown. Distribution. India.

**Etymology.** The new species is named after Dr. P. Gowri Shankar, founder director of Kalinga Foundation, Karnataka, India for his exceptional and unparalleled works, contributions to the study of the King Cobra over the past two decades, his contributions towards to the advancement of herpetology and his unwavering support to APR during Siang Expedition 2022.

**Comparative diagnosis.** Apart from the differences given in the key, the new species can be distinguished from *M. chiani* sp. nov. by the following characters: head  $1.3 \times as$  wide as long in anterior view ( $1.6 \times in M. chiani sp. nov.$ ), face  $2.4 \times as$  wide as long ( $1.7 \times in M. chiani sp. nov.$ ), epicnemial area with incomplete groove behind epicnemial carina (with complete groove in *M. chiani* sp. nov.) and area dentipara of propodeum wider than long (longer than wide in *M. chiani* sp. nov.).

#### Microleptes sandeshkaduri Ranjith & Humala, sp. nov.

https://zoobank.org/AF1C5F1F-F0AE-45D3-9BE2-84581D070A35 Figs 7, 8

**Material examined.** *Holotype* • female INDIA: Arunachal Pradesh, Kuming River side, 25°98'78"N, 94°98'04"E, 777 m.a.s.l., sweep net, 20.x.2022, coll. A.P. Ranjith (ZSIK) Regd. No. ZSI/WGRC/IR/INV.27408.

**Description. Holotype, female.** Body length 3.8 mm, fore wing length 2.9 mm. *Head.* Head 1.3 × as wide as long in anterior view (Fig. 7B) and 1.2 × as wide as long in dorsal view (Fig. 7C); face flat, smooth, elevated anteriorly below antennal sockets and forming acute protrusion, sparsely setose, 2.2 × as wide as long (Fig. 7A, B); clypeus about 2.5 × as wide as long anteriorly, smooth, with lower margin convex (Fig. 7B); tentorial pits round (Fig. 7B); malar space 1.4 × basal width of mandible, with subocular sulcus; mandible broad with single broad tooth (Fig. 7B); temple smooth, setose (Fig. 7A); frons sparsely punctate; vertex smooth and sparsely setose (Fig. 7C); eye glabrous, 1.1 × as long as temple in dorsal view (Fig. 7B, C); OOL : diameter of lateral ocellus : POL = 1.5 : 1.0 : 1.0; antenna with 14 flagellomeres; scape subcylindrical, medial flagellomeres as long as wide (Fig. 7A–C); first flagellomere 0.9 × as long as second flagellomere, 1.6 × as long as wide; second flagellomere 1.5 × as long as wide.

**Mesosoma.** Mesosoma 2.0 × as long as high (Fig. 7E); dorsal part of pronotum crenulated medially, with transverse wrinkles anteriorly (Fig. 7D); pronotum laterally crenulated in middle (Fig. 7E); mesoscutum flat in lateral view, smooth, sparsely setose, with a pair of elongate pits postero-laterally (Fig. 7D, E); notaulus shallow, only impressed anteriorly (Fig. 7D); scuto-scutellar groove wide, smooth, without crenulations (Fig. 7D); scutellum smooth, setose, glabrous medially (Fig. 7D); mesopleuron smooth, setose (Fig. 7E); mesopleural furrow narrowly crenulated (Fig. 7E); epicnemial carina present, joining with subtegular ridge and forming a smooth crenulated continuous groove anteriorly (Fig. 7E); metapleuron coarsely rugose, sparsely setose (Fig. 7E); propodeum rugose, smooth baso-laterally; area superomedia narrowing anteriorly, widened medially, parallel-sided apically with crenulations laterally; costula indistinct; posterior transverse carina present; area dentipara longer than wide, rugose; pleural carina complete (Fig. 7F).

*Legs.* Femora robust (Fig. 7A); hind coxa smooth (Fig. 8A); hind femur 3.8 × as long as wide; hind tibia 4.6 × as long as wide; hind basitarsus 4.4 × as long as wide.



**Figure 7.** *Microleptes sandeshkaduri* Ranjith & Humala, sp. nov., holotype, female **A** habitus, lateral view **B** head, anterior view **C** head, dorsal view **D** mesosoma, dorsal view **E** mesosoma, lateral view **F** propodeum, dorsal view.

*Wings.* Wings hyaline (Fig. 8D); pterostigma 2.8 × as long as wide; fore wing vein 2r&RS joining to pterostigma in middle, 1.3 × as long as 2rs-m; fore wing vein 2rs-m as long as M between 2rs-m and 2m-cu; vein 1cu-a slightly postfurcal (Fig. 8D); hind wing with nervellus (vein CU) intercepted in middle (Fig. 8D).

*Metasoma*. First metasomal tergite distinctly longitudinally striate-rugose, setose with strong dorsal carina, polished posteriorly (Fig. 8C);  $1.9 \times$  as long as wide; spiracle situated at middle of tergite (Fig. 8A); second tergite polished, sparsely setose,  $0.9 \times$ 



**Figure 8.** *Microleptes sandeshkaduri* Ranjith & Humala, sp. nov., holotype, female **A** metasoma, lateral view **B** metasoma, dorsal view **C** first metasomal tergite, dorsal view **D** wings.

as long as wide posteriorly, with distinct small thyridium (Fig. 8B); third tergite polished, sparsely setose,  $0.8 \times as$  long as wide posteriorly (Fig. 8B); tergites 4–7 polished, sparsely setose (Fig. 8B); hypopygium straight posteriorly; ovipositor hardly exposed; sheath setose apically,  $0.1 \times as$  long as hind tibia (Fig. 8A, B).

**Colour.** Body predominantly black; antenna except scape and pedicel, pterostigma, wing veins, hind coxa dark brown; scape, pedicel, mandible, maxillary and labial palps, tegula, fore and mid legs, hind leg except coxa and ovipositor sheath yellow.

Male. Unknown.

#### Distribution. India.

**Etymology.** The new species is named after Mr. Sandesh Kadur, Director of Felis Creations, Honorary Fellow of ATREE, Senior Fellow of the International League of Conservation Photographers and a National Geographic Explorer for his outstanding contributions towards the documentation, conservation and protection of the planet's biodiversity.

**Comparative diagnosis.** The new species is similar to *M. splendidulus* in having the median flagellomeres distinctly transverse and first flagellomere sharply widened apically. In addition to the differences given in the key, the new species differs from *M. splendidulus* in having the following characters: malar space  $1.4 \times as$  long as basal width of mandible ( $0.8 \times in M.$  splendidulus) and the first flagellomere  $0.8 \times as$  long as the second ( $1.1 \times in M.$  splendidulus).

#### Microleptes tehriensis Ranjith & Humala, sp. nov.

https://zoobank.org/A51FEE8E-3643-417D-BDED-2678E4FAD763 Figs 9, 10

**Material examined.** *Holotype* • male INDIA: Uttarakhand, Tehri, 10.viii.2019, coll. P. Girish Kumar (ZSIK) Regd. No. ZSI/WGRC/IR/INV.27409. Paratypes, 8 males with same data as holotype (AIMB).

Description. Holotype, male. Body length 4.5 mm, fore wing length 3.7 mm.

*Head.* Head  $1.2 \times as$  wide as long in anterior view (Fig. 9B) and  $1.5 \times as$  wide as long in dorsal view (Fig. 9C); face flat, punctate, elevated anteriorly below antennal sockets, forming an acute protrusion, setose,  $1.8 \times as$  wide as long (Fig. 9A, B, D); clypeus transverse, smooth, with lower margin slightly convex (Fig. 9B); tentorial pits round (Fig. 9B); malar space distinctly long,  $1.7 \times basal$  width of mandible, with subocular sulcus (Fig. 9B, D); mandible broad with single broad tooth (Fig. 9B); lateral temples smooth, setose (Fig. 9D); frons and vertex smooth and sparsely setose (Fig. 9C); eye glabrous,  $1.4 \times as$  long as temple in dorsal view (Fig. 9B, C); OOL : diameter of lateral ocellus : POL = 1.4 : 1.1 : 1.0; antenna with 17 flagellomeres; all flagellomeres longer than wide (Fig. 9A); flagellomeres 1-2 with tyloids as longitudinal carinae; first flagellomere  $0.7 \times as$  long as second flagellomere,  $2.4 \times as$  long as wide; second flagellomere  $3.4 \times as$  long as wide.

**Mesosoma.** Mesosoma 1.9 × as long as high (Fig. 9F); dorsal part of pronotum crenulated medially (Fig. 9E); lateral pronotum laterally with a set of subparallel transverse ridges medially, smooth posteriorly (Fig. 9F); mesoscutum flat in lateral view, punctate, setose with a pair of elongate pits postero-laterally (Fig. 9E, F); notaulus shallow, present anteriorly (Fig. 9E); scuto-scutellar groove wide, smooth, without crenulations (Fig. 9E); scutellum smooth, sparsely setose (Fig. 9E); mesopleuron smooth, setose (Fig. 9F); mesopleural furrow widely crenulated (Fig. 9F); epicnemial carina present, joining with subtegular ridge and forming a crenulated continuous groove anteriorly (Fig. 9F); metapleuron coarsely rugose, setose (Fig. 9F); propodeum rugose;



**Figure 9.** *Microleptes tehriensis* Ranjith & Humala, sp. nov., holotype, male **A** habitus, lateral view **B** head, anterior view **C** head, dorsal view **D** head, ventro-lateral view **E** mesosoma, dorsal view **F** mesosoma, lateral view.

area superomedia irregularly rugulose, narrowing basally and apically, costula indistinct; posterior transverse carina present; area dentipara longer than wide, smooth medially rest rugulose; pleural carina complete (Fig. 10A).

*Legs.* Femora slender (Fig. 9A); hind coxa rugose dorsally (Fig. 10B, C); hind femur  $5.6 \times$  as long as wide, somewhat bent upwards in profile; hind tibia  $6.5 \times$  as long as wide; hind basitarsus  $8.0 \times$  as long as wide.



Figure 10. *Microleptes tehriensis* Ranjith & Humala, sp. nov., holotype, male **A** propodeum, dorsal view **B** first metasomal tergite, dorsal view **C** metasoma, lateral view **D** metasoma, dorsal view **E** male genitalia **F** wings.

*Wings.* Wings hyaline (Fig. 10F); pterostigma 3.0 × as long as wide; fore wing vein 2r&RS joining to pterostigma in middle, 2.7 × as long as 2rs-m; fore wing vein 2rs-m as long as M between 2rs-m and 2m-cu; vein 1cu-a oblique and distinctly postfurcal (Fig. 10F); hind wing with nervellus (vein CU) intercepted below middle (Fig. 10F).

*Metasoma*. First tergite rugose in anterior half, longitudinally striate in posterior half, setose with indistinct pair of dorsal carinae,  $2.1 \times$  as long as its maximum width, spiracle situated at middle of tergite (Fig. 10B, C); second tergite with distinct

thyridium, granulate with indistinct longitudinal wrinkles anteriorly, and subpolished posteriorly, setose,  $0.9 \times$  as long as wide posteriorly (Fig. 10D); third tergite smooth, setose,  $0.7 \times$  as long as wide (Fig. 10D); tergites 4–7 smooth, setose (Fig. 10D); posterior margin of apical sternite without a median process; gonostyle almost polished, with apico-lateral patch of setae (Fig. 10C, E).

**Colour.** Body predominantly black; antenna, mandible, pterostigma, wing veins, metasoma, hind coxa, tibia and tarsus dark brown; maxillary and labial palps, tegula, fore and mid legs, hind femur and trochanters yellowish-brown.

Female. Unknown.

Distribution. India.

Etymology. The new species is named after the type locality, Tehri.

**Comparative diagnosis.** The new species is similar to *M. orientalis*. Apart from the differences given in the key it can be distinguished from *M. orientalis* by the following characters: antenna slenderer, with 17 flagellomeres (16 flagellomeres in *M. orientalis*) and hind femur 5.6 × as long as wide, concave dorsally (4.6 × as long as wide and convex dorsally in *M. orientalis*).

#### Microleptes xinbinensis Sheng & Sun, 2014

Figs 11, 12

**Material examined.** 1 female and 2 males, INDIA • Arunachal Pradesh, Yingku, Malaise trap, 17.v.2023, coll. Sahanashree, R. (AIMB).

Description. Female. Body length 3.5 mm, fore wing length 2.6 mm.

*Head.* Head as wide as long in anterior view (Fig. 11B) and  $1.2 \times$  as wide as long in dorsal view (Fig. 11C); face flat, punctate, setose,  $1.4 \times$  as wide as long;  $0.5 \times$  as wide as head (Fig. 11B); clypeus moderately transverse, smooth, with lower margin convex (Fig. 11B); tentorial pits transverse (Fig. 11B); malar long with distinct subocular sulcus,  $1.4 \times$  basal width of mandible (Fig. 11B); mandible broad, with single broad blunt tooth (Fig. 11B); temple polished, with sparse setae (Fig. 11D); frons and vertex smooth and sparsely setose (Fig. 11C); compound eye with short setae,  $1.2 \times$  as long as temple in dorsal view (Fig. 11B, C); OOL : diameter of lateral ocellus : POL = 1.3 : 1.0 : 1.0; antenna with 15 flagellomeres; medial flagellomeres slightly longer than wide (Fig. 11A); first flagellomere  $1.2 \times$  as long as second flagellomere,  $4.2 \times$  as long as wide; second flagellomere  $3.5 \times$  as long as wide.

**Mesosoma.** Mesosoma  $1.8 \times as$  long as high (Fig. 11D); dorsal part of pronotum crenulate medially, with medial pit (Fig. 11C, E),; pronotum lateral smooth and polished (Fig. 11D); epomia absent (Fig. 11D); mesoscutum flat in lateral view (Fig. 11D), punctate, setose with a pair of elongate pits postero-laterally (Fig. 11E); notaulus short and weak, only impressed anteriorly (Fig. 11E); scuto-scutellar groove smooth, without crenulations (Fig. 11E); scutellum smooth (Fig. 11E); mesopleuron smooth (Fig. 11D); mesopleural furrow narrowly crenulated (Fig. 11D); epicnemial carina present, joining with subtegular ridge, not forming crenulated groove anteriorly (Fig. 11D); metapleuron smooth with transverse wrinkles medially, sparsely setose



Figure 11. *Microleptes xinbinensis* Sheng & Sun, female A habitus, lateral view B head, anterior view C head, dorsal view D head and mesosoma, lateral view E mesosoma, dorsal view F propodeum, dorsal view.

(Fig. 11D); propodeum smooth, area superomedia nearly parallel-sided, with few transverse wrinkles medially; anterior transverse carina well developed; posterior transverse carina present; area dentipara as long as wide; pleural carina complete (Fig. 11F).

*Legs.* Femora slender (Fig. 11A); hind coxa rugose antero-dorsally (Fig. 12B, C); hind femur widened posteriorly,  $5.4 \times$  as long as wide; hind tibia  $6.0 \times$  as long as wide; hind basitarsus  $7.6 \times$  as long as wide.



**Figure 12.** *Microleptes xinbinensis* Sheng & Sun, female **A** metasoma, lateral view **B** metasoma, dorsal view **C** first metasomal tergite, dorsal view **D** wings.

*Wings.* Wings hyaline (Fig. 12D); pterostigma  $2.9 \times as$  long as wide; fore wing vein 2r&RS joining to pterostigma in middle,  $1.8 \times as$  long as 2rs-m; fore wing vein 2rs-m  $2.3 \times as$  long as M between 2rs-m and 2m-cu; fore wing vein 1cu-a distinctly postfurcal (Fig. 12D); hind wing with nervellus (vein CU) intercepted in middle.

*Metasoma.* First tergite smooth in anterior half, irregularly longitudinally wrinkled in posterior half, with indistinct dorsal carina and sparse setae,  $3.5 \times as$  long as

its maximum width, spiracle situated at middle of tergite (Fig. 12C); second tergite with distinct thyridium, smooth, setose,  $1.1 \times as$  long as wide posteriorly (Fig. 12B); third tergite smooth, setose,  $0.6 \times as$  long as wide posteriorly (Fig. 12B); tergites 4–6 polished, scarcely setose (Fig. 12B); hypopygium straight posteriorly; ovipositor hardly exposed; sheath apically densely setose,  $0.1 \times as$  long as hind tibia (Fig. 12A).

**Colour.** Body predominantly black; scape, pedicel, flagellomeres 1–5, maxillary and labial palps, tegula, legs except hind tibia basally and hind basitarsus, thyridium yellow, flagellomeres 6–15, hind tibia basally, hind basitarsus, pterostigma, wing veins, hypopygium and ovipositor sheath brown.

Male. Similar to female, antennae with tyloids on flagellomeres 5–7.

Distribution. India and China.

**Notes.** The species was described from Liaoning province of China (East Palaearctic) and known only from a male specimen (Sheng and Sun 2014). This is the first description of the female and a first record of the species from the Oriental region.

## Discussion

Only 14 species were known in the genus *Microleptes* prior to our study, with the majority of them (12 species) distributed in the Holarctic region. One of the main reasons for the greater diversity of the genus in the Holarctic region is that it has been comparatively well studied there (Schwarz 1991; Dasch 1992; Humala 2003, 2007; Sheng and Sun 2014). The species *M. splendidulus* having the widest range has been reported from Palaearctic and Nearctic regions (Yu et al. 2016). Apart from *M. splendidulus*, only one other species, *M. rallus*, has also been reported from Nearctic region. The *Microleptes* fauna of the Oriental region has been so poorly studied that only one species, *M. malaisei*, has been recorded from Myanmar (Kasparyan 1998). The present study enriches our knowledge on the distribution of the genus to the southern part of Oriental region, with the discovering of five new species from south India and Thailand.

Based on the updated distribution range for *Microleptes*, it can be assumed that the center of species diversity of the genus *Microleptes* is confined to the East Palaearctic and Oriental regions, thus this particular area may have played a defining role in the historical process of formation of this group. Given the wide distribution of some species, such as *M. splendidulus*, the possibility of discovering more species with a wider range of distribution cannot be neglected. This applies both to the discovery of new still undescribed species, and to the possible revealing of a wider distribution of already known species. This is further supported, for example, by the new distribution record of *M. xinbinensis* from India, which was previously known only from Northeast China (Sheng and Sun 2014).

Moreover, the expansion of the area of ongoing research in the Oriental region can certainly result in the revealing of even more *Microleptes* species unknown to science, since such researches are still very rare and not systematic. In addition, the comparative rarity of these Darwin wasps in nature (most of the new species described in our study

are represented by single individuals) and, as a consequence, the scarcity of materials on *Microleptes* in collections from the Oriental region should be taken into account.

All of this point to the fact that taxonomic studies of the subfamily in the Oriental region are largely insufficient, as so far only one species from Myanmar has been described (Kasparyan 1998). Continued study of Microleptinae would be very interesting, because, in addition to discovering new species, it could possibly provide new data on the biology of *Microleptes*, which are extremely scarce. In turn, these data may provide further evidence that Microleptinae belong to the subfamily group Ichneumoniformes, as suggested by Santos (2017) and Bennett et al. (2019), or provide a rationale for rejecting this assumption. In the meantime, this research can be considered as a first attempt to reveal the higher species diversity of *Microleptes* in this area.

## Acknowledgements

We thank Drs Sheng Mao-Ling (National Forestry and Grassland Administration, China) and Jin-Kyung Choi (Yeungnam University, South Korea) for sending requested images of *Microleptes*. We are very grateful to the subject editor, Gavin Broad (Natural History Museum, London, UK) and Andrey I. Khalaim (Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia) for valuable comments. APR is grateful to Dr Girish Kumar (Zoological Survey of India) for the specimens. APR is financially supported by a postdoctoral fellowship from the Rachadaphiseksomphot Fund, Graduate School, Chulalongkorn University. This research is financially supported by Thailand Science Research and Innovation Fund Chulalongkorn University and Chulalongkorn University, Rachadaphiseksomphot Fund (RU66\_008\_2300\_002) and RSPG Chula to BAB. The study of A.E. Humala was carried out under state order to the Karelian Research Centre of the Russian Academy of Sciences (Forest Research Institute). APR & DRP acknowledge National Geographic Society (NGS-71945c-20), Global Conservation, USA for the financial assistance for Siang Expedition 2023 and Schlinger Foundation USA and Prof Michael Irwin (University of Illinois, Urbana) for financial support for the collections.

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RESEARCH ARTICLE



# Review of Bicarinibracon Quicke & Walker and Chelonogastra Ashmead (Hymenoptera, Braconidae, Braconinae) in China, with the description of two new species

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 $\label{eq:academiceditor:J.M.Jasso-Martínez | Received \\ 8 \\ October 2024 | \\ Accepted \\ 4 \\ November 2024 | \\ Published \\ 26 \\ November 2024 | \\ Published \\ 20 \\ November 2024 | \\ Publishe$ 

https://zoobank.org/D846F64B-3D9B-4E46-B6EE-992147EAD5BC

**Citation:** Li Y, van Achterberg C, Yan C-J, Chen X-X (2024) Review of *Bicarinibracon* Quicke & Walker and *Chelonogastra* Ashmead (Hymenoptera, Braconidae, Braconinae) in China, with the description of two new species. Journal of Hymenoptera Research 97: 1285–1299. https://doi.org/10.3897/jhr.97.138683

#### Abstract

The species of two genera (*Bicarinibracon* Quicke & Walker and *Chelonogastra* Ashmead) of the subfamily Braconinae (Hymenoptera, Braconidae) from China are reviewed and 6 species are recognized, including 2 new species (*Bicarinibracon concolor* **sp. nov.** and *Chelonogastra rugosa* **sp. nov.**), which are described and illustrated. *Bicarinibracon carini* Chishti & Quicke, 1993 is reported from China for the first time. Keys to the Chinese species of the genera *Bicarinibracon* and *Chelonogastra* are provided.

## Keywords

Aphrastobraconini, Braconini, new record, new species, Oriental

# Introduction

*Bicarinibracon* Quicke & Walker, 1991, and *Chelonogastra* Ashmead, 1900 are two small genera of the subfamily Braconinae (Hymenoptera: Braconidae) with 5 and 8 described species worldwide, respectively (Yu et al. 2016). Both genera used in the tribe

Braconini Nees, but now belong to the tribe Aphrastobraconini Ashmead (Quicke et al. 2023). *Bicarinibracon* occurs in the Oriental and Australasian regions, and *Chelonogas-tra* mainly in the Afrotropical, Eastern Palaearctic and Oriental regions (Yu et al. 2016). The biology of both genera is still unknown. In this paper, we report three *Bicarinibra-con* species in China, of which one species is new to science (*B. concolor* sp. nov.) and one species is new to China (*B. tricarinatus* (Cameron, 1897)), and three *Chelonogastra* species in China, of which one species is new to science (*C. rugosa* sp. nov.).

In the present paper, the new species are described and illustrated and keys to Chinese species of *Bicarinibracon* and *Chelonogastra* are provided.

## Materials and methods

Specimen of *Bicarinibracon tricarinatus* (Cameron, 1897) was collected by sweeping nets and kept in 100% ethanol. While specimens of *Bicarinibracon concolor* sp. nov. and *Chelonogastra rugosa* sp. nov. were collected by Malaise traps. Monthly collected specimens from Malaise traps were kept in 100% ethanol. They were mounted on point-cards or with #3 insect pins.

The recognition of the subfamily Braconinae and tribes Braconini and Aphrastobraconini, based on van Achterberg (1990, 1993), Chen and van Achterberg (2019) and Quicke et al. (2023); the terminology and measurements used in this paper, follow van Achterberg (1988, 1993); and for additional references see Yu et al. (2016). The medial length of the third metasomal tergite is measured from the posterior border of the second suture to the posterior margin of the tergite.

Photographs were made with a Keyence VHX-2000 digital microscope and a Canon 6D mark II digital camera with Laowa 25mm f2.8 + 2.5–5.0 X, and apex of antenna and ovipositor with Mitutoyo 10 x. The photos were slightly processed (mainly cropped and the background modified) in Photoshop 2024. For the descriptions and measurements an Olympus SZX7 and Leica M125 stereomicroscopes were used. The specimens are deposited in the College of Chemistry and Life Sciences, Chengdu Normal University, Chengdu (**CDNU**) and in the Institute of Zoology, Chinese Academy of Sciences, Beijing (**IZCAS**).

## Results

#### Genus Bicarinibracon Quicke & Walker, 1991

Figs 1–4

*Bicarinibracon* Quicke & Walker, 1991: 419. Type species: *Atanycolus tricolor* Szépligeti, 1900.

**Diagnosis.** Body medium-sized. Median segments of antenna square or slightly longer than wide (Figs 1, 3), apical antennal segment rather acute, with short spine; in lateral

view scapus nearly truncate and dorsally longer than ventrally (Figs 2k, 4i); eye glabrous, not or weakly emarginated (Figs 2g, 4g); face punctate, and often with a more or less distinct triangular median area (Figs 2g, 4g); clypeus with distinct dorsal carina (Figs 2g, 4g); malar suture relatively long and distinct (Figs 2i, 4i); labio-maxillary complex normal, not elongate (Figs 2i, 4i); frons distinctly concave behind antennal sockets, with deep median groove, smooth (Figs 2h, 4h); mesosoma largely smooth and shiny (Figs 2c, 4c); notauli smooth and moderately depressed (Figs 2d, 4d); mesoscutum smooth and evenly setose; scutellar sulcus comparatively wide, with developed crenulae (Figs 2d, 4d); metanotum with or without mid-longitudinal carina; propodeum with two sub-medial carinae and nearly reaching to its anterior margin, and with distinctly lamelliform carinae sub-laterally (Figs 2d, 4j); angle between veins 1-SR and C+SC+R of fore wing about 50°; fore wing vein SR1 not reaching the tip (Figs 2a, 4a); fore wing veins 1-SR+M and 1-M not or rarely weakly curved subbasally (Figs 2a, 4a); fore wing vein cu-a interstitial; fore wing vein CU1b medium-sized, slender and reclivous (Figs 2a, 4a); vein 3-CU1 of fore wing slender; fore wing vein r oblique and shorter than width of pterostigma; second submarginal cell of fore wing long and narrow, nearly subparallelsided or slightly narrowing distally (Figs 2a, 4a); hind wing vein SC+R1 distinctly longer than vein 1r-m (Figs 2b, 4b); hind wing with only 1 hamulus on vein R1, membrane largely glabrous near vein cu-a (Figs 2b, 4b); claws medium-sized, ventral lobe obtuse (Figs 2f, 4f); metasomal tergites largely sculptured; median area of first metasomal tergite strongly convex, with well-developed dorsal and dorso-lateral carinae and a mediolongitudinal carina, often connected with several transverse carinae laterally (Figs 2j, 4k); second metasomal tergite with small smooth medio-basal area, and connected to median carina posteriorly, median carina extends up to posterior margin of tergite and lateral grooves developed (Figs 2e, 4e); second metasomal suture deep and crenulate (Figs 2e, 4e); third and fourth metasomal tergites with antero-lateral grooves, and lateroposterior corner protruding, more or less smooth (Figs 1, 3); third to fifth metasomal tergites with rather weak transverse posterior grooves (Figs 2e, 4e); hypopygium medium-sized and slightly apically acute, not emarginate medio-apically; ovipositor normal, subapically upper valve with nodus, and its lower valve with teeth ventrally (Figs 2l, 4l). Biology. Unknown.

Distribution. Australasian; Oriental.

## Key to Chinese species of the genus Bicarinibracon Quicke & Walker

## Bicarinibracon carini Chishti & Quicke, 1993

Bicarinibracon carini Chishti & Quicke, 1993: 232.

#### Biology. Unknown.

**Distribution.** Oriental (China-Taiwan).

**Note.** Chishti and Quicke (1993) reported this species from Taiwan (China), but no specimens of this species are available for this study.

#### Bicarinibracon concolor sp. nov.

https://zoobank.org/2CF47E8C-9424-40A1-84ED-97F9F7CA86F0 Figs 1, 2

**Type material.** *Holotype:* CHINA • ♀; Hainan Prov., Wanning, Xinglong Tropical Botanical Garden; 18°43'51"N, 110°11'24"E; 30.vi–9.x.2021; Wang Zheng leg.; No. MT2, WZ44, 2022011 (CDNU).

**Diagnosis.** This new species has the body colouration very similar to *Bicarinibracon luteus* Quicke & Walker, but can be separated from the latter by the following characters: postero-lateral lobes of third and fourth metasomal tergites rounded and not strongly protruding (acute and strongly protruding in *B. luteus*); third to fifth metasomal tergites largely longitudinally striate (only medially striate, but more confused rugulose posteriorly and laterally in *B. luteus*); hind wing vein 1r-m relatively long, 0.6 times the length of vein SC+R1 (0.4 times in *B. luteus*); first metasomal tergite with 2 strong and complete transverse carinae running between dorsal and dorso-lateral carinae (without crenulae in *B. luteus*); antenna largely dark brown, except for scapus brownish (largely brownish mustard-yellow but terminal few antennomeres mid-brown in *B. luteus*).

**Description.** Holotype,  $\mathcal{Q}$ , length of body 6.0 mm, of fore wing 5.6 mm, of ovipositor sheath 3.2 mm.

**Head.** Antenna incomplete, 40 segments remaining; median segments 1.3 times longer than its width; third segment 1.6 times longer than its width, 1.3 and 1.4 times longer than fourth and fifth respectively, the latter 1.3 times longer wide; length of maxillary palp 0.6 times height of head; malar suture long and distinct, with sparse short setae (Fig. 2i); clypeus height: inter-tentorial distance: tentorio-ocular distance = 5: 10: 9; clypeus with sparse long setae (Fig. 2i); eye glabrous, weakly emarginate (Fig. 2g); face moderately densely punctate, with dense and long setae (Fig. 2g); eye



Figure 1. *Bicarinibracon concolor* sp. nov., ♀, holotype, habitus lateral.

height: shortest distance between eyes: head width = 9: 12: 23; frons moderately concave behind antennal sockets, largely smooth except for a few weak punctures, with some sparse short setae and a strong median groove (Fig. 2h); vertex with sparse weak punctures and some short setae (Fig. 2h); minimum distance between posterior ocelli: minimum diameter of elliptical posterior ocellus: minimum distance between posterior ocellus and eye = 6: 7: 20; length of malar space 1.8 times basal width of mandible; in dorsal view length of eye 2.4 times temple; temples moderately densely setose, and gradually narrowed behind eyes (Fig. 2h).

*Mesosoma.* Length of mesosoma 1.5 times its height (Fig. 2c); pronotum largely glabrous (Fig. 2c); anterior half of notauli deeply impressed and posterior half shallow (Fig. 2d); mesoscutum evenly densely setose; scutellar sulcus comparatively wide, with sparse (only 8) crenulae (Fig. 2d); scutellum densely setose posteriorly (Fig. 2d); metanotum convex medially, with a developed median carina anteriorly (Fig. 2d); propodeum densely setose, and somewhat longer laterally, propodeal carinae complete (Fig. 2d).

*Wings.* Fore wing (Fig. 2a): SR1: 3-SR: r = 34: 20: 5; 1-SR+M rather weakly curved subbasally, 1.7 times as long as 1-M; 2-SR: 3-SR: r-m = 12: 20: 9; CU1b 0.7 times as long as 3-CU1; angle between 1-SR and C+SC+R ca. 50°; cu-a interstitial. Hind wing (Fig. 2b): 1r-m straight; SC+R1: 2-SC+R: 1r-m = 40: 18: 25.

*Legs.* Length of fore femur: tibia: tarsus = 15: 18: 25; length of hind femur: tibia: basitarsus = 17: 20: 8; length of femur, tibia and basitarsus of hind leg 3.0, 6.6 and 4.5 times their maximum width, respectively; hind tibial spurs 0.3 and 0.4 times as long as hind basitarsus; hind femur, tibia and tarsus densely setose, setae of tarsus rather short.



**Figure 2.** *Bicarinibracon concolor* sp. nov.,  $\bigcirc$ , holotype **a** fore wing **b** hind wing **c** mesosoma, lateral view **d** mesosoma, dorsal view **e** metasoma, dorsal view **f** hind leg, lateral view **g** head, front view **h** head, dorsal view **i** head, lateral view **j** first metasomal tergite, dorsal view **k** scapus outer side, lateral view **l** apex of ovipositor, lateral view **m** apex of hind leg, lateral view.

*Metasoma.* Length of first metasomal tergite about 0.8 times as long as its apical width; lateral area of first tergite comparatively wide, with 2 strong and complete transverse carinae running between dorsal and dorso-lateral carinae, and with 3 transverse carinae both sides of medio-longitudinal carina (Fig. 2j); second tergite 1.7 times wider than medially long, largely coarsely striate-sculptured except the smooth medio-basal area, lateral grooves converging posteriorly (Fig. 2e); second suture strongly crenulate, narrow and weakly curved medially, widened laterally (Fig. 2e); third to fifth metasomal tergites largely longitudinally striate-sculptured (Fig. 2e); postero-lateral lobes of third and fourth metasomal tergites smooth, rounded and not strongly protruding (Fig. 1); sixth metasomal tergite smooth and shiny; hypopygium acute apically, not reaching level of apex of metasoma; ovipositor sheath 0.6 times as long as fore wing.

**Colour.** Largely yellowish (Fig. 1), but antenna (except for scapus brownish), eyes, mandible apically and claws dark brown (Figs 1, 2f, g, k); notaular area and median mesoscutal lobe posteriorly pale yellow (Fig. 2d); ovipositor sheath black (Fig. 1); wing membrane yellowish, pterostigma and veins pale brown (Fig. 2a, b).

Biology. Unknown.

Distribution. Oriental (China- Hainan).

**Etymology.** Named after the yellowish body: "concolor" is Latin for "coloured uniformly".

#### Bicarinibracon tricarinatus (Cameron, 1897)

Figs 3, 4

- *Bicarinibracon tricarinatus* Cameron, 1897: 33; Szépligeti, 1904: 37; Ramakrishna Ayyar, 1924: 354.
- Campyloneurus tricarinatus (Cameron): Ramakrishna Ayyar, 1928: 55; Shenefelt, 1978: 1665.

Bicarinibracon tricarinatus (Cameron): Chishti & Quicke, 1993: 235.

**Material.** CHINA • 1♀; Yunnan Prov., Xishuangbanna Xiaomengyang; 850 m; 14.VI.1957; Wang Shuyong leg.; No. IOZ(E)1964572 (IZCAS).

Biology. Unknown.

Distribution. Oriental (China-Yunnan; India; Sri Lanka).

Note. This species is new to the fauna of China.

#### Genus Chelonogastra Ashmead, 1900

Figs 5, 6

*Chelonogastra* Ashmead, 1900: 139; Watanabe, 1937: 16; Shenefelt, 1978: 1669; Quicke, 1987: 107. Type species: *Chelonogastra koebelei* Ashmead, 1900 (monobasic and original designation).

Iphiaulax (Chelonogastra): Fahringer, 1928: 589.



Figure 3. *Bicarinibracon tricarinatus* (Cameron, 1897), ♀, habitus lateral.

Diagnosis. Body small to medium-sized; terminal antennomere often rather acute apically (Fig. 60); in lateral view scapus gradually narrowed basally, truncate apico-laterally, ventrally more or less as long as dorsally (Fig. 6n); eye setose, weakly emarginated (Fig. 6j); face coarsely rugose or punctate, often densely setose (Fig. 6j); clypeus without dorsal carina (Fig. 6j); malar suture often sculptured (Fig. 6l); labio-maxillary complex normal, not elongate (Fig. 6l); frons weakly concave behind antennal sockets, with some setae and a median groove (Fig. 6k); occiput normal (Fig. 6k), or sometimes with distinct lateral tubercles; mesosoma densely setose (Fig. 6c); middle lobe of mesoscutum nearly truncate anteriorly, not strongly produced in front of the lateral lobes (Fig. 6d); notauli moderately deep and complete, sometimes only shallow subposteriorly (Fig. 6d); precoxal suture absent; pleural suture smooth; scutellar sulcus moderately wide and crenulate (Fig. 6d); metanotum convex medially, and with a short median carina anteriorly (Fig. 6e); propodeum largely smooth and densely setose, without medio-longitudinal carina or groove (Fig. 6e); propodeal spiracle round, near middle of propodeum, and without tubercle above it (Fig. 6c); angle between veins 1-SR and C+SC+R of fore wing about 60°; vein SR1 not reaching tip of fore wing (Fig. 6a); fore wing veins 1-M and 1-SR+M nearly straight (Fig. 6a); fore wing vein cu-a more or less interstitial (Fig. 6a); fore wing



**Figure 4.** *Bicarinibracon tricarinatus* (Cameron, 1897),  $\bigcirc$  **a** fore wing **b** hind wing **c** mesosoma, lateral view **d** mesosoma, dorsal view **e** metasoma, dorsal view **f** hind leg, lateral view **g** head, front view **h** head, dorsal view **i** head and scapus outer side, lateral view **j** propodeum, dorsal view **k** first metasomal tergite, dorsal view **l** apex of ovipositor, lateral view.

vein CU1b medium-sized, slender and reclivous (Fig. 6a); second submarginal cell of fore wing moderately short, and subparallel-sided (Fig. 6a); hind wing vein SC+R1 distinctly longer than vein 1r-m (Fig. 6b); membrane more or less evenly setose or largely glabrous near vein cu-a (Fig. 6b); lobes of tarsal claws usually large, with setae (Fig. 6h); metasoma

robust; metasomal tergites (at least second and third) often largely and coarsely sculptured (Fig. 6f); first metasomal tergite largely coarsely sculptured except for the median area, which slightly convex and largely smooth, and without medio-longitudinal carina (Fig. 6m); lateral grooves of first metasomal tergite wide and crenulate; second metasomal tergite with a small rugose medio-basal area and connected to median carina posteriorly, lateral grooves crenulate (Fig. 6f); second metasomal suture deep and crenulate (Fig. 6f); third to fifth metasomal tergites with antero-lateral areas, and latero-posterior corner more or less protruding (Fig. 6g); female with posterior margin of fifth metasomal tergite broadly emarginate (Fig. 6g); hypopygium medium-sized and apically acute; upper valve of ovipositor without nodus subapically, and its lower valve without ventral teeth (Fig. 6i).

Biology. Unknown.

Distribution. Oriental, Afrotropical, Eastern Palaearctic.

## Key to Chinese species of the genus Chelonogastra Ashmead

1	Body with head and metasoma black, mesosoma reddish yellow; medio-basal
	area of second metasomal tergite coarsely rugose C. rugosa sp. nov.
_	Body almost entirely black; medio-basal area of second metasomal tergite
	smooth2
2	Fourth and fifth metasomal tergites similar striate as first three tergites and
	without granulation; body length 6.0-8.0 mm C. formosana
_	First three metasomal tergites coarsely rugose, fourth and fifth tergites granu-
	late; body length 5.5–6.0 mm <i>C. koebelei</i>

## Chelonogastra formosana Watanabe, 1937

*Chelonogastra koebelei* forma *formosana* Watanabe, 1937: 17. *Chelonogastra formosana* Watanabe: Watanabe, 1961: 363; Chou, 1981: 73.

#### Biology. Unknown.

**Distribution.** Oriental (China-Taiwan; Thailand; Japan).

**Note.** Watanabe (1937) reported this species from Taiwan (China), but no specimens of this species are available for this study.

## Chelonogastra koebelei Ashmead, 1900

*Chelonogastra koebelei* Ashmead, 1900: 139, 1906: 195; Watanabe, 1934: 184, 1937: 17; Chou, 1981: 73. *Iphiaulax (Chelonogastra) koebelei* (Ashmead): Fahringer, 1928: 591.

## Biology. Unknown.

Distribution. Oriental (China-Taiwan; Thailand; Japan).

Note. Watanabe (1934) reported this species from Taiwan (China), but no specimens of this species are available for this study.

## Chelonogastra rugosa sp. nov.

https://zoobank.org/4B41AAE4-970F-464A-8799-364EF5CB3BFE Figs 5, 6

**Type material**. *Holotype:* CHINA •  $\bigcirc$ ; Hainan Prov., Danzhou, Southern Medicinal Botanical Garden; 19°30'50.46"N, 109°30'1.05"E; 30.IX–31.X.2020; Chen Longlong leg.; No. HN4, LSX901, 2022021 (CDNU). *Paratypes:* CHINA •  $2\bigcirc \bigcirc$ ; same data as for holotype; No. HN5, LSX903, 2022051–2022052 (CDNU) •  $2\bigcirc \bigcirc$ ; Hainan Prov., Wenchang Tongguling Nature Reserve, road side; 137m; 19°40'19.19"N, 111°0'44.6"E; 4–15.III.2020; Xu Chunyang leg.; No. TGL2, PYQ401, 2022053–2022054 (CDNU) •  $1\bigcirc$ ; Hainan Prov., Wenchang Tongguling Nature Reserve, cropland; 11 m; 19°40'19.19"N, 111°0'44.6"E; 15.iv–2.v.2020; Xu Chunyang leg.; No. TGL3, PYQ413, 2022055 (CDNU).

**Diagnosis.** This new species with very similar metasoma to *Chelonogastra formosana* Watanabe, 1937, but can be separated from the latter by the following characters: mesoscutum reddish yellow (black in *C. formosana*); relatively small-sized, length of body of female 2.5–3.9 mm (6.0–8.0 mm in *C. formosana*); occiput without lateral tubercle (with distinct lateral tubercles in *C. formosana*); medio-basal area of second metasomal tergite coarsely rugose (smooth in *C. formosana*).



Figure 5. Chelonogastra rugosa sp. nov., ♀, holotype, habitus lateral.



**Figure 6.** *Chelonogastra rugosa* sp. nov., Q, holotype **a** fore wing **b** hind wing **c** mesosoma, lateral view **d** mesosoma, dorsal view **e** metanotum and propodeum, dorsal view **f** second and third metasomal tergites, dorsal view **g** fourth and fifth metasomal tergites, dorsal view **h** hind leg, lateral view **i** apex of ovipositor, lateral view **j** head, front view **k** head, dorsal view **l** head, lateral view **m** first metasomal tergite, dorsal view **n** scapus outer side, lateral view **o** apex of antenna.

**Description.** Holotype,  $\mathcal{Q}$ , length of body 2.7 mm, of fore wing 3.0 mm, of ovipositor sheath 1.0 mm.

Head. Antenna with 31 segments; apical antennal segment rather acute, with short spine, 2.7 times longer than its maximum width (Fig. 60); penultimate segment 1.9 times longer than its width, and 0.8 times as long as apical antennomere; median segments 1.5 times longer than wide; third segment 1.4 times longer than wide, 1.0 and 1.0 times longer than fourth and fifth, respectively, the latter 1.5 times longer than wide; length of maxillary palp 0.6 times height of head; malar suture rugose, and densely setose (Fig. 6l); clypeus height: inter-tentorial distance: tentorio-ocular distance = 19: 37: 20; clypeus with sparse, long setae (Fig. 6l); eye with sparse short setae, weakly emarginate (Fig. 6j); face with some punctures, and densely setose (Fig. 6j); eye height: shortest distance between eyes: head width = 12: 13: 25; frons sparsely punctate, and weakly concave behind antennal sockets, with a median groove (Fig. 6k); vertex largely smooth except for a few weak punctures, and with some sparse short setae (Fig. 6k); minimum distance between posterior ocelli: minimum diameter of elliptical posterior ocellus: minimum distance between posterior ocellus and eye = 6: 4: 11; length of malar space 2.1 times longer than basal width of mandible; in dorsal view length of eye 2.7 times temple; temples sparsely setose, and directly narrowed behind eyes (Fig. 6k); occiput without lateral tubercle (Fig. 6k).

*Mesosoma.* Length of mesosoma 1.4 times its height (Fig. 6c); notauli developed and complete (Fig. 6d); mesoscutum densely short setose; scutellar sulcus comparatively wide and deep, with crenulae (Fig. 6d); scutellum densely short setose, especially posteriorly (Fig. 6d); metanotum convex medially, with median carina (Fig. 6e); propodeum largely smooth, but with sparse setae medially, and dense, long setae laterally, without medio-longitudinal carina or groove (Fig. 6e).

*Wings.* Fore wing (Fig. 6a): angle between 1-SR and C+SC+R approximately 62°; SR1: 3-SR: r = 48: 27: 11; 1-SR+M straight, 2.0 times as long as 1-M; 2-SR: 3-SR: r-m = 5: 9: 4; 2-SR+M largely not sclerotised; CU1b 0.6 times as long as 3-CU1; cu-a interstitial. Hind wing (Fig. 6b): 1r-m straight; SC+R1: 2-SC+R: 1r-m = 17: 5: 6.

*Legs.* Length of fore femur: tibia: tarsus = 24: 34: 21; length of hind femur: tibia: basitarsus = 19: 25: 10; length of femur, tibia and basitarsus of hind leg 2.5, 6.6 and 4.7 times their maximum width, respectively; hind tibial spurs 0.3 and 0.4 times as long as hind basitarsus; hind femur, tibia and tarsus densely setose, setae of tarsus rather short.

*Metasoma.* Length of first metasomal tergite 0.8 times its apical width, median area convex and reticulate sculptured posteriorly (Fig. 6m); lateral grooves of first tergite comparatively wide, with crenulae; second tergite largely coarsely sculptured, including medio-basal area (Fig. 6f); antero-lateral grooves of second tergite moderately narrow and shallow, with crenulae; second suture crenulate, wide and distinctly curved medially, narrow laterally (Fig. 6f); third to fifth tergites largely coarsely sculptured except apically, and with antero-lateral grooves (Fig. 6f, g); hypopygium acute apically, not reaching level of apex of metasoma; ovipositor sheath 0.3 times as long as fore wing.

**Colour.** Head largely black (Fig. 5), but mandible whitish (except apically) (Fig. 6j); mesosoma largely reddish yellow (Fig. 6c, d, e); fore legs largely blackish brown except femur apically, tibia and tarsus reddish yellow (Fig. 5); middle and hind legs blackish brown (Figs 5, 6h); metasoma blackish brown (Fig. 6f, g); ovipositor sheath black (Fig. 5); wing membrane infuscated, pterostigma and veins dark brown (Fig. 6a, b).

*Variation.* Length of body of female 2.5–3.9 mm, of fore wing of female 2.9–4.3 mm, and of ovipositor sheath 0.8–1.7 mm; antenna of female with 33 antennomeres; apical antennomere 2.0 times longer than its maximum width; penultimate antennomere 1.7 times longer than its maximum width, and 0.8 times as long as apical antennomere; length of mesosoma 1.1–1.3 times its height.

Biology. Unknown.

Distribution. Oriental (China- Hainan).

**Etymology.** Named after the entirely coarsely rugose second to fifth metasomal tergites: "rugosa" is Latin for "rugose".

## Acknowledgements

The authors thank Huayan Chen for providing the specimens. We also thank Mrs Hong Liu (IZCAS) for the loan of specimens. We are grateful to the editor and reviewers for improving this paper. This work was supported by the General Program of National Natural Science Foundation of China (32100360), the Sichuan Provincial Natural Science Foundation Project (2024NSFSC1321), the Foundation of Chengdu Normal University Talent Introduction Research Funding (YJRC202009, No. 111/111158701), the Special Funding for Tianfu Emei Talent Project (51000022T000004883381) and the Key International Joint Research Program of National Natural Science Foundation of China (31920103005).

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RESEARCH ARTICLE



# Integrative taxonomic revision of the Nearctic Perilampus hyalinus species complex (Hymenoptera, Chalcidoidea, Perilampidae) resolves 100 years of confusion about the host associations of P. hyalinus Say

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Academic editor: Ankita Gupta   Received 28 July 2024   Accepted 17 October 2024   Published 5 December	2024

**Citation:** Yoo JJ, Darling DC (2024) Integrative taxonomic revision of the Nearctic *Perilampus hyalinus* species complex (Hymenoptera, Chalcidoidea, Perilampidae) resolves 100 years of confusion about the host associations of *P. hyalinus* Say. Journal of Hymenoptera Research 97: 1301–1383. https://doi.org/10.3897/jhr.97.133255

#### Abstract

The enigmatic Nearctic parasitoid *Perilampus hyalinus* Say (Hymenoptera: Chalcidoidea: Perilampidae) has long been suspected as a species complex with a wide range of host associations and differing modes of parasitism. In this study we clarify the status of this species by combining morphological evidence, two genes (COI and ITS2) and host information and recognize ten species in the *P. hyalinus* species complex in the Nearctic region. Eight new species are described: *Perilampus arcus* Yoo & Darling, **sp. nov.**, *P. neodiprioni* Yoo & Darling, **sp. nov.**, *P. monocteni* Yoo & Darling, **sp. nov.**, *P. neodiprioni* Yoo & Darling, **sp. nov.**, *P. monocteni* Yoo & Darling, **sp. nov.**, and *P. ute* Yoo & Darling, **sp. nov.**, *P. seneca* Yoo & Darling, **sp. nov.**, *P. sonora* Yoo & Darling, **sp. nov.**, and *P. ute* Yoo & Darling, **sp. nov.** A reared specimen with a COI sequence is designated as the Neotype of *P. hyalinus* Say establishing this species as either a hyperparasitoid that parasitizes dipteran parasitoids of Orthoptera or a parasitoid of dipteran kleptoparasites of Crabronidae and Sphecidae that provision their nests with Orthoptera. *Perilampus sirsiris* (Argaman) and four of the new species are hyperparasitoids, parasitizing hymenopteran and dipteran parasitoids of Lepidoptera. *Perilampus neodiprioni* and *P. monocteni* can develop as both primary parasitoids of Diprionidae (Hymenoptera) and as hyperparasitoids, parasitizing dipteran and hymenopteran parasitoids of diptrioni sawflies. *Perilampus neodiprioni* is strictly associated with *Neodiprion* sawflies, and *P. monocteni* is associated with *Monoctenus* sawflies.

#### **Keywords**

COI, ITS2, key, morphology, new species, parasitoid, species delimitation, systematics

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# Introduction

The *Perilampus hyalinus* species group contains the most conspicuous species of *Perilampus* in the Western Hemisphere. Specimens are large (3–5 mm) and brightly iridescent in color and are frequently collected on flowers. It is one of the 6 species groups recognized by Smulyan (1936) in the last comprehensive study of the genus and three species were recognized, two of which were new: *Perilampus carolinensis* and *P. regalis*. All remaining specimens were referred to the already enigmatic *P. hyalinus* Say.

*Perilampus hyalinus* Say has been shrouded in confusion for at least 100 years, since biological studies of these parasitoids indicated divergent host associations and modes of parasitism (Smith 1912; Kelly 1914; Smith 1958) and suggested that there were morphological differences in the first-instar larvae or planidia associated with various hosts (Ford 1922; Tripp 1962). The search for morphological differences of the adults that were correlated with these biological differences is still best summarized by Burks (1979:771), "This may be a species complex, rather than a single species; careful rearings have produced specimens, at present indistinguishable, that are either primary or secondary parasites".

Resolving the status of *P. hyalinus* could have important implications for the biological control of insect pests important to agriculture and forestry. Careful rearing studies have revealed *P. hyalinus* (*s.l*) as primary parasitoids attacking *Neodiprion* sawflies (Hymenoptera: Diprionidae), which are serious forest pests particularly in boreal forests (Alfaro and Fuentealba 2016; Johns et al. 2016). But this nominal species is also a common hyperparasitoid, parasitizing dipteran (Sarcophagidae and Tachinidae) and hymenopteran (Ichneumonoidea) primary parasitoids of Lepidoptera and Orthoptera (Smith 1912; Kelly 1914; Clausen 1940; Smith 1958), thereby possibly interfering with population regulation of insect herbivores by the primary parasitoids.

To clarify the status of the *P. hyalinus* species group, Yoo (2023) has incorporated molecular data from two genes (COI and ITS2) along with a critical analysis of morphological characters to identify 25 "candidate" species in which morphology and genes were in agreement, and 5 "candidate" species with unique combinations of morphological character states consistent across multiple specimens. A phylogenetic analysis of the molecular data indicated that the *P. hyalinus* species group is comprised of two strongly supported monophyletic species complexes, both of which contain species in the Nearctic and Neotropical regions (Fig. 1, modified from Yoo 2022): the *P. carolinensis species* complex (including *P. carolinensis* Smulyan, *P. regalis* Smulyan and 5 undescribed species, Yoo and Darling, in preparation) and the *P. hyalinus* species complex (including *P. hyalinus*). Phylogenetic analyses of the combined COI and ITS2 data suggest that the 9 Nearctic species of the *P. hyalinus* species complex belong to three separate clades of the *P. hyalinus* species group (Fig. 1).

In this paper we revise the *P. hyalinus* species complex and recognize 10 Nearctic species using morphology, molecular data (COI and ITS2), and host information. We also designate a Neotype for *Perilampus hyalinus* Say. Most of Thomas Say's type



**Figure 1.** Maximum likelihood tree of *Perilampus hyalinus* species group retrieved from the combined analysis of COI and ITS2 (modified from Yoo 2023). Bootstrap support values are shown on the left side of the nodes. The roman numerals and black dots adjacent to the nodes indicate the major morphological clades recovered as monophyletic (I = *P. hyalinus* species group; II = *P. carolinensis* species complex; IIa = "pseudocarolinensis" clade; IIb = *P. carolinensis* clade; III = *P. hyalinus* species complex; IIIa = *P. hyalinus* clade 1; IIIb = *P. hyalinus* clade 2; IIIc = *P. hyalinus* clade 3; IIId = "regalishyalinus" clade. The morphospecies designation for the sequences is marked by vertical bars, colored according to their placements within their respective morphological subgroups. The names of the species described herein are indicated in white boxes.

material is regarded as lost and the surviving Say specimens are in the Museum of Comparative Zoology (MCZ), Harvard University (Mawdsley 1993). There are no specimens of Chalcidoidea described or identified by Say in the MCZ and a Neotype needs to be designated to fix the name *Perilampus hyalinus* objectively. The new species described and recognized herein present "exceptional need" (as defined by Article 75.3 of the International Code of Zoological Nomenclature [fourth edition] 1999) justifying the designation of a Neotype. We also discuss reasons for the diverse host associations in the *P. hyalinus* species complex and suggest areas for future research on the Nearctic species.

# Methods

# Morphology

Specimens were examined with a Leica MZ7.5 stereo zoom microscope and were illuminated with a Leica 20-watt halogen light source, filtered through a strip of translucent Mylar<sup>®</sup> film. Images of specimens were taken with a Keyence digital microscope VHX-7000 series, and edited with Adobe® Illustrator CC ver. 21.0.2 (Adobe Systems Inc., California, USA). The material examined and descriptions for each species were generated by a series of R coding commands and an Excel spreadsheet; the R-codes are freely available on GitHub (https://github.com/esdarling/r-taxonomy). The Excel spreadsheet for the species descriptions was output from Lucid Builder 3.3 (University of Queensland, Australia). Morphological terms mostly follow Darling (1983), Gibson (1997), and Darling and Yoo (2021) with the following modifications and additional terms. Frontal carina is a raised knife-edged ridge extending from the vertex (Fig. 2B: fc) ventrad along the margin of the parascrobal area (Fig. 2A: psa) to near the lower eye margin (Fig. 2A: fc). The pronotum is "carinulate" if it has a raised carina running along the upper posterior margin visible from dorsal view (Fig. 2H: ca). This state was discovered and termed as "bicarinulate" by Argaman (1990), but we prefer the term "carinulate" because only one distinct carina can be observed. The setae on the face are considered sparse if the distance between two adjacent setal pores is usually about equal to or longer than the length of the setae (Fig. 4I), or dense, if the distance between two adjacent setal pores is usually shorter than the length of the setae (Fig. 14I). Pits on male scape are depressions or indentations that have pores (Fig. 3F). Pores on the male scape are well documented for various groups of Chalcidoidea such as Torymidae (Goodpasture 1975), Perilampidae (Darling 1983), Eulophidae (Dahms 1984), and Aphelinidae (Shirley et al. 2019). Also referred to as release-and-spread structures (RRS), these pores are connected to glandular cells within the scape and suggest the release and spread of pheromone for mate-recognition during courtship (Isidoro et al. 1996). Courtship in Chalcidoidea often involves elaborate movements of male antennae (e.g. Girault and Sanders 1910; Barass 1960). The male scape of Perilampidae has conspicuous pits that contain pores (Darling 1983) and are likely
RRS. The scape morphology of males, e.g. the distributions and shape of pores and pits, are useful for species discrimination in Perilampidae and other Chalcidoidea (e.g. Darling 1983; Shirley et al. 2019; Darling and Yoo 2021). Interestingly, many female specimens of the P. hyalinus species group and other species of Perilampidae also have pits, albeit distinctively fewer in numbers and often inconspicuous or entirely absent (Fig. 3D, E cf. Fig. 3F), and do not show consistent interspecific variability. In addition, the pits on the female scape are restricted to mesad on the anterior surface, covering no more than  $0.2 \times$  scape length. It is unclear if the pits on the female scape contain pores. The pits on scape are considered sparse if separated by distance usually longer than diameter of pits (Fig. 7F, G), dense if separated by distance usually equal to or shorter than the diameter of pits (Fig. 17G, H). The pitted area of the male scape in the P. hyalinus species group is never swollen anteriad, in contrast to several species in the other groups with a swollen pitted area. The axillar shelf is a horizontal cliff-like edge on the axilla extending from the anterior to posterior margin of the axilla in lateral view (Fig. 2F: axsh). Males usually have more bulbous eyes and larger ocelli than females which results in shorter lateral ocellar line, ocular ocellar line, and postocellar line in males.

All measurements were taken with the Keyence Communication software, either directly from the specimens or from digital images, in which case care was taken to avoid problems associated with parallax. The measurements of each species were taken from four to five specimens per sex. Holotype and paratypes were measured for each new species. The primary type for the previously described Nearctic P. hyalinus complex species could not be borrowed for measurement (e.g. P. sirsiris). For this species, the measurements were taken from conspecific specimens that were sequenced and/or with collection localities close to that of the types. Most of the following abbreviations for measurements follow Darling (1983) and Gibson (1997): AL, anellus length; AxH, axillula height at midpoint; AxL, axillula length; CH, clypeus height; CW, clypeus width; EH, eye height; EL, eye length; FC, frontal carina width across maximum diameter of median ocellus in dorsal view; FCLO, shortest distance between frontal carina and lateral ocellus; Fu#L, funicular segment length; Fu#W, funicular segment width; HH, head height; HL, head length; HW, head width in dorsal view; PSA, parascrobal area width at maximum eye width; LPP, lateral panel of pronotum width; LOD, lateral ocellus diameter; LOL, lateral ocellar line, the shortest distance between the median and a lateral ocellus; ML, mesosoma length in lateral view; MW, mesosoma width in dorsal view; MOD, median ocellus diameter; MSL, malar space length; MSC, length of mesoscutum in lateral view; OOL, ocular ocellar line, the shortest distance between the eye and a lateral ocellus; PL, pedicel length; PN, pronotum length in dorsal view; POL, postocellar line, the shortest distance between the lateral ocelli ; PPT, prepectus width; PW, pronotum width in dorsal view; PSW, width of parascrobal area at maximum eye length; SC, length of mesoscutellum in lateral view; SCH, supraclypeal area height; SCW, supraclypeal area width; SW, scrobe width at maximum width of head in anterior view; WL, wing length; WW, wing width. In addition to specified ratios (e.g. POL/OOL), POL, OOL, and LOL were compared with LOD as ratios (LOD: POL: OOL: LOL).

### Material examined

Specimens were examined from the following collections: American Museum of Natural History, New York City, NY, United States (AMNH); California State Collection of Arthropods, Sacramento, CA, United States (CSCA); California Academy of Sciences, San Francisco, CA, United States (CAS); Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, ON, Canada (CNC); Centre for Biodiversity Genomics, University of Guelph, Guelph, ON, Canada (CBG); Cornell University Insect Collection, Ithaca, NY, United States (CUIC); University of Guelph Insect Collection, Guelph, ON, Canada (DEBU); Entomological Museum at Utah State University, Logan, UT, United States (EMUS); Field Museum of Natural History, Chicago, IL, United States (FMNH); Florida State Collection of Arthropods, Gainesville, FL, United States (FSCA); Great Lakes Forestry Centre, Sault Ste. Marie, ON, Canada (GLFC); Illinois Natural History Survey, Champaign, IL, United States (INHS); Ministry of Agriculture, Fisheries and Food in Québec, Québec City, QC, Canada (MAPAQ); Museum of Comparative Zoology, Harvard University, Cambridge, MA, United States (MCZC); Natural History Museum, Berlin, Germany (MNHB); National Museum of Natural History, Paris, France (MNHN); Hungarian National Museum, Budapest, Hungary (HNHM); North Carolina State University Insect Collection, Raleigh, NC, United States (NCSU); Natural History Museum, London, United Kingdom (NMHUK); the Royal Ontario Museum, Toronto, ON, Canada (ROM); Snow Entomological Museum Collection, Lawrence, KS, United States (SEMC); Texas A&M University, College Station, TX, United States (TAMU); University of Arkansas, Fayetteville, AR, United States (UAAM); University of Arizona Insect Collection, Tucson, AZ, United States (UAIC); University of California, Davis, CA, United Staes (UCDC); University of Central Florida, Orlando, FL, United States (UCFC); University of Colorado Museum, Boulder, CO, United States (UCMC); Entomology Research Museum, University of California, Riverside, CA, United States (UCRC); W.R. Enns Entomology Museum, University of Missouri, Columbia, MO, United States (UMRM); Smithsonian National Museum of Natural History, Washington, DC, United States (USNM); Insect Collection, University of Texas, Austin, TX, United States (UTIC); Wisconsin Insect Research Collection, University of Wisconsin-Madison, WI, United States (WIRC); J.B. Wallis/R.E. Roughley Museum of Entomology, University of Manitoba, Winnipeg, MB, Canada (WRME). The primary types of the previously described species of the *P. hyalinus* species group were studied by examining available specimens or images sent by the repositories the repositories (Suppl. material 6). A summary of the non-type specimens examined is provided for each species in the Suppl. materials. The specimens of particular interest that are mentioned in Variation and/or Remarks sections or that were unsequenced and collected from outside the Nearctic region are listed as Additional Material Examined. The label data of holotypes are reported as verbatim.

## **DNA** sequencing

Hind legs and/or middle legs were removed from the specimens of each morphospecies for DNA extraction. The molecular work was done either Canadian Centre for DNA Barcoding (CCDB) at the University of Guelph or in the Laboratory of Molecular Systematics (LMS) at Royal Ontario Museum. At LMS, DNA was extracted using a Qiagen DNeasy Blood and Tissue Kit following the manufacturer's instructions and DNA was eluted with 50 µl of AE buffer. Each 25 µl PCR reaction consisted of 1 µl of template DNA, 18.89 µl ddH2O, 0.56 µl dNTPs [10 mM], 0.05 µl Platinum Taq (Invitrogen), 1 µl [0.01 mM] each of the universal COI primers LCO1490 and HCO2198 (Folmer et al. 1994) and 2.5 µl 10 × PCR buffer (Invitrogen). PCR thermo-cycling conditions were an initial hot start of 94 °C for 1 min, 5 cycles of denaturation at 94 °C for 30 s, annealing at 42 °C for 40 s and extension at 72 °C for 1 min, then 35 cycles of denaturation at 94 °C for 30 s, annealing at 46 °C for 40 s and extension at 72 °C for 1 min, with a final extension at 72 °C for 5 min. Three microliters of PCR products were combined with 3 µl loading dye and visualised using 1% agarose gel. Only amplicons with single, intense bands were sequenced. Before sequencing the remaining 23 µl of PCR product was treated with 0.5 ul of ExoSAP-IT (Applied Biosystems) and 1.5 µl ddH2O and placed in a thermocycler under the following conditions: 37 °C for 15 min, 80 °C for 15 min, and then a 4 °C hold. Each sequencing reaction consisted of 2 µl of PCR product along with 0.5 µl BIG DYE 3.1 reagent (Applied Biosystems), 0.5 µl LCO1490/HCO2198 primer, 5 µl ddH20 and 2 µl 5 × sequencing buffer (Invitrogen) and were then run on an ABI 3730 capillary sequencer (Applied Biosystems). At CCDB, DNA was extracted using the automated CCDB glass fiber membrane method for 96-well plates (Ivanova et al. 2006). PCR amplification and sequencing reactions followed standard CCDB protocols (Hajibabaei et al. 2005). Identical primers were used in both institutions for PCR amplification: primers LepF1 (5'- ATTCAACCAAT CAT-AAAGATATTGG-3') and LepR1 (5'TAAACTTCTGGATGTCCAAAAAATCA-3') were used for COI; and ITS2F (5'TGTGAACTGCAGG ACACATG-3') and ITS2R2 (5'-TCTCGCCTGCTCTGAGGT-3') were used for ITS2. At CCDB, various mixes of primers were also used for additional amplifications for the taxa with poor quality DNA. The majority of the assembled sequences were uploaded to and downloaded from the Barcode of Life Data Systems (Ratnasingham and Hebert 2007). Prior to alignment, trace files of COI sequences were inspected with Chromas ver. 2.6.6 (Technelysium Pty Ltd., Helensvale, Australia) and edited where necessary for quality control.

# Molecular analyses

The *Perilampus platigaster* species group is regarded as the sister group to the *P. hya-linus* species group based on two putative morphological synapomorphies, frontal carina and finger-like axillula (Darling 1996), and was used as the outgroup. COI sequences were aligned with MUSCLE algorithm (Edgar 2004) implemented in

MEGA ver. 10.1.6 (Kumar et al. 2018) with default settings. ITS2 sequences were aligned with MAFFT v.5 online server (Katoh 2013) with default settings except for the alignment strategy was changed to L-INS-i, and scoring matrix for the sequences was changed to 1PAM/K=2. COI and ITS2 datasets were concatenated with MEGA ver. 10.1.6, using only the specimens that were successfully sequenced for both genes. COI and ITS2 sequences were trimmed with MEGA ver. 10.1.6 to a maximum length of 600 bp and 450 bp, respectively. Sequences shorter than 50% of the maximum alignment length were excluded from the analyses. jModelTest (Darriba et al. 2012) implemented in IQ-TREE ver.2.1.3 (Nguyen et al. 2015) was used to select the most suitable nucleotide substitution models for the phylogenetic analyses, restricted to only those supported by MrBayes, for the analyses under Bayesian Information Criterion: GTR +I+G4 for COI; and HKY+G4 for ITS2. Maximum likelihood (ML) and Bayesian phylogenetic inference (BI) analyses were conducted for both single and concatenated datasets, using IQ-TREE ver.2.1.3 and MrBayes ver. 3.2.7 (Huelsenbeck et al. 2001; Ronquist et al. 2012), respectively. Each ML analysis was conducted in IQ-TREE ver.2.1.3, with 1000 initial parsimony trees, 20 best trees retained during search, and 1000 ultrafast bootstrap iterations for branch support (Hoang et al. 2018). The convergence was evaluated by inspecting the trace plots with Tracer ver. 1.7.1 (Rambaut et al. 2018) to verify if all estimated sample sizes (ESS) were > 200. The first 25% of the samples were discarded as burn-in, and the remaining trees were used to construct the 50% majority rule consensus tree. All trees were visualized with Figtree ver. 1.4.4 (Rambaut 2018) and further edited with Adobe® Illustrator CC ver. 21.0.2.

The pairwise uncorrected p-distances within and between preliminary species inferred from morphology were calculated in PAUP\* 4.0a169 (Swofford 2003) using minimal evolution and constraining negative branch lengths to be non-negative, ignoring gaps for affected sites, with equal rates for variable sites, and estimating variation for all substitutions. For each morphospecies, the minimum interspecific distances to the nearest neighbor and the maximum intraspecific distances were obtained.

Three molecular species delimitation methods were employed for each locus to estimate the number of molecular operational taxonomic units (MOTUs): Automatic Barcoding Gap Discovery (ABGD) (Puillandre et al. 2011), Barcode Index Number (BIN) system (Ratnasingham and Hebert 2013), and Poisson Tree Processes (PTP) (Zhang et al. 2013). The finalization of preliminary species was based on comparison across the partitioning of morphospecies and MOTUs, further supported with available host information. ABGD delimits MOTUs by recursively partitioning the data using the barcode gap between pairwise interspecific and intraspecific distances (Puillandre et al. 2011). In ABGD, the position of the barcode gap is inferred based on a range of genetic intraspecific divergences (P) and relative gap width (X) defined a priori. In this study, ABGD method was performed on the online web application (https://bioinfo.mnhn.fr/abi/public/abgd/abgdweb.html) with pairwise uncorrected p-distances calculated with PAUP. Default P values from 0.001 to 0.1 were used for both the COI and ITS2 datasets. The number of steps was set to 30, and the X

value of 0.5 was analyzed. ABGD resulted in highly variable number of MOTUs across the P values, likely due to the lack of clear barcoding gaps (Yoo 2023). The partitioning schemes from Yoo (2023) that were best corroborated by morphology and other delimitation methods were presented as the most biologically plausible (Puillandre et al. 2011). The initial and recursive partitions at P = 0.0057-0.0067was selected for COI. The recursive partition at P = 0.0036 - 0.0067 was selected for ITS2. The BIN system is another distance-based species delimitation method. Barcode of Life Data Systems (Ratnasingham and Hebert 2007) automatically assigned BINs to each sequence with Refined Single Linkage Analysis (RESL) which delimits molecular operational taxonomic unit based on a 2.2% threshold of sequence divergence, then refined by Markov clustering (Ratnasingham and Hebert 2013). Since BOLD currently assigns BINs only for COI, this method could not be applied for the ITS2 sequences. PTP is a tree-based species delimitation method which models speciation rates using the number of substitutions obtained from branch lengths of phylogenetic tree (Zhang et al. 2013). Under the assumption that there are a significantly higher number of substitutions between species than within species, the method identifies the transition points between speciation and coalescent processes (Zhang et al. 2013). The PTP analyses were performed using the online web application (https://species.h-its.org) using the above ML trees obtained from IQ-TREE ver.2.1.3 as inputs. 500,000 MCMC generations, thinning value of 100, a burn-in of 10%, and outgroups were removed to improve the species delimitation. MCMC chains did not converge despite using the available maximum number of generations (500,000), thus only the results of maximum likelihood solutions are reported. With ITS2, the inclusion of the complete *P. hyalinus* species group data set resulted in grouping of the majority of the species in the *P. hyalinus* species complex into two molecular taxonomic units (MOTUs) while the exclusion of most divergent species such as those in the *P. carolinensis* species complex partitioned MOTUs closer to morphology and COI (Yoo 2023). This is likely due to the greater degree of uneven branch length distributions between P. carolinensis species complex and the most members in the *P. hyalinus* species complex in ITS2. Because PTP assumes constant speciation and coalescent rates across phylogeny (Zhang et al. 2013), the algorithm may have classified longer branches outside the P. hyalinus species complex as speciation processes, while classifying the mostly shorter branches within the species complex as coalescence processes (Yoo 2023). Therefore, the results from two separate PTP analyses with ITS2 were merged to obtain the total MOTU partitioning scheme.

### Species distributions

The species distribution maps were made with the online GIS tool SimpleMappr (Shorthouse 2010), and further edited with Adobe<sup>®</sup> Illustrator CC ver. 21.0.2 (Adobe Systems Inc., California, USA). The complete data for each specimen, including species, type status, locality information with coordinates and sequencing information is

archived on the TMS Collections Management System (ROM) and will be added to the Global Biodiversity Information Facility (www.GBIF.org) after publication and the validation of the new species.

### Host associations

The host association of individual specimens was obtained from the associated labels, available host remains, and/or publications. Where necessary, the host names were updated to reflect the current nomenclature. In many instances, the dipteran or ichneumonid primary parasitoid hosts pupated inside the cocoons or pupae of their herbivore hosts. This necessitated a careful examination of the inner contents of the cocoons and pupae to determine whether the *Perilampus* had developed as primary or hyperparasitoids. The sawfly cocoons and lepidopteran pupae from which *Perilampus* exited were either dissected (Fig. 26B cf. 26A) or their interiors were examined through the exit hole (Fig. 26A: eh) using halogen light sources. The presence of parasitoid cocoons (Fig. 26C, E: Ic) or puparia (Fig. 26D, F, H: Tp) indicated the development as hyperparasitoids, while their absence (Fig. 26B, G) indicated primary parasitoids.

# Results

The molecular analysis provides strong support for both the *P. hyalinus* species group and the *P. hyalinus* species complex—both the ML and BI analyses yielded similar tree topologies (Fig. 1, Suppl. material 1: BS  $\ge$  96, PP = 1). In addition, the *P. hyalinus* species complex is further divided into three well supported major clades (Figs 1, Suppl. material 1: BS  $\ge$  86, PP  $\ge$  0.90) and eight of nine Nearctic morphospecies, including the parasitoids associated with *Neodiprion* sawflies, show well supported monophyly with the combined data (Figs 1, Suppl. material 1 BS  $\ge$  95, PP = 1) or at least one or both loci (Suppl. materials 2–4, COI BS  $\ge$  92, PP  $\ge$  0.76; ITS2 BS  $\ge$  90, PP  $\ge$  0.94). The eight species were also successfully delimited with at least one gene (Suppl. materials 2, 5). The molecular analysis pertaining to the entire Western Hemisphere and phylogenetic structure within the *P. hyalinus* species group are discussed in detail in Yoo (2023).

The BINs assigned for each specimen by BOLD are shown in the material examined. The current BINs (December 28, 2023) and the number of BINed specimens are indicated in the remarks section for each species. The pairwise uncorrected distances for each gene for the Nearctic species are summarized in Table 1. The minimum interspecific divergences with COI range from 1.2% to 4.6%, and maximum intraspecific divergences range from 0.7% to 2.3%. The minimum interspecific divergences with ITS2 range from 0.7% to 4.5%, and maximum intraspecific divergences range from 0 to 0.7%. The overlap of minimum interspecific and maximum intraspecific divergences suggests the absence of a global barcode gap (Wiemers and Fiedler 2007; Kvist 2016) in the Nearctic *P. hyalinus* species complex in both COI and ITS2.

	P. arcus	P. crassus	P. neodiprioni	P. hyalinus	P. pilosus	P. seneca	P. sirsiris	P. sonora	P. ute
P. arcus	0/0-1.2	4.5	4.1	3.4-4.5	4.1-4.2	0.7	4.5-4.8	3.1	2.1-2.8
P. crassus	4.0-5.5	0/0.2-0.5	2.8	1.0	2.4	3.8	2.4-2.8	3.4-3.5	4.5-5.2
P. neodiprioni	4.0-5.3	2.7-3.7	0/0-0.9	1.7	2.4	3.4	1.7-2.1	2.8	4.5-4.9
P. hyalinus	4.2-6.2	1.6-4.0	3.0-4.7	0/0-2.3	1.4	2.8	1.4-1.7	2.4	3.4-4.2
P. pilosus	3.5-4.4	2.3-3.6	2.3-3.4	1.2-2.9	0/0-1.0	3.4	2.1-2.4	2.4	4.1-4.9
P. seneca	2.5 - 4.0	4.0-5.3	3.4-4.7	4.3-6.7	3.8-5.2	0/0.2-0.7	3.8-4.1	2.4	1.4-2.1
P. sirsiris	3.3-4.5	2.2-4.1	1.3-2.6	2.1-3.8	1.3-2.2	3.2-5.0	0-0.3/0-1.3	3.1-3.5	4.5-5.6
P. sonora	3.9-5.8	4.2-6.3	4.0-5.2	4.6-6.5	3.7-4.8	3.4-5.4	3.5-4.7	0-0.3/1.0-1.3	3.8-4.5
P. ute	3.1-4.4	3.7-5.5	3.2-4.2	4.1-6.5	4.1-6.5	2.2-3.0	2.9-4.7	4.0-5.2	0-0.7/0.3-2.0

**Table 1.** Pairwise uncorrected p-distances for two genes among Nearctic members of the *Perilampus hyalinus* species complex. Intraspecific distances are along the diagonal, ITS2/COI. Interspecific distances for COI are below diagonal, for ITS2 are above diagonal.

### Perilampus hyalinus species group

Figs 2A, B, D, F, H, 3

#### Family Perilampidae Főrster, 1856

#### Genus Perilampus Latreille, 1809

Taltonos Argaman, 1990 (subjective synonym, Darling, 1996).

#### P. hyalinus species group sensu Smulyan (1936) and Darling (1996)

**Description. Female.** Color: head and body entirely or at least partially brightly iridescent (Fig. 2A, H).

Head: in anterior view weakly transverse, slightly wider than high, HW/HH 1.2-1.3; slightly wider than pronotum, HW/PW 1.1-1.2. Frontal carina: distinct, extended from posterior margin of median ocellus (Fig. 2B) to near lower eye margin (Fig. 2A); in dorsal view narrow near median ocellus. Ocelli: median ocellus in line with lateral ocelli or only slightly advanced (Figs 2B, 12G). Eye: slightly shorter than head height, EH/HH 0.6–0.7. Vertex: rounded behind. Occiput: with vertical groove below vertex, with subparallel costulae; occipital carina absent. Malar space (Fig. 2A): with oblique striae obliterating malar sulcus (Fig. 2D). Clypeus (Fig. 3A): weakly transverse to strongly transverse, CW/CH 1.3-1.6; lateral sulci straight or weakly curved, strongly divergent; with small and indistinct tentorial pits; epistomal sulcus concave, deeper and more distinct than lateral sulci; ventral margin concave or nearly flat. Supraclypeal area (Fig. 3A): subquadrate; shorter and narrower than clypeus, SCH/CH 0.5–0.6. Scape (Figs 3C–E): length about  $0.6 \times EH$ ; narrow throughout; pits absent or if present distad covering no more than 0.2 × scape length (Figs 3 D, E). Flagellum (Fig. 3I): anellus transverse, AL/PL about 0.3; Fu1 subquadrate, Fu1L/Fu1W 1.0–1.1; subequal to or slightly longer in length than pedicel, Fu1L/PL 1.0-1.3; Fu2 subquad-



**Figure 2.** The morphological characters of *Perilampus hyalinus* species group (A B D H F) and other *Perilampus* species groups (C E G I) **A** head, anterior-oblique view, *P. seneca* **B** vertex, dorsal view, *P. neodiprioni* **C** vertex, dorsal view, *P. aunatus* **D** malar space, *P. seneca* **E** malar space, *P. platigaster* **F** axilla and axillula, *P. hyalinus* **G** axilla and axillula, *Perilampus* sp. **H** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **I** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **I** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **I** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **I** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **I** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **I** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **I** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **I** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **I** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **I** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **I** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **I** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **I** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **I** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **I** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **I** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **I** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **I** pronotum and mesoscutum, posterior oblique view, *P. neodiprioni* **B** attack and axillular shelf; ca, carina; fc, frontal carina; ms, malar space; msl, malar sulcus; not, notaulus; psa, parascrobal area. **[A** ROME182769; **B**, **H** ROME162273; **C** ROME162320; **D** ROME199563; **E** ROME141508; **F** ROME162229; **G** ROME182831; **I** DHJPAR0038540]. Scale bars: 250 µm (**A–C, H, I** 



Figure 3. Sexual dimorphism in the *Perilampus hyalinus* species group A female head, anterior view, *P. seneca* B male head, anterior view, *P. seneca* C female scape anterior margin, *P. seneca* D female scape inner margin, *P. seneca* E female scape inner margin, *P. neodiprioni* F male scape anterior margin, *P. seneca* I female head, dorsal view, *P. seneca* H male head, dorsal view, *P. seneca* I female flagellum, *P. seneca* K female habitus, dorsal view, *P. neodiprioni* L male habitus, dorsal view, *P. neodiprioni*. Abbreviation: scp, scape. [A ROME199563; B ROME183976; C, D ROME199531; E ROME198219; F ROME198147]. Scale bars: 250 μm (A, B, G–J); 100 μm (C–F); 500 μm (K, L).

rate or transverse, Fu3–Fu7 transverse; clava 4-segmented, C1–3 as long dorsad as ventrad, with distinct terminal button (C4).

Mesosoma: slightly longer than wide, ML/MW 1.2–1.3. Pronotum: carinulate (Fig. 2H); short, PN/MSC about 0.2; shorter along midline, 0.5–0.7 length laterad;

anterior margin sharp, all rows of punctures on same plane. Lateral panel of pronotum: without flange (Fig. 4D) or with flange below level of mesothoracic spiracle in posterior oblique view (Fig. 16D: arrow); anterior margin sharp, all rows of punctures on same plane. Prepectus: wide and triangular; differentiated from pronotum with distinct suture; ventral strap short, without row of alveolae; central area of lateral panel smooth, with foveae along dorsal and posterior margins. Mesoscutum (Fig. 2H): midlobe without tubercle; notaulus distinct and continuous, uninterrupted by sculpture of mesoscutum. Mesoscutellum: without tubercle; slightly longer than mesoscutum, SC/MSC 1.2–1.3; strongly vaulted, frenum ventrad and not visible in the dorsal view. Axilla: with axillar shelf (Fig. 2F). Axillula: elongate and finger-like, AxL/AxH usually 2.0 or greater (Fig. 2F). Metanotum: short, length  $0.4-0.5 \times$  length of propodeum along midline. Propodeum: width about 3 × length along midline; submedian area smooth to weakly imbricate, with foveae or groove laterad median carina, delimited laterad and ventrad by complete plicae, dorsad by transverse band of foveae; callus with angulate process below spiracle, and alveolate-rugose, with alveolae sometimes obliterated below spiracle; nucha with transverse to arcuate rugae. Fore wing: elongate, WL/WW 2.3-2.4; hyaline, with yellow or brown venation; parastigma swollen with weak equilateral triangular process; postmarginal vein  $0.7-0.8 \times as$  long as marginal vein; stigmal vein  $0.3-0.4 \times$  as long as marginal vein; stigma with weak uncus.

Metasoma: petiole short and straplike, with weak transverse wrinkles; petiolar flange short with ventral margin of upper area with shallow emargination mesad; antecostal sulcus transverse, with weak vertical carinae laterad and smoothened mesad; Mt2 with trapezoidal demarcation and shallow median groove, imbricate and wrinkled anteriad, and smooth posterad without lateral protruberances along midline, posterior margin straight and sparsely setose; Gt3 smooth.

**Male.** As in female, except: Color: mesonotum sometimes nearly entirely black or with cupreous iridescence (Fig. 3L cf. Fig. 3K). Eye: in dorsal view often more bulbous (Fig. 3H cf. Fig. 3G). Ocellus: often larger (Fig. 3H cf. Fig. 3G). Ocellar ratios LOD: POL: OOL: LOL: often shorter. Frontal carina: distance from lateral ocellus usually shorter. Malar space: MSL/EH often shorter. Flagellum: slightly wider (Fig. 3J cf. Fig. 3I). Scape (Fig. 3F): in anterior view weakly expanded distad,  $1.3-1.4 \times$  width above radicle; with distinct pits on anterior surface (Fig. 3F cf. Fig. 3D, E); pitted surface not swollen in lateral view. Aedeagus: without a pair of lateral spines.

**Diagnosis.** The *P. hyalinus* species group is characterized by: brightly iridescent coloration (Fig. 2A, H), distinct frontal carina extended from posterior margin of median ocellus (Fig. 2B cf. Fig. 2C) to near lower eye margin (Fig. 2A), oblique costae obliterating malar sulcus (Fig. 2D cf. Fig. 2E), carinulate pronotum (Fig. 2H cf. Fig. 2I), distinct and uninterrupted notaulus (Fig. 2H), axilla with axillar shelf (Fig. 2F cf. Fig. 2G), and elongate and finger-like axillula (Fig. 2F cf. Fig. 2G). The *P. platigaster* species group has a similar structure of the frontal carina, axilla, and axillula, but is distinguished by having a malar sulcus (Fig. 2E cf. Fig. 2D) and the general body color black with or without weak iridescent reflections (Fig. 2I cf. Fig. 2H).

**Distribution.** The *P. hyalinus* species group occurs exclusively in the Western Hemisphere, from the southern Canada to Argentina.

**Host association.** The previously published host records indicate that species are mostly hyperparasitoids, parasitizing dipteran (Tachinidae and Sarcophagidae) and hymenopteran parasitoids (Ichneumonoidea) of Lepidoptera, Orthoptera, and rarely, Phasmatoidea and Coleoptera (e.g. Smith 1912; Smith 1958; Pitts et al. 2002; Janzen and Hallwachs 2009). Smith (1912) gave a detailed description of the biology of *P. hyalinus* Say as an indirect hyperparasitoid—the planidia actively searches and burrows into the host of the primary parasitoid (e.g. caterpillars), but can only feed and develop on the dipteran or hymenopteran parasitoids. There are relatively fewer cases of primary parasitoids in the *P. hyalinus* species group, and the best documented are the parasitoids of *Neodiprion* sawflies (Hymenoptera: Diprionidae) (Tripp 1962).

Remarks. This species group was hypothesized as a monophyletic group based on morphological characters (Darling 1996) and was well corroborated in our combined analysis of COI and ITS2 (Fig. 1). The oblique costae obliterating the malar sulcus (Fig. 2D) is the only shared and putatively derived character exclusive to this species group. Other character states (e.g. frontal carina) are widely distributed across Perilampidae in varying combinations, and a comprehensive phylogenetic analysis of this family is required to understand their evolution. Yoo (2023) recognized two clades in the P. hyalinus species group supported by COI+ITS2 and morphology: the P. carolinensis species complex, which has a parascrobal area abruptly narrowed in lateral view and the lateral panel of pronotum without a flange (Fig. 1 Clade II), and the *P. hyalinus* species complex which has a parascrobal area usually gradually narrowed in lateral view and the lateral panel of pronotum with or without a flange (Fig. 1 Clade III). The P. hyalinus species complex is further divided into three major clades which are congruent in genetic and morphological characters, for example the density of pits on the male scape, the shape of the lateral panel of the pronotum, and color of the mesonotum in females (Yoo 2023). The species in the P. hyalinus clade 3 (IIIc, Fig. 1), including P. arcus, P. seneca, and P. ute, are distinguished by a usually densely pitted male scape (Figs 17G, 17H, 19H, 19I, 21G, 21H) and the lateral panel of pronotum with a triangular flange (Figs 16D, 18D, 20D). The species in the P. hyalinus clade 1 (IIIa, Fig. 1), including P. sonora, can be recognized by the cupreous mesonotum in females (Fig. 22B), in addition to the usually sparse pits on the male scape (Fig. 23G, H) and the lateral panel of the pronotum that lacks a triangular flange (Fig. 22D). The P. hyalinus clade 2 species (IIIb, Fig. 1), including P. crassus, P. neodiprioni, P. hyalinus, P. monocteni, P. pilosus, and P. sirsiris, also has a sparsely pitted male scape (Figs 5G, H, 7F, G, 9G, H, 11G, H, 13G, H, 15F, G) and the lateral panel of pronotum without a triangular flange (Figs 4D, 6D, 8D, 10D, 12D, 14D). But the P. hyalinus clade 2 species do not have the strong cupreous mesonotum in females (e.g. Fig. 4B), except in P. pilosus (Fig. 15A).

## Key to the Nearctic P. hyalinus species group

1 Parascrobal area in lateral view abruptly narrowed towards lower eye margin (A, B); outer orbit with long and wide smooth area (A, B); lower face sparsely setose (C, D)......*P. carolinensis* species complex, 2









3(1) Median ocellus advanced to form a narrow triangle with lateral ocelli (C); lower face densely setose, with dense and widely distributed setae laterad torulus (A female, B male, circled); lateral panel of pronotum without flange (D, lateral view; E, oblique posterior view); male scape sparsely pitted (F). [Southwestern U.S and Northwestern Mexico]...*P. pilosus* Yoo & Darling, sp. nov.



Ocellar triangle variable (d, e); lower face sparsely (a female) or densely setose (b, c male), with sparse (a, circled) or dense and narrowly distributed setae laterad torulus (b, c, circled); lateral panel of pronotum without (f, posterior oblique view) or with flange (g, posterior oblique view); male scape variable......4





Parascutal carina (a, circled) broadly curved, without flange (b, c) ......6



5(4) Lateral panel of pronotum without flange or with small rounded flange in posterior oblique view (A); parascutal carina usually angulate (B), rarely steeply curved (C); male scape sparsely pitted (D)......*P. sirsiris* (Argaman)





6(4) Mesonotum cupreous in both sexes (A female, B male); lateral panel of pronotum without flange in posterior oblique view (C); male scape with short pitted area, about 0.3 × scape length, and pits sparse (D, E). [Southwestern U.S to Southern Mexico] ...... *P. sonora* Yoo & Darling, sp. nov.







Mesoscutal lateral lobes usually punctate along notaulus (a, b); lateral panel of pronotum without flange (c) or with small rounded flange (d); median ocellus in line with lateral ocelli or advanced and forming a narrow triangle (e); axilla areolate-rugose (f, g) or carinate ventrad; male scape sparsely pitted (h)......9







9(7) Ventral margin of clypeus nearly straight, weakly iridescent (A, B); mesoscutal lateral lobes sculpture along notaulus always strongly punctate (C, D)..... *P. crassus* Yoo & Darling, sp. nov.



 Ventral margin of clypeus concave and black (a, b); sculpture of lateral lobe of mesoscutum along notaulus weaker, rarely smooth (c, d) ......10





11(10) Axillula usually with piliferous punctures dorsad (arrows, A, B); mesofemoral depression variable, often imbricate-alveolate (C, D); inner margins at apex of mesoscutellum gradually diverging (E, F). [Parasitoids of *Neodiprion* spp. or hyperparasitoids, parasitizing their dipteran and hymenopteran parasitoids]......*P. neodiprioni* Yoo & Darling, sp. nov.





#### Perilampus hyalinus Say, rev. stat.

Figs 4, 5, 24A, B

Perilampus hyalinus Say, 1829:79. (original description, sex not indicated). Type locality: USA, Pennsylvania. Type material: Type lost. Neotype. "USA:OH: Montgomery Co. New Carlisle 39.989583, -84.029056, Ex. Ceracia dentate, Ex. Melanoplus femurrubrum prob. 26.x.2014 M. D. Sheaffer". The neotype is point-mounted (Male ROME204130, USNM). BOLD:AEA0382. ROM Online Collection.

*Perilampus entellus* Walker, 1843:103 (original description). Type locality: Ohio, USA. Type Material. Lectotype, B.M. Type Hym. 5.2285, NHMUK014583126 (Images examined).

*Perilampus aciculatus* Provancher, 1889:199 (original description). Type locality: Ottawa, Canada. Type material. Lectotype, 1359, Université Laval, Québec City, Canada (Images examined). Note: Year of publication incorrect as 1887 in subsequent references to *P. aciculatus* (see Barron 1975:391).

Perilampus aciculatus, Lectotype, Gahan and Rohwer 1918:106.

Perilampus aciculatus Smuylan, 1936:380 (tentative synonym of P. hyalinus Say).

Perilampus aciculatus Peck, 1963:519 (subjective synonym of P. hyalinus Say).

Perilampus aciculatus Burks, 1963:1259 (subjective synonymy "probably correct").

Perilampus entellus, Lectotype, Burks 1975:150 (subjective synonym of P. hyalinus Say).

Taltonos hyalinus (Say). Argaman, 1990:205 (new combination).

Taltonos aciculatus (Provancher), Argaman, 1991:5 (new combination).

Taltonos entellus (Walker), Argaman, 1991:9 (new combination).

Perilampus hyalinus Say. Darling, 1996:113 (*Taltonos*, subjective synonym of *Perilampus*).
Perilampus aciculatus Darling, 1996:113 (*Taltonos*, subjective synonym of *Perilampus*).
Perilampus entellus Darling, 1996:113 (*Taltonos*, subjective synonym of *Perilampus*).
Perilampus aciculatus, New synonymy based on Neotype designation herein.
Perilampus entellus, New synonymy based on Neotype designation herein.

**Material examined.** CANADA: 77 females, 47 males. USA: 67 females, 31 males. (Suppl. materials).

Additional material examined. CANADA: 1 female. Ontario: 1 female. Durham R.M., Glen Major Forest: (1 female: ROME152664-ROME; BOLD:AEA0382; ITS2). MEXICO: 2 females. Jalisco: 1 female. (1 female: ROME200751-HNHM). Sonora: 1 female. (1 female: ROME162260-USNM).

**Description. Female** (Fig. 4). Length: 2.9–4.4 mm. Color: head iridescent greenish blue or violet; mesosoma and metasoma iridescent greenish blue or violet; clypeus ventral margin black (Fig. 4I); antenna with scape and pedicel weakly iridescent greenish blue or violet, flagellum brown or black, lighter ventrad and distad.

Head (Fig. 4G–I): in dorsal view transverse, width slightly greater than twice length, HW/HL 2.1–2.2. Frontal carina: in anterior view straight to weakly sinuate below midlevel of eye; in dorsal view gradually narrowed V shape around median ocellus, FC/MOD 1.5–1.9; distance from lateral ocellus short to long, FCLO/LOD 0.6–1.0. Scrobal cavity (Fig. 4H): in anterior view wide, SW/HW about 0.5. Ocelli (Fig. 4G):



Figure 4. *Perilampus hyalinus* Female A habitus, lateral view B habitus dorsal view C lateral lobe of mesoscutum along notaulus D lateral panel of pronotum, posterior oblique view E axillula F axilla G head, dorsal view H head, anterior view I lower face J parascutal carina K mesoscutellum apex L, M mesofemoral depression. [A ROME185913; B, K ROME189058; C, M ROME185947; D, F ROME189056; E, G ROME162229; H ROME167636; I ROME189060; L ROME162246]. Scale bar: 1 mm (A).



**Figure 5.** *Perilampus hyalinus* Male **A** habitus, lateral view **B** lateral panel of pronotum and parascutal carina, posterior oblique view **C** head, anterior view **D** head, dorsal view **E** lower face **F** lateral lobe of mesoscutum along notaulus **G**, **H** scape. [**A** Neotype, ROME204130; **B–D**, **F**, **G** ROME182798; **E** ROME167638; **H** ROME189059]. Scale bars: 1 mm (**A**); 100 μm (**G**, **H**).

a line between anterior margin of lateral ocelli nearly bisecting median ocellus. POL/ OOL 1.7–1.9. Ocellar ratios LOD: POL: OOL: LOL 1, 3.3–3.5, 1.8–2.0, 1.2–1.4. Vertex: with strong to weak transverse striations, without large piliferous punctures. Parascrobal area: in lateral view gradually narrowed towards lower eye margin; width narrow, PSW/EL about 0.3; sculpture strongly to weakly striate, without large piliferous punctures. Gena: entirely or mostly striate along outer eye margin with narrow and short smooth area, striate behind. Malar space: MSL/EH 0.2–0.3. Lower face (Fig. 4H, I): with setae sparse laterad torulus, and usually sparse below. Clypeus (Fig. 4I): CW/CH 1.3–1.5; ventral margin concave; setae evenly distributed, or with small bare area without setae medially.

Mesosoma (Fig. 4B–F, J–M): Lateral panel of pronotum: slightly narrower than or about as wide as prepectus, LPP/PPT 0.7–0.9; without flange below level of mesothoracic spiracle in posterior oblique view (Fig. 4D). Mesofemoral depression: smooth, weakly imbricate (Fig. 4L), or rugulose (Fig. 4M). Mesoscutum: punctures angulate, with narrow or slightly wide and weakly coriarious interspaces (Fig. 4B); lateral lobe usually weakly punctate with coriarious or smooth interspaces along notaulus (Fig. 4C); parascutal carina broadly curved, acuminate (Fig. 4J). Mesoscutellum: apex with inner margin gradually or abruptly diverging (Fig. 4K); punctures angulate, with narrow or slightly wide and weakly coriarious interspaces. Axilla (Fig. 4F): in lateral view imbricate dorsad and rugose-areolate or carinate ventrad. Axillula (Fig. 4E): smooth dorsad. Fore wing: stigma small, 2.0–2.5 × as wide as postmarginal vein.

**Male** (Fig. 5). Length: usually smaller, 2.6–3.8 mm. As in female, except: Color: mesonotum sometimes with weak cupreous iridescence. Frontal carina (Fig. 5D): distance from lateral ocellus shorter, FCLO/LOD 0.5–0.6. Scape (Fig. 5G, H): pits sparse, covering  $0.3-0.4 \times$  scape length.

**Diagnosis.** *Perilampus hyalinus* is morphologically similar to *P. neodiprioni*, but the axillula is always smooth dorsad without piliferous punctures (Fig. 4E cf. Fig. 8E), the sculpture of the mesofemoral groove is usually smooth to weakly imbricate or rugulose (Fig. 4L, M cf. Fig. 8L, M), and the inner margins of the apex of the mesoscutellum are often abruptly diverged (Fig. 4K cf. Fig. 8K).

**Distribution** (Fig. 25A). Throughout USA and southern Canada, and possibly western Mexico: Canada (Alberta, British Columbia, Manitoba, New Brunswick, Ontario, Quebec), USA (Arizona, Colorado, Illinois, Indiana, Kansas, Maryland, Montana, New York, North Dakoda, Oklahoma, Pennsylvania, Utah, Washington, Wisconsin), Mexico (Sonora, Jalisco).

Host associations. *Perilampus hyalinus* is a hyperparasitoid, attacking dipteran parasitoids of Orthoptera and dipteran kleptoparasites of Crabronidae and Sphecidae provisioning with Orthoptera and rarely parasitoids of dipteran parasitoids attacking Phasmida (ROME204120). Hosts: Tachinidae (Diptera). *Ceracia dentata* (Coquillett) from *Melanoplus femurrubrum* (De Geer) (Acrididae). Tachinidae from Phasmatidae. Sarcophagidae (Diptera). *Sarcophaga* sp. from *Melanoplus sanguinipes* (Fabricius). Sarcophagids from Tettigoniidae and Oecanthinae collected in the nests of *Isodontia mexicana* (Saussure) (Sphecidae) (Medler 1965). *Senotainia trilineata* (Wulp) and *S. vigilans* 

Allen from nests of *Tachysphex terminatus* (Smith) and *T. validus* Cresson (Crabronidae) (Spofford and Kurczewski 1984). Possibly *Nemestrinidae* (Diptera) from *M. sanguinipes*. Unidentified Diptera from *Melanoplus differentialis* (Thomas). Unidentified parasitoid of *Orphullela* sp. (Acrididae).

**Variation.** A female from Ontario (ROME152664), Canada, has a smooth vertex. COI and ITS2 suggest that this specimen is a rare morphological variant of *P. hyalinus*.

Remarks. The identity of *P. hyalinus* has long been obscured by the presumed lost type specimen (Mawdsley 1993) and the morphological similarity of specimens exhibiting different parasitism strategies and host associations (Burks 1979). Say's (1829) original description contains neither host information nor sufficient details on morphology for determining with certainty which of the Nearctic species treated herein should be regarded as *P. hyalinus* Say. To clarify this situation a neotype is designated herein, a reared specimen collected near the original type locality (Pennsylvania) which establishes this species as a parasitoid of dipteran parasitoids and dipteran kleptoparasites associated with Orthoptera. This species is supported by molecular analyses in both genes (Fig. 1, Suppl. material 5) and there are 14 BINed specimens, including the neotype on BOLD (AEA0382) collected and reared from throughout the range of this species. Perilampus hyalinus Say is the most abundant species in collections in the eastern Nearctic region. This species is morphologically close to P. neodiprioni, and can usually be distinguished by the sculpture of its axillula dorsad and mesofemoral groove. However, these characters are not always reliable distinguishing these two species (see Remarks in P. neodiprioni). While these characters are not always reliable distinguishing these two species, they are clearly differentiated in both COI and ITS2 (Fig. 1)

### Perilampus sirsiris (Argaman)

Figs 6, 7, 24C

*Ichneumon cyaneus* Brullé, 1846:21 (Plate V, #4). Type locality: USA, "Carolina". Type material: **Holotype.** "Carolina". (Female Paris EY35408, MHNH) (images examined).

Perilampus cyaneus Dalla Torre, 1898:355 (new combination ?).

- *Perilampus hyalinus* Viereck, 1910:647 (subjective synonym *P. cyaneus* ?, cited by Peck 1963).
- *Taltonos sirsiris Argaman*, 1990:15. Replacement name, *Perilampus cyaneus* Brullé (nec Fabricius 1798).

*Perilampus sirsiris* Darling, 1996:113 (*Taltonos*, subjective synonym of *Perilampus*). *Perilampus eucyaneus* Özdikmen, 2011. Unnecessary replacement name.

**Material examined.** CANADA: 4 females, 8 males. USA: 17 females, 11 males. (Suppl. materials).

**Description. Female** (Fig. 6). Length: 2.5–4.5 mm. Color: head iridescent greenish blue or violet, usually without black coloration between lateral ocellus and frontal



Figure 6. *Perilampus sirsiris* Female A habitus, lateral view B habitus, dorsal view C lateral lobe of mesoscutum along notaulus D, E lateral panel of pronotum, posterior oblique view F parascutal carina G head, dorsal view H head, anterior view I lower face J head, lateral view K mesoscutellum apex L mesofemoral depression. [A, B, D, F, H, J, K ROME182764; E, G, L ROME189054; I ROME182766]. Scale bar: 1 mm (A).



Figure 7. *Perilampus sirsiris* Male A habitus, lateral view B lateral panel of pronotum, parascutal carina, and axilla, posterior oblique view C head, dorsal view D head, anterior view E lateral lobe of mesoscutum along notaulus F, G scape. [A ROME162278; B ROME204099; C ROME199527; D ROME162281;
F ROME152680; E ROME162281; G ROME185910]. Scale bars: 1 mm (A); 100 μm (F, G).

carina; mesosoma, and metasoma iridescent greenish blue or violet; clypeus ventral margin black (Fig. 6I); antenna with scape and pedicel weakly iridescent greenish blue or violet, flagellum brown or black, lighter ventrad and distad.

Head (Fig. 6G-J): in dorsal view transverse, width slightly greater than twice length, HW/HL 2.1-2.2. Frontal carina: in anterior view straight to weakly sinuate below midlevel of eye; in dorsal view gradually narrowed V shape around median ocellus, FC/MOD 1.5-1.9; distance from lateral ocellus short, FCLO/LOD 0.6-0.7. Scrobal cavity (Fig. 6H): in anterior view wide, SW/HW about 0.5. Ocelli (Fig. 6G): a line between anterior margin of lateral ocelli reaching anterior margin of median ocellus. POL/OOL 1.7-2.0. Ocellar ratios LOD: POL: OOL: LOL 1, 3.1-3.3, 1.6-1.9, 1.0-1.1. Vertex: with strong to weak transverse striations, without large piliferous punctures. Parascrobal area: in lateral view gradually narrowed towards lower eye margin; width narrow, PSW/EL about 0.3; sculpture strongly to weakly striate, or rarely smooth, without large piliferous punctures. Gena (Fig. 6J): entirely or mostly striate along outer eye margin with narrow and short smooth area, striate behind. Malar space: MSL/EH 0.2-0.3. Lower face (Fig. 6H, I): with setae sparse laterad torulus, and usually sparse below. Clypeus (Fig. 6I): CW/CH 1.3-1.4; ventral margin concave; setae evenly distributed, or with small bare area without setae medially.

Mesosoma (Fig. 6B - F, K, L): Lateral panel of pronotum: slightly narrower than prepectus, LPP/PPT 0.7–0.8; without flange or with small rounded flange below level of mesothoracic spiracle in posterior oblique view (Fig. 6D, E). Mesofemoral depression: usually smooth, weakly imbricate, or rugulose (Fig. 6L). Mesoscutum: punctures angulate, with narrow or slightly wide and weakly coriarious interspaces (Fig. 6B); lateral lobe weakly punctate with coriarious or smooth interspaces (Fig. 6C), or smooth, along notaulus; parascutal carina usually angulate, rarely steeply curved, often weakly flanged (Fig. 6F, arrow). Mesoscutellum: apex with inner margins gradually or abruptly diverging (Fig. 6K); punctures angulate, with narrow or slightly wide and weakly coriarious interspaces. Axilla: in lateral view imbricate dorsad and carinate or rugose-areolate ventrad. Axillula: smooth dorsad. Fore wing: stigma small, 2.0–2.5 × as wide as postmarginal vein.

**Male** (Fig. 7). Length: usually smaller, 1.7–3.8 mm. As in female, except: Color: mesonotum sometimes with weak cupreous iridescence. Frontal carina (Fig. 7C): distance from lateral ocellus shorter, FCLO/LOD 0.3–0.4. Scape (Fig. 7F. G): pits sparse, covering about 0.4 × scape length.

**Diagnosis.** *Perilampus sirsiris* and *P. arcus* are the only Nearctic species with steeply curved or angulate parascutal carina often with a flange (Fig, 6F, 7B, 20E, 21B cf. Figs 8J, 9B). *Perilampus sirsiris* differs from *P. arcus* in usually having an angulate parascutal carina (Fig. 6F cf. Fig. 20F), a flat lateral panel of pronotum or with a small rounded flange in posterior oblique view (Fig. 6D, E cf. Fig. 20D), and the male scape with sparsely pitted surface distad (Fig. 7F, G cf. Fig. 21G, H).

**Distribution (Fig. 25C).** Throughout USA and southern Canada: Canada (Ontario, Quebec, British Columbia), USA (Arkansas, Florida, Kansas, Maryland, Missouri, Montana, Oregon, Texas, West Virginia).

Host association. *Perilampus sirsiris* is a hyperparasitoid, a parasitoid of dipteran and hymenopteran parasitoids of Lepidoptera, rarely of hymenopteran parasitoids of

argid sawflies. Hosts: Tachinidae (Diptera) from *Hyphantria cunea* (Drury) (Erebidae) and *Malacosoma disstria* Hübner (Lasiocampidae). Sarcophagidae (Diptera) from *Neophasia menapia* (C. & R. Felder) (Pieridae). Braconidae (Hymenoptera). *Cotesia hyphantriae* (Riley) from *Hyphantria cunea* (Drury). Ichneumonidae (Hymenoptera) from *Arge* sp. (Hymenoptera).

**Variation.** There is a rare variant from Manitoulin Island, Ontario, a male (ROME152661) which has a wide bare area without setae on the clypeus similar to *P. monocteni*, but confirmed as *P. sirsiris* by the steeply curved parascutal carina and COI and ITS2.

Remarks. The descriptions of P. sirsiris provided in Brullé (1846) and Argaman (1990) are insufficient for species discrimination, but the holotype of this species is intact (MNHN). The images of the holotype sent by the MNHN (Fig. 24C) provided sufficient morphological details for associating the holotype with one of the common Nearctic species based on the key and redescription provided herein. Argaman's descriptions of color and pronotal flange ("Head and sides of thorax golden-green to bluish", "with a triangularly acute lobe opposite to upper top of prepectus") do not match the holotype of *P. cyaneus*. Due to the dubious nature of the type specimen listed in his annotated checklist, where he states that the holotype is in his private collection (Argaman 1991), Argaman clearly did not examine Brullé's type. It is likely that the "Types" in Argaman's checklist represent the specimens he regards as conspecifics, rather than the actual extant types (Darling 1996). We examined two additional NHMH specimens from Jalisco, Mexico misidentified as P. sirsiris by Argaman (1991), identified herein as a female P. hyalinus (ROME200751) and male P. ute (ROME200740). The only other literature record of *P. sirsiris* is Graenicher (1909), which mentions the preference of P. hyalinus and P. sirsiris for flowers of Erigeron canadensis Linnaeus. However, given the poor description of P. sirsiris by Brullé and the absence of an indication that Graenicher had examined the type, it is unclear if the observed species was indeed P. sirsiris.

The steeply curved or angulate parascutal carina often with a flange (Figs 6F, 7B) is one of the key diagnostic features of *P. sirsiris. Perilampus arcus* (Figs 20E, 21B) also has a similarly modified parascutal carina, but the phylogenetic placement of the two species (Fig. 1) suggests convergent evolution within the *P. hyalinus* species complex. This state is also widely distributed in other species of Perilampidae, including some species of the *P. platigaster* species group, and is almost certainly derived independently. Both genes and species delimitation methods support *P. sirsiris* (Fig. 1, Suppl. material 5) and there are 10 BINed specimens on BOLD (AEM7685) from throughout the range of this species (Quebec to Texas) and one specimen (ROME185904, Missouri) with a COI sequence reared from *Hyphantia cunea*.

*Perilampus sirsiris* parasitizes dipteran and hymenopteran parasitoids of Lepidoptera, which feed on the leaves of deciduous trees. Interestingly, the hosts of *P. sirsiris* also include sarcophagid parasitoids of the pine butterfly, *N. menapia* (Pieridae)—this is the only species associated with pines other than *P. neodiprioni*, the hypothesized sister species of *P. sirsiris* (Fig. 1) (see Remarks for *P. neodiprioni* below).

### Perilampus neodiprioni Yoo & Darling, sp. nov.

https://zoobank.org/E1D68A20-14BD-4FAE-864E-99E9FE508E38 Figs 8, 9

Type locality. Canada, Ontario, Haliburton County.

**Type material.** *Holotype.* "CANADA: ONT. Haliburton Hwy 16, 3.8 m. E. Minden Ex: *Neodiprion lecontei* in red pine plantation. VIII.28.93. DC Darling", "Lab Reared 1994 S. Perlman M.Sc. thesis", "BOLD COI-5P Sequence, 325bp". The holotype is card-mounted (Female ROME183975, ROM). ROM Online Collection.

*Paratypes.* CANADA: 3 males. Ontario: 3 males. Nipissing Dist., Algonquin P.P., Cameron Road: (3 males: ROME152669-CNC; BOLD:AEE8879; ITS2; ROME152668-ROME; BOLD:AEE8879; ITS2; ROME183971-ROME; BOLD:AEE8879). USA: 1 female, 2 males. Massachusetts: 1 female, 2 males. Franklin Co., Montague, Montague Plains WMA: (1 female: ROME162273-USNM; BOLD:AEE8879; ITS2. 2 males: ROME162275-ROME; BOLD:AEE8879; ITS2; ROME162274-USNM; BOLD:AEE8879; ITS2).

**Material examined.** CANADA: 79 females, 97 males. USA: 36 females, 33 males. (Suppl. materials).

Additional material examined. Belize: 9 females, 4 males. Stann Creek District: 9 females, 4 males. 4 1/2 mis., Stann Creek Valley: (4 females: ROME185928-USNM; ROME185929-USNM; ROME199572-USNM; ROME199573-USNM. 1 male: ROME185926-USNM); 5 1/2 mi Stann Creek Valley: (1 male: ROME201411-FSCA); Stann Creek Valley: (5 females: ROME185927-USNM; ROME199574-USNM; ROME199575-USNM; ROME199576-USNM; ROME199578-USNM. 2 males: ROME199571-USNM; ROME199577-USNM).

**Etymology.** The specific epithet is a noun in the genitive case meaning "of *Neodiprion*", in reference to the species' predilection for pine sawflies and their primary parasitoids.

**Description. Female** (Fig. 8). Length: 3.5–5.0 mm. Color: head iridescent greenish blue or violet, usually without black coloration between lateral ocellus and frontal carina; mesosoma, and metasoma iridescent greenish blue or violet; clypeus ventral margin black (Fig. 8I); antenna with scape and pedicel weakly iridescent greenish blue or violet, flagellum brown or black, lighter ventrad and distad.

Head (Fig. 8G–I): in dorsal view transverse, width slightly greater than twice length, HW/HL 2.1–2.2. Frontal carina: in anterior view straight to weakly sinuate below midlevel of eye; in dorsal view gradually narrowed V shape around median ocellus, FC/MOD 1.5–1.9; distance from lateral ocellus short, FCLO/LOD 0.6–0.7. Scrobal cavity: in anterior view wide, SW/HW about 0.5. Ocelli (Fig. 8G): a line between anterior margin of lateral ocelli reaching anterior margin of median ocellus or nearly bisecting median ocellus. POL/OOL 1.8–2.0. Ocellar ratios LOD: POL: OOL: LOL 1, 3.0–3.3, 1.6–1.8, 1.1–1.4. Vertex: with strong to weak transverse striations, without large piliferous punctures. Parascrobal area: in lateral view gradually narrowed towards lower eye margin; width narrow, PSW/EL about 0.3; sculpture strongly to weakly striate, rarely smooth, without large piliferous punctures. Gena: entirely or mostly stri-

ate along outer eye margin with narrow and short smooth area, striate behind. Malar space: MSL/EH 0.2–0.3. Lower face (Fig. 8H, I): with setae sparse laterad torulus, and usually sparse below. Clypeus (Fig. 8I): CW/CH 1.3–1.4; ventral margin concave; setae evenly distributed, or with small bare area without setae medially.

Mesosoma (Fig. 8B–F, J–M): Lateral panel of pronotum: slightly narrower than or about as wide as prepectus, LPP/PPT 0.7–0.9; without flange or with small rounded flange below level of mesothoracic spiracle in posterior oblique view (Fig. 8D). Mesofemoral depression: imbricate-alveolate (Fig. 8L, M), or weakly imbricate, rugulose, or smooth. Mesoscutum: punctures angulate, with narrow or slightly wide and weakly coriarious interspaces (Fig. 8B); lateral lobe usually weakly punctate with coriarious interspaces along notaulus (Fig. 8C); parascutal carina broadly curved, acuminate (Fig. 8J). Mesoscutellum: apex with inner margins gradually diverging (Fig. 8K), rarely rounded; punctures angulate, with narrow or slightly wide and weakly coriarious interspaces. Axilla: in lateral view imbricate dorsad and rugose-areolate (Fig. 8F) or carinate ventrad. Axillula (Fig. 8E): usually with one or more piliferous punctures dorsad. Fore wing: stigma small, 2.0–2.5 × as wide as postmarginal vein.

**Male** (Fig. 9). Length: usually smaller, 2.7-3.8 mm. As in female, except: Color: mesonotum sometimes with weak cupreous iridescence. Frontal carina (Fig. 9D): distance from lateral ocellus shorter, FCLO/LOD 0.5–0.6. Scape (Fig. 9G, H): pits sparse, covering  $0.3-0.4 \times$  scape length.

**Diagnosis.** *Perilampus neodiprioni* can usually be distinguished by an axillula with one or more piliferous punctures dorsad (Fig. 8E cf. Fig. 4E). The specimens with a smooth axillula are most similar to *P. hyalinus*, but can often be differentiated by the strongly imbricate to imbricate-alveolate sculpture of the mesofemoral depression (Fig. 8L, M cf. Fig. 4L, M); and the gradually diverging inner margins of the apex of the mesoscutellum (Fig. 8K cf. Fig. 4K).

**Distribution (Fig. 25B).** South-eastern Canada and central and eastern USA: Canada (Ontario, Quebec), USA (Arkansas, Florida, Illinois, Massachusetts, Michigan, New York, North Carolina, Texas, Virginia, West Virginia, Wisconsin). Possibly Belize (Stan Creek District).

Host association. Perilampus neodiprioni can develop as a primary parasitoid attacking Neodiprion sawflies (Fig. 26B), or as a hyperparasitoid that parasitizes dipteran (Fig. 26D) and hymenopteran parasitoids of Neodiprion sawflies (Fig. 26C, E). Hosts: Diprionidae (Hymenoptera). Neodiprion pratti banksianae Rohwer. Neodiprion excitans Rohwer. Neodiprion lecontei (Fitch). Neodiprion merkeli Ross. Neodiprion pinetum (Norton). Neodiprion rugifrons Middleton. Neodiprion swainei Middleton Neodiprion virginianus Rohwer. Tachinidae (Diptera). Vibrissina spinigera (Townsend) from N. swainei (Tripp 1962). Tachinids from N. lecontei and N. virginianus Ichneumonidae (Hymenoptera). Olesicampe lophyri (Riley) and Endasys subclavatus (Say) from N. swainei (Tripp 1962). Ichneumonids from N. lecontei.

**Remarks.** Both COI and ITS2 support *P. neodiprioni* as a distinct species (Fig. 1, Suppl. material 5). There are 10 BINed specimens on BOLD (AEE8879) collected from the eastern and central Nearctic region north of Mexico, most of which are reared from



Figure 8. *Perilampus neodiprioni* Female A habitus, lateral view B habitus, dorsal view C lateral lobe of mesoscutum along notaulus D lateral panel of pronotum, posterior oblique view E axillula F axilla G head, dorsal view H head, anterior view I clypeus J parascutal carina K mesoscutellum apex L, M mesofemoral depression. [A–E, G, H, J, L Paratype, ROME162273; F, M Paratype, ROME198146; I ROME181757; K ROME189061]. Scale bar: 1 mm (A).



Figure 9. Perilampus neodiprioni Male A habitus, lateral view B lateral panel of pronotum, parascutal carina, and axilla C head, anterior view D head, dorsal view E lower face F lateral lobe of mesoscutum along notaulus G, H scape. [A–D, F Paratype, ROME162274; E ROME185922; G ROME152634; H Paratype, ROME97556]. Scale bars: 1 mm (A); 100 μm (G, H).

Diprionidae that feed on pine trees. There are no completely reliable morphological characters to distinguish *P. neodiprioni* from *P. hyalinus* Say, the hyperparasitoids associated with Orthopteroidea. Imbricate-alveolate sculpture on the mesofemoral groove are found only in *P. neodiprioni*, but weakly imbricate, rugose, or smooth sculpture of mesofemoral groove are found in both species. Likewise, mesoscutellar teeth at the apex with steeply diverging inner margins are found only in *P. hyalinus*, but gradually diverging inner margins are found in both species. The presence of one or more piliferous punctures on axillula dorsad is a unique state found only in *P. neodiprioni* in the *P. hyalinus* species group. But its diagnostic value is somewhat limited because the axillula is punctate in 72% and smooth in 28% of the total studied specimens (n = 188). And the proportion of specimens with punctate axillula seems to show geographical variation: 84% of 136 specimens in the northeastern USA and southeastern Canada, fewer than half in the central USA (9 of 20) and Florida (7 of 25), and all the specimens from Belize (17) are punctate.

Genetic analysis suggests there are at least two distinct COI clades of *P. neodiprioni* in the Nearctic region: Ontario and Massachusetts; and Virginia, West Virginia, and Texas (Suppl. material 2). However, these COI clades are delimited as a single species by the distance-based methods (Suppl. material 5). The geographical distribution of each clade coincides with the post-glacial re-colonization pathways of *N. lecontei* populations from the Atlantic coast and Texas refugia (Bagley et al. 2016). This pattern is likely an indication of the fragmentation and genetic differentiation of *P. neodiprioni* populations during glaciation, and eventual post-glacial range expansion of parasitoids following their recolonizing sawfly hosts prior to secondary contact. ITS2 showed no genetic differentiation between the populations and both distance- and tree-based methods merged both populations as a single species (Suppl. materials 2, 5). This probably represents active interbreeding between the P. neodiprioni populations, which would result in full recombination of nuclear DNA, whereas the variation of nonrecombinant COI accumulated during isolation was retained after secondary contact (Després 2019). Sequencing of Floridan specimens could reveal if there is a third distinct population of *P. neodiprioni* originated from the proposed southern glacial refugia near North and South Carolina that expanded their distribution with the sawfly hosts toward Florida (Bagley et al. 2016). The Belize specimens failed to sequence, and their potential genetic differentiation is yet to be explored. Specimens from Ontario and Massachusetts, which form one of the two COI clades, were selected as the type series.

*Perilampus neodiprioni* is the only species in the *P. hyalinus* species complex that exhibits an exclusive association with pine sawflies, more commonly as a primary parasitoid but also as a hyperparasitoid. An exception is a single *P. neodiprioni* specimen reared from *Diprion similis* (Hartig) in Ontario (ROME207314), but it lacks associated host remains and the collector had noted the uncertainty in their identification in the collection form. While it isn't surprising that *P. neodiprioni* can develop on *D. similis*, this sawfly species is non-native in the Nearctic region and not relevant to the evolutionary history of *P. neodiprioni*.

A large number of *P. neodiprioni* specimens were reared from *Neodiprion lecontei* cocoons in the 1940s at the Dominion Parasite Laboratory (DPL) in Belleville, Ontar-
io and subsequently transferred to the CNC. The 230 reared *P. neodiprioni* specimens are predominantly primary parasitoids (215) and only 15 are hyperparasitoids, 14 parasitoids of Ichneumonidae and one parasitoid of Tachinidae. The reared specimens from the other localities are also comprised of mostly primary parasitoids. Of the total 62 reared *P. neodiprioni* specimens associated with pine sawfly cocoons, 49 are primary parasitoids of *Neodiprion* spp., 13 are hyperparasitoids, of which 11 are parasitoids of Ichneumonidae and two are parasitoids of Tachinidae. There are however, two reared series that are only or mostly hyperparasitoids: Masschusetts (ROME162273-162275, 3 of 3) and Arkansas (ROME152640–152643, 185915, 185916, and 185956, 6 of 7). Tripp (1962) and Wilkinson (1966) also documented Perilampus developing as both primary and hyperparasitoids associated with pine sawflies. It is unclear if P. neodiprioni can develop as hyperparastioids of the other primary parasitoids of pine sawflies with equal success. For example, Tripp (1962) and Hinks (1971) reported rare to no cases of Perilampus developing as hyperparasitoid on Diptera, but Wilkinson (1966) reported predominance of hyperparasitoids on Diptera. Reared specimens examined in this study show that it is rarer for *P. neodiprioni* to develop on dipteran parasitoids than on hymenopteran parasitoids in both the DPL collection (0.4% vs 6%) and from other localities (3.2% vs 17.7%).

*Neodiprion* species are often serious pests in boreal forests (Alfaro and Fuentealba 2016; Johns et al. 2016) which suggests that *P. neodiprioni* could be an effective biological control agent, but this is complicated because this species can develop both as a primary parasitoid and as a hyperparasitoid. Evaluation of the biocontrol potential of *P. neodiprioni* will depend on the relative prevalence of other hymenopteran and dipteran primary parasitoids and their effectiveness as biological control agents —*P. neodiprioni* as a hyperparasitoid could interfere with the population dynamics of these strictly primary parasitoids (Schooler et al. 2011).

The shift in ecology from hyperparasitoid associated with Lepidoptera to primary or hyperparasitoid associated with pine sawflies is suggested by the sister species relationship between *P. neodiprioni* and *P. sirsiris* (Suppl. material 1), and their associations with pine trees. *Perilampus sirsiris* is the only known hyperparasitoid in the *P. hyalinus* species complex that is associated with gymnosperms as well as angiosperms. It is possible that the common ancestor of *P. neodiprioni* and *P. sirsiris* was a hyperparasitoid species which expanded the oviposition sites to include pines, where planidia would have encountered both Lepidoptera caterpillars and *Neodiprion* larvae. Pine sawfly larvae were likely suitable hosts for planidia that inadvertently burrowed into this novel host, driving the evolution of parasitoid capable of developing as a primary parasitoid of *Neodiprion* sawflies.

*Perilampus monocteni* Yoo & Darling, sp. nov. https://zoobank.org/296E0AB0-1E13-42EE-AE4E-27444553C977 Figs 10, 11

Type locality. Canada, Ontario, Peterborough County, Aspley.

**Type material.** *Holotype.* "CANADA, Ontario, Aspley No. S64-3469-01, 22.III. 1965 Ex. *Monoctenus juniperinus* On e.w. cedar, Lot 65.418". The *Monoctenus* associated with the holotype was later re-identified as *M. fulvus* (Kevin Barber, personnel communication). The holotype is point-mounted (Female ROME201079, CNC). ROM Online Collection.

*Paratypes.* CANADA: 7 females, 2 males. Ontario: 7 females, 2 males. City of Ottawa., Bells Corners: (5 females: ROME207334-CNC; ROME207332-GLFC; ROME207333-GLFC; ROME207331-ROME; ROME207335-USNM. 2 males: ROME207329-CNC; ROME207328-ROME). Haliburton Co., Haliburton: (1 female: ROME207336-CNC). Peterborough Co., Apsley: (1 female: ROME201078-CNC).

Additional material examined. CANADA: 1 female, 1 male. Ontario: 1 female, 1 male. City of Ottawa., Bells Corners: (1 male: ROME207330-CNC). Renfrew Co., Beachburg: (1 female: ROME201101-CNC).

**Etymology.** The specific epithet is a noun in the genitive case meaning "of *Monoctenus*", in reference to the species' host preference for *Monoctenus* sawflies and their parasitoids.

**Description. Female** (Fig. 10). Length: 2.1–3.8 mm. Color: head iridescent greenish blue or violet; mesosoma and metasoma iridescent greenish blue or violet; clypeus ventral margin black (Fig. 10I, J); antenna with scape and pedicel weakly iridescent greenish blue or violet, flagellum brown or black, lighter ventrad and distad.

Head (Fig. 10G–J): in dorsal view transverse, width slightly greater than twice length, HW/HL 2.1–2.2. Frontal carina: in anterior view straight to weakly sinuate below midlevel of eye; in dorsal view gradually narrowed V shape around median ocellus, FC/MOD 1.5–1.6; distance from lateral ocellus short, FCLO/LOD 0.6–0.7. Scrobal cavity: in anterior view wide, SW/HW about 0.5. Ocelli (Fig. 10G): a line between anterior margin of lateral ocelli reaching anterior margin of median ocellus. POL/ OOL 1.8–2.0. Ocellar ratios LOD: POL: OOL: LOL: 1, 2.9–3.4, 1.8–2.0, 1.0–1.2. Vertex: with strong to weak transverse striations, without large piliferous punctures. Parascrobal area: in lateral view gradually narrowed towards lower eye margin; width narrow, PSW/EL about 0.3; sculpture strongly to weakly striate, without large piliferous punctures. Gena: entirely or mostly striate along outer eye margin with narrow and short smooth area, striate behind. Malar space: MSL/EH about 0.2. Lower face (Fig. 10H, I, J): with setae sparse laterad torulus, and sparse below. Clypeus (Fig. 10I, J): CW/CH 1.4–1.5; ventral margin concave; with wide bare area without setae near dorsal margin, extended ventrad medially.

Mesosoma (Fig. 10B–F, K, L): Lateral panel of pronotum: about as wide as prepectus, LPP/PPT 0.8–0.9; without flange or with small rounded flange below level of mesothoracic spiracle in posterior oblique view (Fig. 10D). Mesofemoral depression: smooth (Fig. 10L), weakly imbricate, or rugulose. Mesoscutum: punctures angulate, with narrow or slightly wide and weakly coriarious interspaces (Fig. 10B); lateral lobe usually weakly punctate with coriarious or smooth interspaces along notaulus (Fig. 10C); parascutal carina broadly curved, acuminate (Fig. 10E). Mesoscutellum: apex



Figure 10. *Perilampus monocteni* Female A habitus, lateral view B habitus, dorsal view C lateral lobe of mesosucutm along notaulus D lateral panel of pronotum, posterior oblique view E parascutal carina F axilla G head, dorsal view H head, anterior view I, J clypeus K mesoscutellum apex L mesofemoral depression. [A, B, D, K Paratype, ROME201078; C Paratype, ROME207336; E, J, L Holotype, ROME201079; F Paratype, ROME207331; G–I Paratype, ROME207334]. Scale bar: 1 mm (A).



**Figure 11.** *Perilampus monocteni* Male **A** habitus, lateral view **B** lateral panel of pronotum, parascutal carina **C** head, anterior view **D** head, dorsal view **E**, **F** clypeus **G**, **H** scape. [**A–C**, **E**, **G** Paratype, ROME207328 **D**, **F**, **H** Paratype, ROME207329]. Scale bars: 1 mm (**A**); 100 μm (**G**, **H**).

with inner margins gradually diverging (Fig. 10K); punctures angulate, with narrow or slightly wide and weakly coriarious interspaces. Axilla: in lateral view imbricate dorsad, and rugose-areolate (Fig. 10F) or carinate ventrad. Axillula: smooth dorsad. Fore wing: stigma small,  $2.0-2.5 \times as$  wide as postmarginal vein.

**Male** (Fig. 11). Length: usually smaller, 2.7–2.9 mm. As in female, except: Color: mesonotum sometimes with weak cupreous iridescence. Frontal carina (Fig. 11D): distance from lateral ocellus shorter, FCLO /LOD 0.3–0.4. Scape (Fig. 11G, H): pits sparse, covering about  $0.4 \times$  scape length.

**Diagnosis.** *Perilampus monocteni* can be distinguished by a clypeus with a wide and bare area without setae near the dorsal margin, which is extended ventrad medially (Figs 10I, J, 11E, F cf. Figs 4I, 5E).

### Distribution (Fig. 25B). Eastern Canada (Ontario).

Host association. *Perilampus monocteni* can develop as a primary parasitoid of cedar sawflies (Fig. 26G), or as a hyperparasitoid, a parasitoid of dipteran parasitoids of cedar sawflies (Fig. 26H). Hosts: Diprionidae (Hymenoptera). *Monoctenus fulvus* (Norton), *M. suffusus* (Cresson). Tachinidae (Diptera). Tachinids from *M. suffusus*.

**Variation.** A female and male reared from *Monoctenus* spp. have slight variations in the clypeal setae. One has two setae on the mostly bare area of the clypeus dorsad (ROME201101), and the other lacks a distinctive bare area on clypeus dorsad (ROME207330). The host records and absence of diagnostic characters specific to the other species suggest that these two specimens are *P. monocteni*.

Remarks. The available specimens of *P. monocteni* are unsuitable for the sequencing method used in this study. Despite the lack of genetic data, the species hypothesis of *P. monocteni* is supported by the distinctive setal distribution pattern on the clypeus and a unique host association. Perilampus monocteni is a paraisitoid strictly associated with Diprionidae similar to P. neodiprioni. However, P. monocteni parasitizes cedar sawflies and their parasitoids, unlike P. neodiprioni which parasitizes pine sawflies and their parasitoids. Of the total six specimens associated with Monoctenus cocoons, three were primary parasitoids of cedar sawflies (ROME207330, 207332, and 207336) and three were hyperparasitoids that parasitized dipteran parasitoids of cedar sawflies. (ROME207328, 207333, and 207335). The known distribution is restricted to eastern Ontario but this may be due to the solitary larval feeding behaviour of Monoctenus spp. (Rose et al. 2010)-in comparison, many Neodiprion spp. are characterized by gregarious larval feeding behaviour (Haack and Mattson 1993) and more conspicuous and more often collected. The combination of sparse pits on a male scape, the lack of a triangular flange on the lateral panel of pronotum, and the female mesoscutum without strong cupreous iridescence suggest that P. monocteni is clearly a member of the P. hyalinus complex clade 2 but its precise phylogenetic placement needs to be determined with genetic data. But if the parasitism associated with conifer-feeding sawflies was derived only once in the P. hyalinus species complex, P. monocteni is probably the sister species of *P. neodiprioni*, which is also a member of clade 2.

#### Perilampus crassus Yoo & Darling, sp. nov.

https://zoobank.org/54557ED2-7D2D-424A-9D8F-519098A2470D Figs 12, 13

#### Type locality. USA, Florida, Gainesville.

**Type material.** *Holotype.* "USA: FL: Alachua Co.: nr. Gainesville airport, 45 m 29°42'0"N, 82°15'40"W 2.Oct.2016 A. Baker, A. Knyshov, J. Zhang swp AB16.028". The holotype is point-mounted (Female ROME182771, UCRC). BOLD:AEE9250/ ITS2. ROM Online Collection.

*Paratypes.* USA: 1 female, 2 males. Florida: 1 female, 2 males. Putnam Co., Ordway-Swisher Biol. Station, Rd. C6: (1 female: ROME189115-MCZC; BOLD:AEE9250; ITS2. 2 males: ROME189062-MCZC; ITS2; ROME189063-MCZC; BOLD:AEE9250; ITS2).

Material examined. USA: 9 females, 4 males. (Suppl. materials).

Additional material examined. CUBA: 1 female. (1 female: ROME189093–USNM).

**Etymology.** The specific epithet is the Latin adjective *crassus* (coarse), in reference to the punctate sculpture on the lateral lobes of the mesoscutum along notaulus.

**Description. Female** (Fig. 12). Length: 3.0–4.8 mm. Color: head iridescent greenish blue or violet; mesosoma and metasoma iridescent greenish blue or violet; clypeus ventral margin entirely iridescent (Fig. 12I); antenna with scape and pedicel weakly iridescent greenish blue or violet, flagellum brown or black, lighter ventrad and distad.

Head (Fig. 12G–J): in dorsal view transverse, width slightly greater than twice length, HW/HL 2.1–2.2. Frontal carina: in anterior view straight to weakly sinuate below midlevel of eye; in dorsal view gradually narrowed V shape around median ocellus, FC/MOD 1.5–1.7; distance from lateral ocellus short, FCLO/LOD 0.6–0.7. Scrobal cavity: in anterior view wide, SW/HW about 0.5. Ocelli (Fig. 12G): a line between anterior margin of lateral ocelli reaching anterior margin of median ocellus or nearly bisecting median ocellus. POL/OOL 1.7–2.1. Ocellar ratios LOD: POL: OOL: LOL 1, 3.1–3.4, 1.5–1.9, 1.1–1.3. Vertex: with strong to weak transverse striations, without large piliferous punctures. Parascrobal area: in lateral view gradually narrowed towards lower eye margin; width narrow, PSW/EL about 0.3; sculpture strongly to weakly striate, without large piliferous punctures. Gena (Fig. 12J): entirely striate along outer eye margin, striate posterad. Malar space: MSL/EH 0.2–0.3. Lower face (Fig. 12H, I): with setae sparse laterad torulus, and usually sparse below. Clypeus: CW/CH about 1.4; ventral margin nearly straight; setae evenly distributed, or with small bare area without setae medially.

Mesosoma (Fig. 12B–F, K, L): Lateral panel of pronotum: about as wide as prepectus, LPP/PPT about 0.9; without flange below level of mesothoracic spiracle in posterior oblique view (Fig. 12D). Mesofemoral depression: smooth, rugulose, weakly imbricate, or imbricate-alveolate (Fig. 12L). Mesoscutum: punctures angulate, with narrow or slightly wide and weakly coriarious interspaces (Fig. 12B); lateral lobe strongly punctate with coriarious or smooth interspaces along notaulus (Fig. 12C); parascutal



Figure 12. Perilampus crassus Female A habitus, lateral view B habitus, dorsal view C lateral lobe of mesoscutum along notaulus D lateral panel of pronotum, posterior oblique view E parascutal carina F axilla G head, dorsal view H head, anterior view I lower face J head, lateral view K mesoscutellum apex L mesofemoral depression. [A–H, J, L Holotype, ROME182771 I Paratype, ROME189085 K Paratype, ROME189115]. Scale bar: 1 mm (A).



**Figure 13.** *Perilampus crassus* Male **A** habitus, lateral view **B** lateral panel of pronotum, parascutal carina, and axilla, posterior oblique view **C** head, anterior view **D** head, dorsal view **E** lower face **F** lateral lobe of mesoscutum along notaulus **G**, **H** scape. [**A**, **B**, **G** Paratype, ROME189063; **C**, **E**, **F** Paratype, ROME189062; **H** Paratype, ROME189117]. Scale bars: 1 mm (**A**); 100 µm (**G**, **H**).

carina broadly curved, acuminate (Fig. 12E). Mesoscutellum: apex with inner margins gradually or abruptly diverging (Fig. 12K); punctures angulate, with narrow or slightly wide and weakly coriarious interspaces. Axilla: in lateral view imbricate dorsad and rugose-areolate (Fig. 12F) or carinate ventrad. Axillula: smooth dorsad. Fore wing: stigma small,  $2.0-2.5 \times as$  wide as postmarginal vein.

**Male** (Fig. 13). Length: usually smaller, 3.0-3.8 mm. As in female, except: Frontal carina (Fig. 13D): distance from lateral ocellus as wide or shorter, FCLO/LOD 0.5-0.6. Scape (Fig. 13G, H): pits sparse, covering about  $0.3 \times$  scape length.

**Diagnosis.** *Perilampus crassus* can be distinguished by a weakly iridescent and nearly straight ventral margin of clypeus (Figs 12I, 13E cf. Figs 8I, 18I). Also, the lateral lobe of mesoscutum is more strongly punctate along the notaulus than in the other species with punctate sculpture (Figs 12C, 13F cf. Figs 4C, 5F, 8C, 9F).

**Distribution (Fig. 25A).** Central and southern USA: USA (Arkansas, Florida, Kansas, New Mexico, Texas). Possibly Cuba.

Host association. Hosts unknown.

**Remarks.** This species is supported by both genes (Fig. 1, Suppl. material 5), and there are three BINed specimens on BOLD (AEE9250) from Florida. Only specimens from Florida were successfully sequenced and the degree of intraspecific genetic variability in this species is unclear. A single specimen collected from avocado fruit imported from Cuba (ROME189093) suggests that the distribution of *P. crassus* extends to the Greater Antilles.

## Perilampus pilosus Yoo & Darling, sp. nov.

https://zoobank.org/1C7022C2-2C90-4627-BF19-CF0C558ACC3D Figs 14, 15

Type locality. USA, Texas, 3.5 mi SE La Sauceda.

**Type material.** *Holotype.* "USA, Texas, Presidio Co. Big Bend Ranch SNA McGuirks Tanks on desert willows 12.V.1990, R Wharton". The holotype is point-mounted (Female ROME182765, TAMU). BOLD:AEF0151/ITS2. ROM Online Collection.

*Paratypes.* USA: 3 females, 3 males. Arizona: 2 females. Graham Co., Pinaleno Mountains, Ash Creek near Cluff Ranch Wildlife Area, 14 km SW Pima, 32°47.69'N, 109°51.42'W: (1 female: ROME152679-CNC; ITS2). Pinaleno Mountains, Gilespie Wash, 10 km W Jct. 191 on hwy 266, 32°33'91"N, 109°45'59"W: (1 female: ROME182819-USNM; BOLD:AEF0151). California: 1 female, 1 male. San Bernardino Co., Joshua Tree N.P., 29 Palms, JTNP, Oasis of Mara, 34°07'42"N, 116°02'19"W: (1 female: ROME189067-UCRC; COI; ITS2. 1 male: ROME189068-UCRC; BOLD:AEF0151; ITS2). Texas: 2 males. Presidio Co., Big Bend Ranch SNA, McGuirks Tanks: (1 male: ROME182761-TAMU; BOLD:AEF0151; ITS2). Big Bend Ranch SNA, McGuirks Tanks, 29°28'34"N, 103°49'12"W: (1 male: ROME182757-TAMU; BOLD:AEF0151; ITS2).



Figure 14. *Perilampus pilosus* Female A habitus, lateral view B habitus, dorsal view C lateral lobe of mesoscutum along notaulus D lateral panel of pronotum, posterior oblique view E parascutal carina F axilla G head, dorsal view H head, anterior view I lower face J head, lateral view K mesoscutellum apex L mesofemoral depression. [A, H Holotype, ROME182765; B, C, E–G, L Paratype, ROME182819; I, J Paratype, ROME189067; K ROME189129; L Paratype, ROME152679]. Scale bar: 1 mm (A).



**Figure 15.** *Perilampus pilosus* Female **A** habitus, dorsal view. Male **B** habitus, lateral view **C** head, anterior view **D** head, dorsal view **E** lower face **F**, **G** scape. [**A** Paratype, ROME189067; **B** Paratype, ROME152727; **C**, **D**, **F** Paratype, ROME182757; **E** Paratype, ROME152714; **G** Paratype, ROME152725]. Scale bars: 1 mm (**B**); 100 μm (**F**, **G**).

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**Material examined.** MEXICO: 5 females. USA: 19 females, 29 males. (Suppl. materials).

Additional material examined. MEXICO: 1 female. Sonora: 1 female. (1 female: ROME189096-UCDC).

**Etymology.** The specific epithet is the Latin adjective *pilosus* (hairy), in reference to the densely setose face.

**Description. Female** (Figs 14, 15A). Length: 3.0–4.4 mm. Color: head, mesosoma, and metasoma iridescent greenish blue or violet with or without weak cupreous mesonotum (Fig. 14B), or iridescent green with strong cupreous mesonotum (Fig. 15A); clypeus ventral margin black (Fig. 14I); antenna with scape and pedicel weakly iridescent greenish blue or violet, flagellum brown or black, lighter ventrad and distad.

Head (Fig. 14G–J): in dorsal view transverse, width slightly greater than twice length, HW/HL 2.1–2.2. Frontal carina: in anterior view straight to weakly sinuate below midlevel of eye; in dorsal view gradually narrowed V shape around median ocellus, FC/MOD 1.5–1.9; distance from lateral ocellus short to long FCLO/LOD 0.6–1.0. Scrobal cavity (Fig. 14H): in anterior view wide, SW/HW about 0.5. Ocelli (Fig. 14G): a line between anterior margin of lateral ocelli nearly bisecting median ocellus or reaching posterior margin of median ocellus. POL/OOL 1.8–2.0. Ocellar ratios LOD: POL: OOL: LOL 1, 2.9–3.5, 1.6–1.8, 1.1–1.4. Vertex: with strong to weak transverse striations, without large piliferous punctures. Parascrobal area: in lateral view gradually narrowed towards lower eye margin; width narrow, PSW/EL 0.2–0.3; sculpture strongly to weakly striate, without large piliferous punctures. Gena (Fig. 14J): entirely striate along outer eye margin, striate posterad. Malar space: MSL/ EH about 0.2. Lower face (Fig. 14H, I): with setae dense and widely distributed laterad torulus, and dense below. Clypeus (Fig. 14I): CW/CH 1.4–1.5; ventral margin concave; setae evenly distributed, or with small bare area without setae medially.

Mesosoma (Fig. 14B–F, K, L): Lateral panel of pronotum: about as wide as prepectus, LPP/PPT 0.8–0.9; without flange below level of mesothoracic spiracle in posterior oblique view (Fig. 14D). Mesofemoral depression: smooth or weakly imbricate (Fig. 14L). Mesoscutum: punctures angulate, with narrow or slightly wide and weakly coriarious interspaces (Fig. 14B); lateral lobe smooth or weakly coriarious along notaulus (Fig. 14C); parascutal carina broadly curved, acuminate (Fig. 14E). Mesoscutellum: apex with inner margins gradually diverging (Fig. 14K); punctures angulate, with narrow or slightly wide and weakly coriarious interspaces. Axilla (Fig. 14F): in lateral view imbricate dorsad and rugose-areolate or carinate ventrad. Axillula: smooth dorsad. Fore wing: stigma small, 2.0–2.5 × as wide as postmarginal vein.

**Male** (Fig. 15B–G). Length: usually smaller, 2.3–3.1 mm. As in female, except: Color: mesonotum with strong or weak cupreous iridescence. Frontal carina: distance from lateral ocellus as wide or shorter, FCLO/LOD 0.5–0.6. Scape: pits sparse, covering  $0.3-0.4 \times$  scape length.

**Diagnosis.** *Perilampus pilosus* can be distinguished by the combination of an advanced median ocellus (Figs 14G, 15D cf. Figs 8G, 9D), dense and widely distributed setae on the face (Figs 14H, 15C cf. Figs 8H, 9C), lateral panel of the pronotum with-

out a flange (Fig. 14D cf. Fig. 16D), and the sparsely pitted male scape (Fig. 15F, G cf. Fig. 17G, H). *Perilampus pilosus* specimens with cupreous mesonota are superficially similar to *P. sonora* (Fig. 15A cf. Fig. 22B) but differ in having dense setae laterad of the torulus (Figs 14I, 15E cf. Figs 22I, 23E).

**Distribution (Fig. 25F).** Southwestern and central USA, and western and southern Mexico: USA (California, New Mexico, Texas), Mexico (Baja California Sur, Morelos, Sonora).

Host association. *Perilampus pilosus* is a hyperparasitoid, parasitizing dipteran parasitoids of Lepidoptera. Hosts: Tachinidae (Diptera). *Chaetogena* sp. from *Hemileuca juno* Packard (Saturniidae).

**Variation.** A female from Sonora, Mexico (ROME189096) has the frontal carina close to the lateral ocellus (FCLO/OD about 0.5) and iridescent olivaceous head.

**Remarks.** This species is supported by both genes (Fig. 1, Suppl. material 5), and there are five BINed specimens on BOLD (AEF0151) from the western and central USA. All specimens except (ROME189067) are grouped as a monophyletic clade in COI (Suppl. material 2). The low COI sequence quality in ROME189067 likely caused its exclusion from the monophyletic clade as evidenced by poor peak shapes in a chromatogram. All specimens including ROME189067 are grouped as monophyletic with both ITS2 and concatenated datasets (Fig. 1, Suppl. material 2).

#### Perilampus seneca Yoo & Darling, sp. nov.

https://zoobank.org/B7D5FBA5-DA48-498D-A32A-C393A3B62404 Figs 16, 17

Type locality. Canada, Ontario, Chaffey's Locks.

**Type material.** *Holotype.* "CANADA, ONT: Frontenac Co., Chaffey's Locks Oct. 6, 1987 DC Darling. Ex: birch", "LAB REARED Ex: tachinid parasite of Hyphantria cunea". The holotype is point-mounted (Female ROME183977, ROME). BOLD:ACF3436. ROM Online Collection.

*Paratypes.* CANADA: 1 male. Ontario: 1 male. Essex Co., Windsor: (1 male: ROME162263-ROME; BOLD:ACF3436; ITS2). USA: 5 females, 1 male. Indiana: 1 female. Posey Co., Harmonie State Park: (1 female: ROME182769-TAMU; BOLD:ACF3436; ITS2). Kentucky: 1 female, 1 male. Jessamine Co., S. of Nicholasville, 37°47'4"N, 84°34'11"W: (1 female: ROME158541-ROME; BOLD:ACF3436; ITS2). Missouri: 1 female. St. Louis Co., St. Louis: (1 female: ROME185906-ROME; BOLD:ACF3436; ITS2). Texas: 1 female. Walker Co., Huntsville: (1 female: ROME185911-TAMU; BOLD:ACF3436; ITS2). West Virginia: 1 female. Hardy Co., 3 mi NE Mathias, 38.9098, -78.8881: (1 female: ROME198142-USNM; BOLD:ACF3436; ITS2).

**Material examined.** CANADA: 13 females, 17 males. USA: 38 females, 29 males. (Suppl. materials).

**Additional material examined.** USA: 2 females, 3 males. Florida: 2 females, 3 males. Alachua Co., Gainesville: (1 male: ROME204136-SEMC). (2 males:



Figure 16. Perilampus seneca Female A habitus, lateral view B habitus, dorsal view C lateral lobe of mesoscutum along notaulus D lateral panel of pronotum, posterior oblique view E parascutal carina F axilla G head, dorsal view H head, anterior view I lower face J head, lateral view K mesoscutellum apex L mesofemoral depression. [A, H, I, J, L Paratype, ROME199563; B, F, G Paratype, ROME182769; C Paratype, ROME158541;
D Paratype, ROME199544; E Holotype, ROME183977; K Paratype, ROME198142]. Scale bar: 1 mm (A).



**Figure 17.** *Perilampus seneca* Male **A** habitus, lateral view **B** lateral panel of pronotum, parascutal carina, and axilla, posterior oblique view **C** head, anterior view **D** head, dorsal view **E** habitus, dorsal view **F** lateral lobe of mesoscutum along notaulus **G**, **H** scape. [**A–C**, **F**, **G** Paratype, ROME183976; **D** Paratype, ROME199551; **E** Paratype, ROME162263; **H** Paratype, ROME199552]. Scale bars: 1 mm (**A**); 100 μm (**G**, **H**).

ROME207380-FSCA; ROME207381-FSCA). Orange Co., Orlando, UCF Campus: (1 female: ROME152729-UCFC; BOLD:ACF3436; ITS2). Walt Disney World, Sec 16 T24S R27E: (1 female: ROME152728-UCFC; BOLD:ACF3436; ITS2).

**Etymology.** The specific epithet is a noun in apposition—a reference to both the Seneca people who are the original inhabitants of the core range of the species and to the county in New York State where most of the specimens were reared.

**Description. Female** (Fig. 16). Length: 2.9–4.4 mm. Color: head iridescent greenish blue or violet with black coloration between lateral ocellus and frontal carina (Fig. 16G, arrow); mesosoma, and metasoma iridescent greenish blue or violet; clypeus ventral margin black (Fig. 16I); antenna with scape and pedicel weakly iridescent greenish blue or violet, flagellum brown or black, lighter ventrad and distad.

Head (Fig. 16G–J): in dorsal view transverse, width slightly greater than twice length, HW/HL 2.1–2.2. Frontal carina: in anterior view straight to weakly sinuate below midlevel of eye; in dorsal view gradually narrowed V shape around median ocellus, FC/MOD 1.5–1.7; distance from lateral ocellus short, FCLO/LOD 0.5–0.6. Scrobal cavity (Fig. 16H): in anterior view wide, SW/HW about 0.5. Ocelli (Fig. 16G): a line between anterior margin of lateral ocelli touching anterior margin of median ocellus. POL/OOL 1.9–2.1. Ocellar ratios LOD: POL: OOL: LOL 1, 2.9–3.2, 1.5–1.8, 1.0–1.2. Vertex: with strong to weak transverse striations, without large piliferous punctures. Parascrobal area: in lateral view gradually narrowed towards lower eye margin; width narrow, PSW/EL 0.2–0.3; sculpture strongly to weakly striate, without large piliferous punctures. Gena (Fig. 16J): mostly striate along outer eye margin with narrow and short smooth area, striate behind. Malar space: MSL/EH about 0.2. Lower face (Fig. 16H, I): with setae sparse or dense and narrowly distributed laterad torulus, and sparse or dense below. Clypeus (Fig. 16I): CW/CH 1.3–1.4; ventral margin concave; setae evenly distributed, or with small bare area without setae medially.

Mesosoma (Fig. 16B–F, K, L): Lateral panel of pronotum: slightly narrower than or about as wide as prepectus, LPP/PPT 0.7–0.9; usually with small triangular flange below level of mesothoracic spiracle in posterior oblique view (Fig. 16D, arrow). Mesofemoral depression: usually smooth (Fig. 16L), rarely weakly rugulose or weakly imbricate ventrad. Mesoscutum: punctures angulate, with narrow and weakly coriarious interspaces (Fig. 16B); lateral lobe smooth or weakly coriarious along notaulus (Fig. 16C); parascutal carina broadly curved, acuminate (Fig. 16E). Mesoscutellum: apex with inner margins gradually diverging (Fig. 16K); punctures angulate, with narrow and weakly coriarious interspaces. Axilla (Fig. 16F): in lateral view imbricate dorsad and carinate ventrad. Axillula: smooth dorsad. Fore wing: stigma small, 2.0–2.5 × as wide as postmarginal vein.

**Male** (Fig. 17). Length: usually smaller, 1.6-3.3 mm. As in female, except: Color: mesonotum with strong or weak cupreous iridescence, and mesoscutellum cupreous laterad (Fig. 17E). Frontal carina: distance from lateral ocellus as wide or shorter, FCLO/LOD 0.3-0.5. Scape (Fig. 17G, H): pits dense, covering 0.3-0.4 × scape length. Lateral panel of pronotum: shape below level of mesothoracic spiracle as in female or with large triangular flange.

**Diagnosis.** *Perilampus seneca* is most similar to *P. ute*, but females can be distinguished by the lateral panel of pronotum which has a small triangular flange (Fig. 16D, arrow cf. Fig. 18D, arrow), and black coloration between the frontal carina and lateral ocelli (Fig. 14G, arrow cf. Fig. 18G). Males of this species can often be differentiated from those of *P. ute* by a smaller flange on the pronotum (Fig. 17B cf. Fig. 19B, C). Males of *P. seneca* with a large triangular flange on the pronotum are similar to those of *P. ute*, but differ in having cupreous iridescence on a mesonotum (Fig. 17E cf. Fig. 19F). Males of *P. seneca* with a small or no flange on lateral panel of pronotum can be confused with *P. sonora*, which also has the strongly cupreous mesonotum (Fig. 17A, E cf. Fig. 23A), but can be distinguished by a densely pitted scape (Fig. 17G, H cf. Fig. 23G, H). In addition, the distribution of *P. seneca* extends to southeastern Canada and eastern USA, while *P. ute* is restricted to the southwestern and central USA.

**Distribution (Fig. 25D).** Southeastern Canada, and central and eastern USA: Canada (Ontario), USA (Arkansas, Arizona, Georgia, Indiana, Kentucky, Maryland, Massachusetts, Missouri, New York, Texas, Virginia, West Virginia, Wisconsin). Possibly southeastern USA and Mexico: USA (Florida), Mexico (Veracruz).

**Host association.** *Perilampus seneca* is a hyperparasitoid, primarily parasitizing dipteran and hymenopteran parasitoids of Lepidoptera (Fig. 26F), rarely parasitizing dipteran parasitoids of Orthoptera and Coleoptera. Tachinidae (Diptera). *Lespesia melalophae* (Allen) from Lepidoptera. *Ormia* sp. from *Amblycorypha oblongifolia* (Tettigoniidae) (ROME162263). Tachinids from *H. cunea* and Chrysomelidae (ROME174210). Braconidae (Hymenoptera). *Cotesia hyphantriae* (Riley) from *Hyphantria cunea* (Drury) (Erebidae). Unidentified parasitoids from *Euchaetes egle* (Drury) (Erebidae).

**Variation.** An unsequenced male from Florida (ROME204136), has a violet mesonotum and two sequenced females from Florida (ROME152728, ROME152729) lack black coloration between the frontal carina and median ocellus. And two unsequenced males from Florida (ROME207380, ROME207381) reared from *Anisomorpha buprestoides* (Pseudophasmatidae, Phasmida) have a violet mesonotum and the lateral lobe of mesoscutum is weakly punctate along notaulus.

**Remarks.** There are uncertainties about the species limit of *P. seneca*. Although *P. seneca* is differentiated from the other Nearctic species in COI (10 BINed specimens on BOLD, ACF3436), there are Neotropical clades (from Argentina, Costa Rica, and Venezuela) with BIN ACF3436 that cannot be delimited from *P. seneca* and each other. Specimens either morphologically indistinguishable from *P. seneca* ("*P. hyalinus* 1" from Costa Rica and Venezuela) or differ only in the body coloration or subtle male scape morphology ("*P. hyalinus* 2, 3, and 16, from Argentina, Costa Rica, and Venezuela, respectively). *Perilampus seneca* and these Neotropical groups are placed together as a single clade in COI (Suppl. material 2). Interestingly, *P. seneca* is rendered paraphyletic by *P. hyalinus* 2 from Argentina which itself is polyphyletic—the first clade of *P. seneca* is the population from Florida, and the second is the northern population. ITS2 does not support the species delimitation and relationships suggested by COI (Suppl. material 2)—each Neotropical group is delimited as reciprocally monophyletic species and show different or unresolved species relationships, and *P. seneca* is an unresolved

polytomy. And *P. seneca* cannot be morphologically distinguished from the types of *P. americanus* Girault and *P. nigriviridis* Girault, both from Paraguay, based on the images provided by ZMHB (Fig. 24D–F).

Despite these uncertainties we hypothesize that *P. seneca* is a recently diverged Nearctic species distinct from the Neotropical groups with similar COI sequences the populations north of Florida are monophyletic for COI albeit with poor support in BI (Suppl. materials 2, 3: BS = 71, PP = 0.53). And *P. seneca* is differentiated from the aforementioned Neotropical groups by ITS2 (Suppl. material 2). The polytomy in the ITS2 trees could be a "soft polytomy" caused by insufficient information from a single gene that can only be resolved with additional genetic data (Maddison 1989). There are ten BINed specimens on BOLD (ACF3436) from the Nearctic region.

The relationships between *P. seneca* and the Neotropical specimens shown in COI unsupported by ITS2 may be due to retention of ancestral polymorphism via incomplete lineage sorting (ILS), introgression events between the Neotropical lineages, and/or insufficient phylogenetic information in ITS2 for this group. The paraphyly of *P. seneca* may be explained by ILS instead of hybridization due to the geographical distance between the two groups. However, two females from Florida (ROME152729, ROME152728) without black coloration between the frontal carina and lateral ocellus, and unsequenced males from Florida (ROME204136, ROME207380, ROME207381) with entirely violet body color in contrast to cupreous body color of northern *P. seneca* suggest there could be two independently evolving lineages in the Nearctic region.

A single *Perilampus* was reared as a parasitoid of Tachinidae in Kentucky, USA (ROME174210) from a series of 1,139 tachinid primary parasitoids of *Acalymma vit-tatum* and *Diabrotica undecimpunctata howardi* (Chrysomelidae) (Skidmore 2018). This is the only Nearctic *P. hyalinus* species complex specimen associated with Coleoptera and is most likely the result of the accidental entry of a planidium into a novel but suitable host, and does not contradict the host preference of *P. seneca* for the parasitoids of Lepidoptera.

#### Perilampus ute Yoo & Darling, sp. nov.

https://zoobank.org/0FDCB57F-2A0C-423C-B06C-34F1CA9C0714 Figs 18, 19

#### Type locality. USA, Colorado, Idledale.

**Type material.** *Holotype.* "USA, Colorado, Jefferson Co., Idledale, Sawmill Gulch, 1981 m, 39°40'N, 105°14'W, 20–27.viii.2001, Malaise, Irwin, Lambkin, Metz & Hauser". The holotype is point-mounted (Female ROME182768, TAMU). BOLD:AEE9091/ITS2. ROM Online Collection.

*Paratypes.* USA: 3 females, 1 male. Arizona: 1 female. Cochise Co., Coronado National Forest, Huachuca Mts., Copper Canyon, 31°21'44"N, 110°18'02"W: (1 female: ROME182763-TAMU; BOLD:AEE9091; ITS2). California: 1 male. San Bernardi-

no Co., Kellers Peak, 34°12'22"N, 117°02'36"W: (1 male: ROME182781-UCRC; BOLD:AEO1509; ITS2). Colorado: 1 female. Jefferson Co., Idledale, Sawmill Gulch, 39°40'N, 105°14'W: (1 female: ROME182768-TAMU; BOLD:AEE9091; ITS2). New Mexico: 1 female. Grant Co., 14 mi N Silver City, Cherry Creek Campground, 32°54.8'N, 108°13.6'W: (1 female: ROME152676-CNC; BOLD:AEE9091; ITS2).

Material examined. USA: 9 females, 5 males. (Suppl. materials).

Additional material examined. MEXICO: 1 male. Jalisco: 1 male. (1 male: ROME200745-HNHM). USA: 1 male. California: 1 male. Mono Co., Golden Gate Mine, 4.6 mi NW Walker: (1 male: ROME201998-CAS).

**Etymology.** The specific epithet is a noun in apposition—a reference to the Ute, indigenous people of the Great Basin regions of present-day Utah and Colorado where the holotype was collected.

**Description. Female** (Fig. 18). Length: 3.0–3.5 mm. Color: head iridescent greenish blue or violet; mesosoma and metasoma iridescent greenish blue or violet; clypeus ventral margin black (Fig. 18I); antenna with scape and pedicel weakly iridescent greenish blue or violet, flagellum brown or black, lighter ventrad and distad.

Head (Fig. 18G–J): in dorsal view transverse, width slightly greater than twice length, HW/HL 2.1–2.2. Frontal carina: in anterior view straight to weakly sinuate below midlevel of eye; in dorsal view gradually narrowed V shape around median ocellus, FC/MOD about 1.5; distance from lateral ocellus short, FCLO/LOD 0.5–0.6. Scrobal cavity (Fig. 18H): in anterior view wide, SW/HW about 0.5. Ocelli (Fig. 18G): a line between anterior margin of lateral ocelli reaching anterior margin of median ocellus. POL/OOL 1.7–1.9. Ocellar ratios LOD: POL: OOL: LOL 1, 2.7–3.1, 1.5–1.8, 1.1–1.2. Vertex: with strong to weak transverse striations, without large piliferous punctures. Parascrobal area: in lateral view gradually narrowed towards lower eye margin; width narrow, PSW/EL 0.2–0.3; sculpture strongly to weakly striate, without large piliferous punctures. Gena: mostly striate along outer eye margin with narrow and short smooth area, striate behind. Malar space: MSL/EH about 0.2. Lower face (Fig. 18H, I): with setae sparse or dense and narrowly distributed laterad torulus, and sparse or dense below. Clypeus (Fig. 18I): CW/CH about 1.4; ventral margin concave; setae evenly distributed, or with small bare area without setae medially.

Mesosoma (Fig. 18B–F, K, L): Lateral panel of pronotum: about as wide or wider than prepectus, LPP/PPT 0.8–1.1; usually with large triangular flange below level of mesothoracic spiracle in posterior oblique view (Fig. 18D, arrow). Mesofemoral depression: usually smooth, rarely weakly rugulose or weakly imbricate ventrad (Fig. 18E). Mesoscutum: punctures angulate, with narrow and weakly coriarious interspaces (Fig. 18B); lateral lobe smooth along notaulus (Fig. 18C), rarely coriarious; parascutal carina broadly curved, acuminate. Mesoscutellum: apex with inner margins gradually diverging (Fig. 18K); punctures angulate, with narrow and weakly coriarious interspaces. Axilla: in lateral view imbricate dorsad and carinate ventrad. Axillula: smooth dorsad. Fore wing: stigma small,  $2.0-2.5 \times$ as wide as postmarginal vein.

Male (Fig. 19). Length: usually smaller, 2.6–2.9 mm. As in female, except: Color: black coloration often present between frontal carina and lateral ocellus, and mesonotum almost



Figure 18. *Perilampus ute* Female A habitus, lateral view B habitus, dorsal view C lateral lobe of mesos-cutum along notaulus D, E lateral panel of pronotum, posterior oblique view F axilla G head, dorsal view H head, anterior view I lower face J head, lateral view K mesoscutellum apex L mesofemoral depression.
[A, C, D, F, G, H Holotype, ROME182768; B, E, I–L Paratype, ROME182763]. Scale bar: 1 mm (A).



**Figure 19.** *Perilampus ute* Male **A** habitus, lateral view **B**, **C** lateral panel of pronotum, posterior oblique view **D** head, anterior view **E** head, dorsal view **F** habitus, dorsal view **G** lateral lobe of mesoscutum along notaulus **H**, **I** Scape. [**A**, **B**, **D–F**, **H** Paratype, ROME182781; **C**, **G**, **I** Paratype, ROME198139]. Scale bars: 1 mm (**A**); 100 μm (**H**, **I**).

entirely black with weak bluish iridescence mesad (Fig. 19F) or rarely green with weak cupreous iridescence laterad. Frontal carina: distance from lateral ocellus shorter, FCLO/LOD 0.3–0.4. Scape (Fig. 19H, I): pits dense, covering about 0.3–0.4 × scape length.

**Diagnosis.** *Perilampus ute* can usually be distinguished by the lateral panel of pronotum with an expanded triangular flange in posterior oblique view (Figs 18D, 19B, C cf. Figs 16D, 17B) and densely pitted male scape (Fig. 19H, I cf. Fig. 15F, G). Females rarely have a small flange on a pronotum as in *P. seneca* (Fig. 18E, arrow), but can be reliably differentiated from the latter by the lack of black coloration between the frontal carina and lateral ocellus (Fig. 18G cf. Fig. 16G, arrow). Males can be confused with *P. seneca* with an expanded triangular flange on the pronotum in posterior oblique view but can be distinguished by the lack of cupreous iridescence on the mesonotum (Fig. 19F cf. Fig. 17E). *Perilampus ute* is restricted to the southwestern and central USA and the range of *P. seneca* extends to southeastern Canada and eastern USA.

**Distribution (Fig. 25F).** Southwestern and southcentral USA, and possibly western Mexico: USA (Arizona, California, Colorado, New Mexico, Utah), Mexico (Jalisco).

Host association. *Perilampus ute* is a hyperparasitoid, parasitizing dipteran parasitoids of Lepidoptera. Hosts: Tachinidae (Diptera), *Lespesia aletiae* (Riley) from *Apatelodes pudefacta* Dyar (Apatelodidae).

**Variation.** An unsequenced male from California (ROME201998) has a greenish iridescence along the midline of a mesonotum with a weak cupreous iridescence laterad.

**Remarks.** *Perilampus ute* is recovered as monophyletic (Fig. 1), but the molecular species delimitation methods identify the specimen from California (ROME182781) as a unique molecular taxonomic unit in COI while merging it with the eastern specimens in ITS2 (Suppl. materials 2, 5). This is likely due to the relatively large genetic divergence in COI between ROME182781 and the eastern specimens (1.7–2.0%), possibly a result of reduced gene flow between disjoint coastal and eastern inland glacial refugia in California (Roberts and Hamann 2015) prior to range re-expansion of the parasitoid populations. There are currently two unique BINs on BOLD assigned for five specimens of this species: AEO1509 for the specimen from California (ROME182781) and AEE9091 for the four specimens from the more eastern regions. The color of the mesonotum is used to differentiate the males of *P. ute* from those of *P. seneca*. However, more thorough genetic sampling is required because only a single male from California has been sequenced and there are no sequenced *P. seneca* specimens from the southwestern USA.

#### Perilampus arcus Yoo & Darling, sp. nov.

https://zoobank.org/92B1492B-F849-4212-9096-5311ADD6415C Figs 20, 21

Type locality. USA, West Virginia, Hardy County, 3 mi NE Mathias.

**Type material.** *Holotype.* "WEST VIRGINIA: Hardy Co. 3 mi NE Mathias 38.9098, -78.8881, 14–31.VII.2007, Malaise David R. Smith". The holotype is point-mounted (Female ROME189051, USNM). BOLD:AEE7608/ITS2. ROM Online Collection.

*Paratypes*. CANADA: 1 male. Ontario: 1 male. Norfolk Co., Normandale Fish Hatchery, 42°43'08"N, 80°20'23"W: (1 male: ROME198214-CNC; BOLD:AEE7608; ITS2). USA: 5 females. Kentucky: 1 female. Jessamine Co., S. of Nicholasville, 37°47'04"N, 84°34'11"W: (1 female: ROME158551-ROME; BOLD:AEE7608). West Virginia: 4 females. Hardy Co., 3 mi NE Mathias, 38.9098, -78.8881: (4 females: ROME185944-USNM; BOLD:AEE7608; ITS2; ROME189050-USNM; ITS2; ROME189052-USNM; BOLD:AEE7608; ITS2; ROME189131-USNM; ITS2).

**Material examined.** CANADA: 2 females, 1 male. USA: 6 females, 1 male. (Suppl. materials).

**Etymology.** The specific epithet is the Latin noun *arcus* (arch), in reference to the steeply curved parascutal carina.

**Description. Female** (Fig. 20). Length: 2.7–4.0 mm. Color: head iridescent greenish blue or violet; mesosoma and metasoma iridescent greenish blue or violet; clypeus ventral margin black (Fig. 20I); antenna with scape and pedicel weakly iridescent greenish blue or violet, flagellum brown or black, lighter ventrad and distad.

Head (Fig. 20G–J): in dorsal view transverse, width slightly greater than twice length, HW/HL 2.1–2.2. Frontal carina: in anterior view straight to weakly sinuate below midlevel of eye; in dorsal view gradually narrowed V shape around median ocellus, FC/MOD 1.5–1.6; distance from lateral ocellus short, FCLO/LOD 0.5–0.6. Scrobal cavity (Fig. 20H): in anterior view wide, SW/HW about 0.5. Ocelli (Fig. 20G): a line between anterior margin of lateral ocelli reaching anterior margin of median ocellus. POL/OOL 1.6–1.9. Ocellar ratios LOD: POL: OOL: LOL 1, 2.5–2.9, 1.6–1.8, 0.8–1.0. Vertex: with strong to weak transverse striations, without large piliferous punctures. Parascrobal area: in lateral view gradually narrowed towards lower eye margin; width narrow, PSW/EL 0.2–0.3; sculpture strongly to weakly striate, without large piliferous punctures. Gena (Fig. 20J): mostly striate along outer eye margin with narrow and short smooth area, striate behind. Malar space: MSL/EH about 0.2. Lower face (Fig. 20H, I): with setae sparse or dense and narrowly distributed laterad torulus, and usually sparse below. Clypeus (Fig. 20I): CW/CH 1.3–1.4; ventral margin concave; setae evenly distributed, or with small bare area without setae medially.

Mesosoma (Fig. 20B–F, K, L): Lateral panel of pronotum: slightly narrower than prepectus, LPP/PPT 0.7–0.8; usually with small triangular flange below level of mesothoracic spracle in posterior oblique view (Fig. 20D, arrow). Mesofemoral depression: usually smooth, rarely weakly rugulose or weakly imbricate ventrad (Fig. 20L). Mesoscutum: punctures angulate, with narrow and weakly coriarious interspaces (Fig. 20B); lateral lobe smooth or weakly punctate along notaulus (Fig. 20C); parascutal carina steeply curved, often weakly flanged (Fig. 20E, arrow). Mesoscutellum: apex with inner margins gradually (Fig. 20K) or abruptly diverging; punctures angulate, with narrow and weakly coriarious interspaces. Axilla (Fig. 20F): in lateral view imbricate dorsad and carinate ventrad. Axillula: smooth dorsad. Fore wing: stigma small, 2.0–2.5 × as wide as postmarginal vein.

**Male** (Fig. 21). Length: usually smaller, 3.1–3.5 mm. As in female, except: Color: mesonotum sometimes with weak cupreous iridescence. Frontal carina: distance from



Figure 20. Perilampus arcus Female A habitus, lateral view B habitus, dorsal view C lateral lobe of mesoscutum along notaulus D lateral panel of pronotum, posterior oblique view E parascutal carina F axilla G head, dorsal view H head, anterior view I lower face J head, lateral view K mesoscutellum apex L mesofemoral depression. [A, D, E Holotype, ROME189051; B, C, H, J, L Paratype, ROME185944; F Paratype, ROME189050; G Paratype, ROME158551; I, K Paratype, ROME189131]. Scale bar: 1 mm (A).



**Figure 21.** *Perilampus arcus* Male **A** habitus, lateral view **B** lateral panel of pronotum, parascutal carina, and axilla **C** head, anterior view **D** head, dorsal view **E** lower face **F** lateral lobe of mesoscutum along notaulus **G**, **H** scape. [**A–E**, **G** Paratype, ROME185954; **F**, **H** Paratype, ROME198214]. Scale bars: 1 mm (**A**); 100 μm (**G**, **H**).

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lateral ocellus shorter, FCLO/LOD 0.3–0.4. Scape (Fig. 21G, H): pits dense, covering about  $0.4 \times$  scape length.

**Diagnosis.** The steeply curved parascutal carina often with a flange distinguishes *P. arcus* from the majority of the species of the *P. hyalinus* species complex (Figs 20E, 21B cf. Figs 16E, 17B). *Perilampus sirsiris* also has a similar parascutal carina (Figs 6F, 7B), but it is always steeply curved in *P. arcus* and usually angulate in *P. sirsiris* (Fig. 20E cf. Fig. 6F). *Perilampus arcus* also differs from *P. sirsiris* by having the lateral panel of pronotum with a small triangular flange in posterior oblique view (Fig. 20D, arrow cf. Fig. 6D, E) and a male scape with a densely pitted surface (Fig. 21G, H cf. Fig. 7F, G). In addition to the shape of the parascutal carina, sparser setae on the lower face usually distinguish *P. arcus* from *P. seneca* (Figs 20I, 21C cf. Figs 16I, 17C), which also has a small triangular flange on the pronotum (Figs 16D, 17B) and a densely pitted male scape (Fig. 17G, H).

**Distribution (Fig. 25E).** Southeastern Canada and eastern USA, possibly southcentral USA: Canada (Ontario), USA (Arkansas, Kentucky, Ohio, West Virginia, Wisconsin).

## Host association. Unknown.

**Remarks.** This species is supported by both genes (Fig. 1, Suppl. material 5), and there are five BINed specimens on BOLD (AEE7608) from eastern Canada and USA. A single female was collected in Arkansas, indicating that the range of *P. arcus* may include the southern USA.

## Perilampus sonora Yoo & Darling, sp. nov.

https://zoobank.org/D3A8E02F-F4C3-4F8E-A133-63BC6E72C27F Figs 22, 23

Type locality. USA, Arizona, Santa Cruz County, Sonoita.

**Type material.** *Holotype.* "ARIZONA: Santa Cruz Co. Sonoita, 2 mi S of town center 31°38'N, 110°39'W, 16–22. VI.2008 Malaise trap in juniper/oak grasslands, EE Grissell". The holotype is point-mounted (Female ROME152670, USNM). BOLD:AEO0861/ITS2. ROM Online Collection.

*Paratypes.* MEXICO: 1 male. Oaxaca: 1 male. 19 mi S San Miguel Suchixtepec at Puente Jalatengo: (1 male: ROME182754-TAMU; BOLD:AEO0861; ITS2). USA: 1 female, 1 male. Arizona: 1 female, 1 male. Cochise Co., Coronado National Forest, Chiricahua Mts., 1 mi N Rustler Park, 31°54'53"N, 109°16'07"W: (1 female: ROME186060-TAMU; BOLD:AEO0861; ITS2). Santa Cruz Co., (1 male: ROME198215-USNM; ITS2).

**Material examined.** MEXICO: 15 females, 3 males. USA: 3 females. (Suppl. materials).

Additional material examined. USA: 1 female. Arizona: 1 female. Cochise Co., Bisbee, 1429 Franklin St., 31°24'23.8"N, 109°55'57.6"W: (1 female: ROME152671-USNM; BOLD:AEO0861; ITS2).



Figure 22. *Perilampus sonora* Female A habitus, lateral view B habitus, dorsal view C lateral lobe of mesoscutum along notaulus D lateral panel of pronotum, posterior oblique view E parascutal carina F axilla G head, dorsal view H head, anterior view I lower face J head, lateral view K mesoscutellum apex L mesofemoral depression. [A, B, D, G, H, J, K Holotype, ROME152670; C, E, I Paratype, ROME186060; L Paratype, ROME189110]. Scale bar: 1 mm (A).



**Figure 23**. *Perilampus sonora* Male **A** habitus, lateral view **B** lateral panel of pronotum, parascutal carina, and axilla, posterior oblique view **C** head, anterior view **D** head, dorsal view **E** lower face **F** lateral lobe of mesoscutum along notaulus **G**, **H** scape. [**A**–**F**, **G** Paratype, ROME182754; **H** Paratype, ROME198215]. Scale bars: 1 mm (**A**); 100 μm (**G**, **H**).

**Etymology.** The specific epithet is a noun in apposition—a reference to both the Sonoran Desert and to the state of Mexico where most of the specimens were collected.

**Description. Female** (Fig. 22). Length: 2.1–3.2 mm. Color: head iridescent olive with cupreous tinge, with or without black coloration between lateral ocellus and frontal carina; pronotum and mesonotum cupreous, prepectus, meso- and metapleuron, and metasoma iridescent bluish violet; clypeus ventral margin black (Fig. 22I); antenna with scape and pedicel weakly iridescent greenish blue or violet, flagellum brown or black, lighter ventrad and distad.

Head (Fig. 22G–J): in dorsal view transverse, width slightly greater than twice length, HW/HL 2.1–2.2. Frontal carina: in anterior view straight to weakly sinuate below midlevel of eye; in dorsal view gradually narrowed V shape around median ocellus, FC/MOD 1.5–1.7; distance from lateral ocellus short to long FCLO/LOD 0.6–1.0. Scrobal cavity (Fig. 22H): in anterior view wide, SW/HW about 0.5. Ocelli (Fig. 22G): a line between anterior margin of lateral ocelli reaching anterior margin of median ocellus or nearly bisecting median ocellus. POL/OOL 1.8–2.1. Ocellar ratios LOD: POL: OOL: LOL 1, 2.9–3.3, 1.5–1.8, 1.1–1.3. Vertex: with strong to weak transverse striations, without large piliferous punctures. Parascrobal area: in lateral view gradually narrowed towards lower eye margin; width narrow, PSW/EL 0.2–0.3; sculpture strongly to weakly striate, without large piliferous punctures. Gena: entirely striate along outer eye margin, striate posterad. Malar space: MSL/EH about 0.2. Lower face (Fig. 22H, I): with setae sparse or dense and narrowly distributed laterad torulus, and sparse or dense below. Clypeus (Fig. 22I): CW/CH 1.4–1.5; ventral margin concave; setae evenly distributed, or with small bare area without setae medially.

Mesosoma (Fig. 22B–F): Lateral panel of pronotum: about as wide as prepectus, LPP/PPT about 0.9; without flange (Fig. 20D) or with small rounded flange below level of mesothoracic spiracle in posterior oblique view. Mesofemoral depression: usually smooth (Fig. 22L), rarely weakly rugulose or weakly imbricate ventrad. Mesoscutum: punctures angulate, with narrow and weakly coriarious interspaces (Fig. 22B); lateral lobe smooth or weakly coriarious along notaulus (Fig. 22C); parascutal carina broadly curved, acuminate. Mesoscutellum: apex with inner margins gradually diverging; Axilla: in lateral view imbricate dorsad and usually carinate (Fig. 22F), rarely rugose-areolate ventrad. Axillula: smooth dorsad. Fore wing: stigma small, 2.0–2.5 × as wide as postmarginal vein.

**Male** (Fig. 23). Length: usually smaller, 2.5-2.8 mm. As in female, except: Frontal carina: distance from lateral ocellus as wide or shorter, FCLO/LOD 0.5-0.6. Scape (Fig. 23G, H): pits sparse, covering about  $0.3 \times$  scape length.

**Diagnosis.** This species is distinguished by the strong cupreous iridescence on the mesonotum of both females and males (Figs 22B, 23A cf. Figs 4B, 5A), in combination with the lateral panel of pronotum without a flange or with a small and rounded flange below the level of mesothoracic spiracle (Figs 22D, 23B cf. Figs 16D, 17B). *Perilampus pilosus* can also have a strong cupreous iridescence on the mesonotum (Fig. 15A), but *P. sonora* has sparser setae laterad of the torulus (Figs 22I, 23E cf. Figs 14I, 15E). Also,

the female metasoma of *P. sonora* is always violaceous but usually mostly greenish in the strongly cupreous *P. pilosus* specimens (Fig. 22A cf. Fig. 15B). *Perilampus seneca* males also often have a strongly iridescent mesonotum (Fig. 17E), but *P. sonora* males differ in having sparser pits on scapes (Fig. 23G, H cf. Fig. 17G, H). And the Nearctic distribution of *P. sonora* is limited to southwestern USA and western Mexico, and the range of *P. seneca* extends to southeastern Canada and eastern USA,

**Distribution (Fig. 25).** Southwestern USA, and western and southern Mexico: USA (Arizona), Mexico (Chiapas, Guerrero, Morelos, Oaxaca, Sonora).

Host association. *Perilampus sonora* is a hyperparasitoid, parasitizing dipteran and hymenopteran parasitoids of Lepidoptera. Hosts: Probably Tachinidae (Diptera) and/ or Ichneumonoidea (Hymenoptera) from *Utetheisa ornatrix* (Linnaeus) (Erebidae). The potential hosts are: *Gymnosoma* sp. (Tachinidae), *Lespesia* sp. (Tachinidae), and *Cotesia* sp. (Braconidae) (G. R. Buckingham, personal communication).

**Variation.** A female from Arizona (ROME152671) has an iridescent green head and weakly iridescent green midlobe of mesoscutum and scutellum. COI and ITS2 suggest that this specimen is a morphological variant of *P. sonora*. A female from Sonora, Mexico (ROME189103), has a strongly transverse clypeus with CW/CH about 1.7.

**Remarks.** The distribution ranges of *P. sonora* and its undescribed Neotropical sister species, *P. hyalinus* 17 (Fig. 1), appear to be divided by the Central Mexican Plateau. *Perilampus sonora* occurs along the western side of the plateau from Chiapas to Arizona (Fig. 25) and the Central American population of *P. hyalinus* 17 is distributed along the eastern side of the plateau from Panama to Tamaulipas, which may indicate allopatric or parapatric speciation. *Perilampus sonora* is supported by both genes (Fig. 1, Suppl. material 5), and there are four BINed specimens on BOLD (AEO0861) from Arizona and Oaxaca, Mexico.

## Discussion

There is considerable complexity in the host associations of the *P. hyalinus* species complex and the host associations and modes of parasitism are congruent with the newly delimited species. *Perilampus hyalinus* Say is a hyperparasitoid that parasitizes Tachinidae and Sarcophagidae (Diptera) parasitoids of Orthoptera or a parasitoid of dipteran kleptoparasites of Crabronidae and Sphecidae (Hymenoptera) that provision their nests with Orthoptera. Two new species are associated with pine sawflies or cedar sawflies, (Diprionidae) and are able to develop as both primary parasitoids or as hyperparasitoids that parasitize the tachinid and ichneumonid parasitoids of diprionid sawflies. And four new species are described for hyperparasitoids, associated with Lepidoptera, parasitizing Tachinidae or Ichneumonoidea.

The molecular analyses and outgroup comparison with the *P. platigaster* species group suggests that hyperparasitoids are basal in the *P. hyalinus* species group and development as a primary parasitoid is derived. These and other host shifts may have been facilitated by parasitism involving the mobile planidial first-instar larva. Planidia



Figure 24. Type specimens of the previously described species of the *Perilampus hyalinus* species complex **A** *P. entellus* Walker (synonym of *P. hyalinus* Say), lectotype, female **B** *P. aciculatus* Provancher (synonym of *P. hyalinus* Say), lectotype, male **C** *P. sirsiris* (Argaman), holotype, female **D** *P. americanus* Girault, holotype, female **E**, **F** *P. nigriviridis* Girault, lectotype, male. Photo credits: **A** ©The Trustees of the Natural History Museum, London (Licensed under CC BY 4.0) **B** Joseph Moisan-De Serres (Ministry of Agriculture, Fisheries and Food in Québec) **C** National Museum of Natural History, Paris **D**, **E**, **F** Museum of Natural History, Berlin.

that successfully make contact and burrow into a novel but suitable host (e.g. sawfly larva) could successfully develop which may ultimately have resulted in the evolution of the species capable of developing as primary parasitoids, e.g., *P. neodiprioni* and *P. monocteni*. Planidia that make contact with a novel but unsuitable host (e.g. Orthoptera) may be "rescued" by subsequent parasitism by primary parasitoids (e.g. Diptera or Hymenoptera) on which the planidia can develop (Perlman 1995), which may have



Figure 25. Distribution of the Nearctic species of the *Perilampus hyalinus* species complex A *P. hyalinus* (green circles) and *P. crassus* (red squares) B *P. neodiprioni* (cyan circles) *P. monocteni* (red stars) C *P. sirsiris*D *P. seneca* E *P. arcus* F *P. pilosus* (yellow stars) *P. ute* (blue triangles) *P. sonora* (red circles).

led to the evolution of parasitoids associated with novel hosts. A well-documented example of host shifts involves *P. hyalinus* Say. This is the only known species to strictly develop as parasitoids which parasitize dipteran parasitoids (Sarcophagidae and Tachinidae) of Orthoptera and dipteran kleptoparasites of Crabronidae and Sphecidae (Hymenoptera) that provision their nests with Orthoptera prey containing planidia (Medler 1965; Spofford and Kurczewski 1984). The planidial larva and indirect parasitism could also explain the overlap in associated caterpillar species by sympatric species of *Perilampus* (e.g., *P. seneca* and *P. sirsiris* associated with *Hyphantria cunea*).

The morphological characters used to distinguish the species in the *P. hyalinus* species complex are often subtle (e.g. widely vs deeply curved parascutal carina) and can show interspecific variation (e.g. the sculpture of axillula in *P. neodiprioni* varies between punctate and smooth). Despite the fine distinctions, these morphological characters should allow the identification of most specimens in the absence of host information or molecular data, particularly series of specimens with males and females. It is noteworthy that eight of ten Nearctic species were successfully delimitated by COI and ITS and that each species has a unique BIN number and is monophyletic on the maximum likelihood and Bayesian trees of the *P. hyalinus* species group (Fig. 1, Suppl. material 1).



Figure 26. Cocoons, pupa, and host remains associated with reared specimens of *Perilampus*. A–C,
E *Neodiprion lecontei* cocoons A, B *P. neodiprioni* as primary parasitoid C, E *P. neodiprioni* as hyperparasitoid, parasitoid of Ichneumonidae D *Neodiprion virginianus* cocoon, *P. neodiprioni* as hyperparasitoid, parasitoid of Tachinidae [insert: tachinid puparium spiracles] F Lepidoptera pupa, *P. seneca* as hyperparasitoid, parasitoid of Tachinidae G, H *Monoctenus suffusus* cocoons G *P. monocteni* as primary parasitoid H *P. monocteni* as hyperparasitoid, parasitoid, parasitoid of Tachinidae (insert: tachinid e [insert: tachinid puparium spiracles]. Abbreviations: eh, emergence hole; ex, *Perilampus* pupa exuvia; Ic, ichneumonid cocoon; Lp, lepidopteran pupa; M, *Monoctenus* remains; Mc, *Monoctenus* cocoon; N, *Neodiprion* remains; Nc, *Neodiprion* cocoon; Tp, tachinid puparium. [associated *Perilampus*: A, B ROME207376 C ROME207377 D ROME198223
E ROME162273 F ROME202000 G ROME207330 H ROME207328]. Scale bars: 1 mm.

The phylogenetic analyses of COI and ITS2 suggest a Neotropical origin of the *P. hyalinus* species complex (Fig. 1, Suppl. material 1). The 9 Nearctic species are distributed across the three separate clades of New World gene trees and the majority of the Nearctic species (5 of 9) belong to the *P. hyalinus* clade 2 (IIIb), whose southernmost species are from Costa Rica (Suppl. material 2). The phylogenetic placements of the Nearctic species suggest independent dispersals of multiple ancestors into the Nearctic region. Intraspecific mitochondrial genetic differentiation suggests that at least two Nearctic species, *P. neodiprioni* and *P. ute*, underwent fragmentation of once widespread populations during the last glacial maximum, approximately 20,000 to 18,000 years ago (Bagely et al. 2016). Small to zero intraspecific divergences in nuclear DNA suggest that these populations experienced subsequent demographic expansion and secondary contact during the post-glacial period.

This revision provides resolution to 100 years of the confusion surrounding P. hyalinus in the Nearctic region. However, the phylogenetic relationships and species diversity of the P. hyalinus species complex in the Mexican transition zone and Neotropical region needs further study (Yoo 2023). Several Nearctic species range into Mexico and/or near to the Isthmus of Tehuantepec. But the scarcity of specimens available for study from Mexico (28) compared to Canada and USA (754) underscores the need for more comprehensive sampling in Mexico for clearer understanding of the distribution of the Nearctic species. And the northern Neotropical range of *P. neodiprioni* needs to be confirmed with molecular sequencing of the populations in Belize. Further investigation with additional genes and sampling in the Neotropical region and Florida is needed to clarify the species status and distribution limit of *P. seneca* and its relationships with the Neotropical groups similar in morphology and COI, especially from Argentina. Finally, the molecular sampling of the parasitoids reared from *Monoctenus* spp. is needed to test the species hypothesis of *P. monocteni* and its phylogenetic relationships with the other species of the *P. hyalinus* species complex.

# Acknowledgements

We would like to thank Andrew Bennett and James O'Hara from CNC for providing their extensive collections and expertise on the hymenopteran and dipteran hosts of the *Perilampus hyalinus* species complex. We are also grateful to Kevin Barber from GLFC for providing specimens and useful insights and feedback. We also extend our gratitude to the staff of the Royal Ontario Museum: Brad Hubley and Brenna Wells for their invaluable technical support and database management, and Kristen Choffe for her expertise in molecular work. Finally, thanks to Emily Darling for her R-code wizardry which greatly facilitated our workflow. This paper was derived in part from a thesis submitted by the first author in partial fulfillment for a M.Sc. degree from the University of Toronto and the members of the supervisory committee are gratefully acknowledged: Douglas C. Currie and Sebastian Kvist.

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# Bayesian inference 50% majority consensus tree for *Perilampus hyalinus* species group based on concatenated dataset of COI and ITS2 (Yoo 2023)

Authors: Jeong Jae Yoo, D. Christopher Darling

Data type: tif

- Explanation note: Bayesian inference 50% majority consensus tree for *Perilampus hyalinus* species group based on concatenated dataset of COI and ITS2 (Yoo 2023). Posterior probabilities above 0.50 are shown on the left side of the nodes.
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#### Maximum likelihood trees of *Perilampus hyalinus* species group retrieved from the separate analyses of COI and ITS2, and the results of morphological analyses (M) and molecular species delimitation (ABGD, BIN, and PTP) (modified from Yoo 2023)

Authors: Jeong Jae Yoo, D. Christopher Darling

Data type: zip

- Explanation note: Maximum likelihood trees of Perilampus hyalinus species group retrieved from the separate analyses of COI and ITS2, and the results of morphological analyses (M) and molecular species delimitation (ABGD, BIN, and PTP) (modified from Yoo 2023). Bootstrap support values are shown on the left sides of the nodes. The grey bars indicate the result of species delimitations, and the letters within represents identical delimited species. Colored bars under M indicate the morphological partitions that can only be accomplished by the subtle differences in body coloration and male scape morphology. The roman numerals and black dots adjacent to the nodes indicate the major morphological clades recovered as monophyletic (I = P. hyalinus species group; II = P. carolinensis species complex; IIa = "pseudocarolinensis" clade; IIb = P. carolinensis clade; III = P. hyalinus species complex; IIIa = P. hyalinus clade 1; IIIb = P. hyalinus clade 2; IIIc = P. hyalinus clade 3; IIId = "regalishyalinus" clade. The morphospecies designation for the sequences is marked by names and vertical bars, which were colored according to their placements within their respective morphological subgroups. The names of the species described herein are indicated in white boxes.
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# Bayesian inference 50% majority consensus tree for *Perilampus hyalinus* species group based on COI (Yoo 2023)

Authors: Jeong Jae Yoo, D. Christopher Darling

Data type: tiff

- Explanation note: Bayesian inference 50% majority consensus tree for *Perilampus hyalinus* species group based on COI (Yoo 2023). Posterior probabilities above 0.50 are shown on the left side of the nodes.
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Link: https://doi.org/10.3897/jhr.97.133255.suppl3

# Supplementary material 4

Bayesian inference 50% majority consensus tree for *Perilampus hyalinus* species group based on ITS2 (Yoo 2023)

Authors: Jeong Jae Yoo, D. Christopher Darling

Data type: tiff

- Explanation note: Bayesian inference 50% majority consensus tree for *Perilampus hyalinus* species group based on ITS2 (Yoo 2023). Posterior probabilities above 0.50 are shown on the left side of the nodes.
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# The summary of congruence between *Perilampus byalinus* species group morphospecies, phylogenetic analyses, the molecular species delimitation methods (ABGD, BIN, PTP) (modified from Yoo 2023)

Authors: Jeong Jae Yoo, D. Christopher Darling

- Data type: xlsx
- Explanation note: The summary of congruence between *Perilampus hyalinus* species group morphospecies, phylogenetic analyses, the molecular species delimitation methods (ABGD, BIN, PTP) (modified from Yoo 2023). The colored bars indicate support for each criterion of candidate species: unambiguous morphological character states; monophyly in both optimality criteria; and molecular delimitation congruent with morphology. The bolded names under Morphology represent the confirmed candidate species. (S) = singleton morphospecies S = DNA singleton Sp = morphospecies divided into multiple groups L = morphospecies lumped with the other sequences + = morphospecies successfully delimited.
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Link: https://doi.org/10.3897/jhr.97.133255.suppl5

# Supplementary material 6

# The type specimens of species previously described in the *Perilampus hyalinus* species group

Authors: Jeong Jae Yoo, D. Christopher Darling

Data type: xlsx

- Explanation note: The type specimens of species previously described in the *Perilampus hyalinus* species group. AMNH = American Museum of Natural History; HNHM
  Hungarian National Museum, Budapest; MNHB = Natural History Museum, Berlin; MNHM = National Museum of Natural History, Paris; NMHUK = Natural History Museum, London; USNM = Smithsonian National Museum of Natural History, Washington D. C.
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#### Material examined

Authors: Jeong Jae Yoo, D. Christopher Darling

Data type: docx

- Explanation note: Material examined for each species other than the types and additional material.
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# Telenomus dendrolimi (Matsumura) (Hymenoptera, Scelionidae) reared from the eggs of Dendrolimus houi (Lajonquiere) (Lepidoptera, Lasiocampidae) from China

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Academic editor: Miles Zhang | Received 11 October 2024 | Accepted 13 November 2024 | Published 6 December 2024

https://zoobank.org/B1496AC6-AF67-4849-B686-1EDCCA3A42B6

**Citation:** Chen H-Y, Talamas E, Lahey Z, Johnson NF, Lu C-D, Liang G-H (2024) *Telenomus dendrolimi* (Matsumura) (Hymenoptera, Scelionidae) reared from the eggs of *Dendrolimus houi* (Lajonquiere) (Lepidoptera, Lasiocampidae) from China. Journal of Hymenoptera Research 97: 1385–1402. https://doi.org/10.3897/jhr.97.139056

#### Abstract

The pine moth, *Dendrolimus houi* (Lajonquiere), is a notorious insect pest of coniferous trees in South China. A gregarious egg parasitoid in the family Scelionidae shows great potential to be mass-reared for the biological control of *D. houi*. This parasitoid is identified as *Telenomus dendrolimi* (Matsumura) based on comparison to paratype specimens of *Telenomus dendrolimusi* Chu, a junior synonym of *T. dendrolimi*. *Telenomus dendrolimi* is redescribed and included in a molecular analysis. In addition to parasitizing *D. houi*, *T. dendrolimi* was found to successfully parasitize six other species under laboratory conditions, with *Antheraea pernyi* (Guérin-Méneville) the most suitable host for mass-rearing.

#### Keywords

Biological control, egg parasitoid, gregarious, taxonomy

#### Introduction

The pine moth, *Dendrolimus houi* (Lajonquiere) (Lepidoptera, Lasiocampidae), is a notorious insect pest of several important conifers including *Cryptomeria japonica* var. *sinensis* Miquel (Cupressaceae), *Cupressus funebris* Endl. (Cupressaceae), *Pinus yunnanensis* Faranch. (Pinaceae), and *Pinus kesiya* Royle ex Gordon in South China, India, Myanmar, Sri Lanka, and Indonesia (Lin et al. 2023). Caterpillars of this moth feed on the leaves and branch tips of coniferous trees and have caused thousands of hectares of dead and dying trees of *Cr. japonica* (Zhang 2013), *Cu. funebris* (He et al. 2018), and *P. kesiya* (Yang 2015) in several provinces of South China. In addition to damaging coniferous trees, the venomous setae of the caterpillars have been reported to cause painful allergic reactions in humans, and to contaminate drinking water in rural areas (Luo et al. 1998).

Attempts to control D. houi in China have mainly focused on chemical insecticides (Zhang 2013), but more environmentally friendly control methods, such as biological control, have been proposed recently (Yang et al. 2017; Lin et al. 2017; Liang et al. 2018; Lin et al. 2023). To date, 25 parasitoid wasp and fly species have been reported to attack D. houi in China (Lin et al. 2017; Liang et al. 2018; Lin et al. 2023), including seven egg parasitoid wasps: Anastatus gastropachae Ashmead, Mesocomys albitarsis (Ashmead), and Mesocomys trabalae (Yao & Yang) (Eupelmidae); Mesopolobus subfumatus (Ratzeburg) (Pteromalidae); Ooencyrtus kuvanae (Howard) (Encyrtidae); Trichogramma dendrolimi Matsumura (Trichogrammatidae); and Telenomus dendrolimi (Matsumura) (Scelionidae). During a comprehensive survey of natural enemies of D. houi across South China in 2021, a gregarious species belonging to the egg parasitoid genus Telenomus Haliday (Scelionidae) was reared from the eggs of D. houi in Xiapu County of Fujian Province. Morphological examination and molecular analyses confirmed that it was T. dendrolimi (Matsumura) and a colony was established and maintained using eggs of Antheraea pernyi (Guérin-Méneville) (Saturniidae) in the laboratory at Fujian Agriculture and Forestry University. This parasitoid species shows potential to be mass-reared for the biological control of D. houi. This study aims to redescribe this species to facilitate future work on the taxonomy of the genus Telenomus and applications of this egg parasitoid in biological control programs.

#### Materials and methods

#### Insect sampling and rearing

A survey for parasitoid species that attack *D. houi* was conducted in five provinces of China in 2021 (Lin et al. 2023). Some parasitized eggs of *D. houi* on *Cryptomeria japonica* var. *sinensis* Miquel trees (Fig. 1) were collected in Xiapu County, Fujian Province (26°49'45.76"N, 119°57'55.3"E). The parasitized eggs were transported to the laboratory at Fujian Agriculture and Forestry University and placed in a 10 cm glass tube maintained at  $26 \pm 1$  °C,  $50 \pm 10\%$  relative humidity (RH) and 12:12 h light/ dark (LD) photoperiod. The eggs were checked daily for the emergence of parasitoids.



**Figure 1.** *Dendrolimus houi* (Lajonquiere) **A** larvae feeding on the leaves of *Cryptomeria japonica* var. *sinensis* **B** adult female (left), male (right) **C** parasitized egg masses on leaves **D** parasitized eggs with a parasitoid emergence hole.

All parasitoids were collected and fed with 20% honey water in a screened plastic box (29 × 17 × 9 cm) held at 25 °C and 12:12 h LD after emerging from the eggs. Fresh eggs of *A. pernyi* were provided to establish a colony in the laboratory. Additional eggs of the lepidopteran families Lasiocampidae (*Dendrolimus kikuchii* Matsumura, *Dendrolimus punctatus* Walker), Noctuidae (*Spodoptera frugiperda* (J.E. Smith), *Spodoptera litura* (Fabricius)), Plutellidae (*Plutella xylostella* (Linnaeus), and Saturniidae (*Actias sinensis* (Walker), *Antheraea pernyi* (Guérin-Méneville), *Caligula japonica* Moore, *Eriogyna pyretorum* Westwood) were used to test their suitability as hosts.

Some parasitoid specimens were preserved in 100% ethanol for further morphological and molecular studies. All voucher specimens are deposited in the Insect Collection of South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China (**SCBG**).

### Morphological terms

Abbreviations and morphological terms used in text: **A1–A12**: antennomere 1–12; **T1–T7**: metasomal tergite 1–7; **S1–S7**: metasomal sternite 1–7. Morphological terminology otherwise generally follows Mikó et al. (2007).

#### DNA extraction and sequencing

Genomic DNA was extracted from a female and a male of T. dendrolimi, T. remus Nixon, and T. dignus (Gahan) using a TIANamp Micro DNA Kit (Tiangen Biotech (Beijing), Co., Ltd.), following an established non-destructive DNA extraction protocol (Taekul et al. 2014). Two molecular markers were amplified: mitochondrial DNA (mtDNA) cytochrome c oxidase 1 (COI) and nuclear 28S rDNA D2-3 (28S). Polymerase chain reactions (PCRs) were performed using Tks Gflex<sup>™</sup> DNA Polymerase (Takara) with primer pairs LCO1490/HCO2198 (Folmer et al. 1994) for COI and D23F/28Sb (Whiting et al. 1997) for 28S. Thermocycling was conducted in a T100<sup>™</sup> Thermal Cycler (Bio-Rad) following the conditions of Yan et al. (2022). Both DNA strands of amplicons were directly sequenced on an Applied Biosystems (ABI) 3730XL using the same primers used for the PCR by Guangzhou Tianyi Huiyuan Gene Technology Co., Ltd. (Guangzhou, China). Forward and reverse sequences were assembled with Geneious 11.0.3. The assembled sequences of each gene were compared via BLAST against the GenBank non-redundant nucleotide database to check for contamination and stop codons in the open reading frame of COI that would indicate pseudogenic DNA (e.g., nuclear mitochondrial DNA, NUMT). The sequences generated from this study are deposited in GenBank (accession numbers are shown in Suppl. material 1).

#### Phylogenetic analyses

The 28S rDNA and COI sequences from T. dendrolimi, T. remus, and T. dignus were combined with the Telenomus 28S rDNA and COI dataset of Polaszek et al. (2021) (excluding Trissolcus thyantae Ashmead), in addition to a COI sequence of Telenomus gregalis Rajmohana (Rajmohana et al. 2024) downloaded from GenBank (KT896659.1). Multiple sequence alignments for each gene were performed separately with MAFFT v7.450 (Katoh and Standley 2013) using the E-INS-i algorithm for 28S and the L-INS-i algorithm (Translation Align feature in Geneious Prime 2024.0.4) for COI. Phylogenetic analyses were conducted in IQ-TREE v. 2.3.6 (Minh et al. 2020) for 28S, COI, and 28S+COI following the methodology of Chen et al. (2021). No partitions were specified in the 28S analysis. Three partitions (one for each codon position) were specified in the COI analysis. Four partitions (28S and one for each codon position of COI) were specified in the combined analysis (Chernomor et al. 2016). In each analysis, the best nucleotide substitution model for each partition was determined with ModelFinder (Kalyaanamoorthy et al. 2017), with the merge option enabled. Branch support was estimated with 1000 ultrafast bootstrap replicates (Hoang et al. 2018) and 1000 replicates of the SH-like approximate likelihood ratio test (SH-aLRT) (Guindon et al. 2010). Each analysis consisted of 100 independent runs, and Trissolcus basalis (Wollaston) was selected as the outgroup.

#### Imaging

Multifocal images of mounted specimens were made using a Nikon SMZ25 microscope with a Nikon DS-Ri 2 digital camera system and a Keyence VHX-970F imaging system. Scanning electron micrographs were produced using a JSM-6360LV scanning electron microscope (JEOL, Tokyo, Japan). Images were post-processed with Adobe Photoshop CS6 Extended.

# **Results and discussion**

#### Biology

*Telenomus dendrolimi* is a gregarious species, with more than one wasp emerging from a single egg of *D. houi*. Under laboratory conditions, it successfully parasitized two species of Lasiocampidae: *D. kikuchii* and *D. punctatus*; and four species of Saturniidae: *A. sinensis*, *A. pernyi*, *C. japonica*, and *E. pyretorum*. Similarly, more than one wasp emerged from a single host egg, indicating gregarious behavior for all of these hosts. Among the six alternative host species, *A. pernyi* was the most promising for mass-rearing of *T. dendrolimi*, with up to 20 wasps (female to male ratio was about 4:1) emerging per egg. Related biological parameters are under investigation and will be reported in future studies.

### Molecular analyses

Six Telenomus specimens belonging to three species were subjected to non-destructive DNA extraction followed by amplification and sequencing of the D2 and D3 regions of the 28S rDNA and the barcode region of COI. Multiple sequence alignments for 28S and COI were 1,134 and 845 characters (nt + gaps), respectively. In the COI single gene (Suppl. material 3) and combined gene analyses (Suppl. material 4), T. dendrolimi was recovered as the sister taxon to T. dalmanni with weak support. Telenomus dendrolimi was the sister taxon to an undescribed species of the Telenomus californicus complex in the 28S single gene analysis (Suppl. material 2), also with weak support. The COI single gene analysis revealed a moderately supported clade of species with gregarious life histories that includes taxa with known biologies, such as T. gregalis, T. moricolus, and T. dendrolimi. Also included in this clade is T. dalmanni, a solitary egg parasitoid of Orgyia antiqua (Linnaeus) (Lepidoptera: Lymantriidae) based on the published literature and rearing records of specimens accessioned in the Museum of Biological Diversity database (The Ohio State University). The newly sequenced T. remus (Note: The GenBank specimen MW452546.1, labeled as Telenomus remus c in Fig. 7, Suppl. material 4) is misidentified as *T. remus* and represents a closely related, potentially undescribed species) and *T. dignus* specimens formed monophyletic groups with other material of the same species deposited in GenBank (Fig. 7).

#### Telenomus dendrolimi (Matsumura)

Figs 2-6

Holcaerus (?) dendrolimi Matsumura, 1925: 44 (original description).

*Telenomus dendrolimi* (Matsumura): Tachikawa 1965: 284, plate 142 (description); Ryu and Hirashima 1985: 31, 47 (description, keyed); Johnson 1992: 584 (cataloged).

Telenomus (Aholcus) dendrolimi (Matsumura): He et al. 2004: 307 (description).

*Telenomus dendrolimusi* Chu, 1937: 60 (original description); Ishii 1938: 105 (junior synonym of *Telenomus dendrolimi* (Matsumura)); Peng and Liu 1992: 1473 (description, distribution).

*Telenomus (Aholcus) dendrolimusi* Chu: Wu and Chen 1980: 79, 81 (keyed); Chen and Wu 1981: 109, 110 (description, keyed); Chen and Tong 1980: 311 (description).

**Description.** Female body length: 1.07-1.21 mm (n = 10). Male body length 0.8-1.0 mm (n = 8).

Color: female body entirely black; antenna dark brown to black, with ventral side paler; coxae and femora of all legs dark brown to black, remainders of legs brown to yellow, with distal tarsomere darker; wings hyaline. Male similar to female, but antenna brown to dark brown, tibiae and tarsi of all legs paler.

*Head.* Female antenna 10-merous; claval formula 1-2-2-2; A2 distinctly longer than wide, A3 and A10 slightly longer than wide, A4 as long as wide, A5–A9 wider than long.

Male antenna 12-merous; A2 slightly longer than wide; A4 and A5, slightly dilated, but A5 modified, with tyloid projecting anteriorly; A6–A11 transverse; A12 1.60 × as long as wide.

Mandible with 3 teeth; clypeus with 4 setae; labrum, medially pointed, flanked by arched concavities; interantennal process present; frons coriaceous, becoming smooth around toruli and malar sulcus; frontal depression indicated by area of effaced micro-sculpture; gena coriaceous behind eye, becoming smooth ventrally and above occipital carina; eyes setose; vertex smoothly rounded onto occiput, without hyperoccipital carina; vertex coriaceous, becoming smooth above occipital carina; occiput entirely smooth; occipital carina present, higher and weaker medially, ventrally extending to posterior articulation of the mandible.

*Mesosoma. Pronotum*: pronotal cervical sulcus present as a smooth furrow; netrion smooth; netrion sulcus complete and distinct.

*Mesonotum*: mesoscutum evenly rounded in lateral view, with reticulate miscrosculpture except smooth narrow area along mesoscutal humeral sulcus; mesoscutal suprahumeral sulcus absent; mesoscutal humeral sulcus indicated by a mostly smooth furrow; mesoscutellum smooth, sparsely setose; axilla smooth, setae present; scutoscutellar sulcus more or less smooth medially, foveate laterally; posterior mesoscutellar sulcus foveate.

*Metanotum*: metascutellum rugose, slightly protruding posteriorly; metascutellar carina present; metanotal trough smooth.

**Propodeum:** metapostnotum medially tapering to a slender point, creating a gap between posterior margin of metanotum and anterior margin of propodeum; lateral



**Figure 2.** *Telenomus dendrolimi* (Matsumura) **A–D** female (OSUC 0071700) **A** dorsal habitus **B** lateral habitus **C** head and mesosoma, dorsal view **D** head and mesosoma, lateral view **E**, **F** male (OSUC 0071702) **E** lateral habitus **F** antenna.

propodeal carina present, fusing with metapleural carina to form perimeter of metasomal depression; metasomal depression mostly smooth, with short rugae radiating from propodeal foramen.

*Mesopleuron*: acropleural sulcus present, continuous with prespecular sulcus, forming a furrow extending ventrally to mesopleural pit; speculum weakly rugose; mesepimeral sulcus complete, foveate; mesopleural pit deep, slightly transverse; ventral mesopleuron smooth; episternal foveae absent; postacetabular patch clearly indicated, without setae; acetabular carina present; postacetabular sulcus indicated by a smooth



**Figure 3.** *Telenomus dendrolimusi* Chu **A**, **B** allotype, male **A** lateral habitus **B** head, anterior view **C–H** paratype, female **C** dorsal habitus **D** lateral habitus **E** head and mesosoma, dorsal view **F** head and mesosoma, lateral view **G** head, anterior view **H** metasoma, dorsal view.



**Figure 4.** *Telenomus dendrolimi* (Matsumura) from Fujian, female (SCBG\_E0010794) **A** dorsal habitus **B** lateral habitus **C** head and mesosoma, dorsal view **D** head and mesosoma, lateral view **E** head, anterior view **F** metasoma, dorsal view.

furrow; length of intercoxal space longer than fore coxae; mesopleural epicoxal sulcus indicated by shallow foveae.

*Metapleuron*: Metapleural carina interrupted by propodeal spiracle; dorsal metapleural area smooth; ventral metapleural area weakly rugose along anterior and posterior margins; metapleural pit present; metapleural sulcus indicated as a weak, shallow groove posterior to the metapleural pit; metapleural epicoxal sulcus indicated by crenulae.



**Figure 5.** *Telenomus dendrolimi* (Matsumura) from Fujian, female (SCBG\_E0010790) **A** antenna, lateral view **B** clava, ventrolateral view **A** head, anterior view **D** head, posterior view **E** mesosoma, dorsal view **F** mesosoma, dorsolateral view **G** metasoma, dorsal view **H** metasoma, ventral view.



**Figure 6.** *Telenomus dendrolimi* (Matsumura) from Fujian, male (SCBG\_E0010786) **A** dorsal habitus **B** lateral habitus **C** antenna, lateral view **D** genitalia, ventral view **E** genitalia, dorsal view.

*Wings.* Length of postmarginal vein about twice as long as stigmal vein. Fore wing apex reaching beyond T6.

*Metasoma.* T1 with 1 pair of sublateral setae, 2 pairs of lateral setae; foveae along anterior T1 distinct, elongate; foveae along anterior T2 distinct, with short costae extending less than ¼ the length of T2; T2 with sparse setae on lateral part of mediotergite and dorsomedial part of laterotergite; T3–T6 with a transverse line of long setae, setae absent along midline; laterotergites 3–6 glabrous; foveae along anterior S1 distinct, with costae extending to mid-length; foveae along anterior S2 distinct, with short costae extending less than ¼ the length of S2; S2 felt field indicated by coriaceous sculpture and setal patch; sparse setation present in posteromedial portion of S2; S3– S5 with a transverse line of long setae, setae absent along midline; S6 setose laterally, without setae along midline.

*Male genitalia.* Length of aedeagal lobe about  $0.3 \times$  length of aedeago-volsellar shaft, distally pointed; digiti large, about half maximum length of aedeagal lobe, with 3 digital teeth, basal ring about  $0.4 \times$  length of aedeago-volsellar shaft.

Species-group placement. Telenomus californicus-complex (Johnson 1984).

Host. Telenomus dendrolimi was reared from field-laid eggs of D. houi and D. punctatus in China, and Dendrolimus spectabilis Butler in Japan. Under labora-



**Figure 7.** Combined 28S and COI maximum likelihood phylogenetic analysis of *Telenomus* using a modified dataset of Polaszek et al. (2021). The number under the scale bar indicates the number of expected nucleotide substitutions per site. Support values (SH-aLRT and UFBoot) are indicated by colored circles at nodes. Terminal labels correspond to the taxa listed in the supplementary table (Suppl. material 1).

tory conditions, its alternative hosts include *D. kikuchii* and *D. punctatus*, *A. sinensis*, *A. pernyi*, *C. japonica*, and *E. pyretorum*.

**Material examined.** Allotype of *Telenomus dendrolimusi* Chu, 1937, • male: CHINA: Tangki (Tangxi), Chekiang (Zhejiang), ex. eggs of *Dendrolimus punctatus* Walker, 11.VI.1934, Joo-Tso Chu (deposited in Zhejiang University). Paratype of *Telenomus dendrolimusi* Chu, 1937, CHINA • 1 female, same data as allotype • 1 female, same data except collected on 22.VI.1933 (deposited in Zhejiang University). Other material • 2 females 1 male, JAPAN: (Kyushu) Hakozaki Fukuoka Jul. 31, 1959 Col. Y. Hirose, host: Egg of *Dendrolimus spectabilis* Butler, OSUC 71700-702 (deposited in OSUC) • 6 females 6 males, CHINA: Fujian, Xiapu County, 26°49'45.76"N, 119°57'55.3"E, ex. eggs of *Dendrolimus houi* (Lajonquiere) feeding on *Cryptomeria japonica* var. *sinensis* Miquel trees, 10.IX.2021, Guang-hong Liang, SCBG-E0010785-0010796 (deposited in SCBG).

**Distribution.** China (Liaoning, Hebei, Shandong, Henan, Jiangsu, Anhui, Fujian, Zhejiang, Jiangxi, Hubei, Hunan, Sichuan, Fujian, Guangdong, Guangxi, Guizhou, Yunnan), Japan, North Korea (Ryu and Hirashima 1985), Russia (Boldaruev 1969).

**Comments.** *Aholcus* Kieffer (Kieffer 1913) was erected for telenomines in which females have 10-merous antennae. *Aholcus* has since been treated as a junior synonym of *Telenomus* Haliday, a subgenus, a valid genus, and again as a junior synonym (Nixon 1935, Nixon 1937, Mineo et al. 2011, Taekul et al. 2014). Regardless of the generic value of the 10-merous female antenna, this character is useful for reducing the number of species that must be compared for identification. Nonetheless, there are dozens of species in this lineage, many of which have been described from Asia. *Telenomus dendrolimi* is a generalist that is known from southeastern China to Japan and may also be present much farther to the west. A reliable morphological diagnosis is not possible until the species of the broader region are revised– an effort that is beyond the scope of this project. However, by advancing the taxonomy of one described species, we are contributing toward this goal, and the combination of the description, images and sequence data provide a means to determine if a specimen is *T. dendrolimi*.

In this study, our identification of reared specimens was facilitated by their association with *Dendrolimus* eggs and matching them to paratype specimens of *T. dendrolimusi* and three non-type specimens of *T. dendrolimi* from Japan.

#### Acknowledgements

We thank Chunhong Wang (Zhejiang University) for imaging the type materials of *Telenomus dendrolimusi* Chu. We also extend our sincerest thanks to Guangyi Dai from Institutional Center for Shared Technologies and Facilities of South China Botanical Garden-CAS for the SEM guidance. This study was supported by the National Natural Science Foundation of China (32370499, 31900346). ZL is a participant of the Oak Ridge Institute for Science and Education (ORISE) Agricultural Research Service (ARS) Research Participation Program, supported by the USDA-ARS U.S. Vegetable Laboratory in Charleston, SC, USA. Elijah Talamas was supported by the Florida Department of Agriculture and Consumer Services, Division of Plant Industry. The

mention of trade names or commercial products in this article is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the USDA.

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Taxa, GenBank accession numbers, species group placement, collection location, and references associated with the sequence data used in the phylogenetic analyses Authors: Hua-Yan Chen, Elijah Talamas, Zachary Lahey, Norman F. Johnson, Ci-Ding Lu, Guang-Hong Liang

Data type: xlsx

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#### 28S ribosomal DNA cladogram of Telenomus

Authors: Hua-Yan Chen, Elijah Talamas, Zachary Lahey, Norman F. Johnson, Ci-Ding Lu, Guang-Hong Liang

Data type: docx

- Explanation note: Numbers on branches to the left of the forward slash indicate SH-aLRT values and numbers to the right of the forward slash are ultrafast boot-strap values.
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Link: https://doi.org/10.3897/jhr.97.139056.suppl2

# Supplementary material 3

#### Mitochondrial cytochrome oxidase I (COI) cladogram of Telenomus

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Data type: docx

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# Combined 28S and mitochondrial cytochrome oxidase I (COI) cladogram of *Telenomus*

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Data type: docx

Explanation note: Numbers on branches to the left of the forward slash indicate SHaLRT values and numbers to the right of the forward slash are ultrafast bootstrap values.Terminal labels correspond to the taxa listed in the Suppl. material 1.

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# Compatibility of released and adventive populations of Ganaspis kimorum Buffington, 2024, (Cynipoidea, Figitidae), parasitoid of the spotted-wing drosophila Drosophila suzukii (Matsumura, 1931)

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Academic editor: Miles Zhang | Received 16 September 2024 | Accepted 5 November 2024 | Published 10 December 2024

https://zoobank.org/31FB5119-BB54-444F-93D3-78C73EFADFA8

**Citation:** Stahl JM, Lisi F, Samarin T, Wang X, Beers EH, Daane KM (2024) Compatibility of released and adventive populations of *Ganaspis kimorum* Buffington, 2024, (Cynipoidea, Figitidae), parasitoid of the spotted-wing drosophila *Drosophila suzukii* (Matsumura, 1931). Journal of Hymenoptera Research 97: 1403–1415. https://doi.org/10.3897/jhr.97.137087

#### Abstract

Taxonomic and host associations have been closely studied within the *Ganaspis brasiliensis* (Ihering, 1905) (Hymenoptera, Figitidae) complex as parasitoids of the spotted-wing drosophila, *Drosophila suzukii* (Matsumura, 1931) (Diptera, Drosophilidae). Initially, five genetic groups (G1–G5) were identified that suggested the existence of cryptic species that vary in their host ranges and geographic distributions. What was referred to as the "G1" strain was recently described as *G. kimorum* Buffington, 2024, and approved for release as a classical biological control agent in the United States and parts of Europe. Concurrently, an adventive population of *G. kimorum* was found in British Columbia, Canada and is likely spreading through parts of the Pacific Northwest such as Washington State, USA. Here, we compare the reproductive compatibility and molecular similarity of laboratory-bred *G. kimorum* (collected in Tokyo, Japan) used for release in the USA and Europe with the adventive population found in Washington State, USA. Cross-breeding experiments between the Tokyo and the adventive population showed successful mating and the production of female offspring, indicating that they are reproductively compatible. For both populations, the mitochondrial *COI* 

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barcode region was sequenced and further confirmed the conspecificity of the Tokyo and adventive Washington populations with published *G. kimorum*. These findings will help to better understand and document the effects of releases of *G. kimorum* and the reproductive success of adventive and released populations.

#### **Keywords**

Biological control, cryptic species, reproductive compatibility

#### Introduction

Some insect species are widely distributed geographically and, as a result, isolated populations can exhibit biological, ecological, and genetic differences due to selective environmental pressure and local adaptation (Hopper et al. 1993). Such intraspecific variability can lead to the differentiation of populations characterized by varying levels of reproductive compatibility (Hopper et al. 1993; Turelli et al. 2001), as well as different biological characteristics that could, for example, impact their effectiveness as biological control agents (Stouthamer et al. 2000; Vallina et al. 2020). Moreover, mating incompatibility among parasitoid biotypes is often attributed to the presence of cryptic species that exhibit differences in genetic, physiological, behavioral, and/ or ecological traits, despite morphological similarity (Bickford et al. 2007; Heraty et al. 2007). For example, there is an increasing realization that maternally inherited endosymbionts, such as Wolbachia or Cardinium present in arthropods, can cause cytoplasmic incompatibility (e.g., Perlman et al. 2014; Gebiola et al. 2016; Bruzzese et al. 2022). In such cases, cross-breedings between males infected with the endosymbiont and uninfected females or females infected with a different endosymbiont strain result in reproductive incompatibility.

In this context, understanding the reproductive status among populations of biological control agents can be crucial to predict the success of multiple introductions and subsequent admixture impact on pest control efforts (Stouthamer et al. 2000; Dayrat 2005; Gebiola et al. 2016). To this aim, laboratory cross-breeding experiments and analyses of genetic diversity of different geographical populations through DNA barcode sequencing or genome assembly can play an essential role in the taxonomic identification and detection of cryptic species, especially for parasitoids employed as biological control agents (Desneux et al. 2009; Seehausen et al. 2020). Here, we investigate two populations of Ganaspis kimorum Buffington, 2024 (Hymenoptera, Figitidae), one of the main parasitoids attacking the spotted-wing drosophila, Drosophila suzukii (Matsumura, 1931) (Diptera, Drosophilidae). When it was first reported from Japanese field collections of wild cherries infested by D. suzukii, it was assigned as the suzukii- type of G. xanthopoda Ashmead (Kasuya et al. 2013) and then later as G. brasiliensis (e.g., Buffington and Forshage 2016; Daane et al. 2016; Giorgini et al. 2019) or G. cf. brasiliensis (e.g., Girod et al. 2018a; Seehausen et al. 2020). Nomano et al. (2017) divided the G. cf. brasiliensis complex, based on DNA sequences of the COI barcode region, into five groups (G1–G5) and reported that two G. cf. brasiliensis groups (G1 and G3) were reared from *D. suzukii* in Asia. Later surveys confirmed that G1 and G3 successfully attacked *D. suzukii* and often co-occur at the same collection sites (Giorgini et al. 2019; Daane et al. 2021), but based on laboratory test have different host ranges with G1 being more specialized on *D. suzukii* than G3 (Girod et al. 2018b; Daane et al. 2021). Based on cross-breeding experiments showing G1 and G3 mating incompatibility, detailed molecular work (Gariepy et al. 2024; Hopper et al. 2024; Seehausen et al. 2024), and taxonomic differences in the ovipositor, G1 and G3 were determined to be separate species and named *G. kimorum* and *G. lupini*, respectively (Sosa-Calvo et al. 2024).

As the most host specific Asian D. suzukii parasitoid, G. kimorum was selected for release as a biological control agent in parts of Europe (Fellin et al. 2023) and the USA (Gariepy et al. 2024), with field release approved for G. kimorum (initially as G. brasiliensis G1 (Tokyo)) and began in Italy in 2021 (Lisi et al. 2022) and the USA in 2022 (Gariepy et al. 2024). Concurrently, an adventive population of Ganaspis sp. (initially reported as G. cf. brasiliensis G1) was discovered in Northwestern North America, first in British Columbia, Canada (Abram et al. 2020), and later across the border in Washington, USA (Beers et al. 2022) and is likely to expand to other regions in the USA. All specimens of the adventive Ganaspis sp. attacking D. suzukii in the Pacific Northwest have thus far been identified (using morphology and DNA barcoding) as G. kimorum, still it is important to confirm if the adventive population is similar to G. kimorum collected in Japan and being released across the USA. Moreover, given the wide distribution of G. kimorum in East Asia (Daane et al. 2016; Girod et al. 2018b; Giorgini et al. 2019), understanding its genetic diversity and potential admixture impact is crucial at the early stage of this biological control program for D. suzukii. Here, we aimed to confirm the reproductive compatibility of the released and adventive populations of G. kimorum and confirm their molecular similarity or dissimilarity through barcoding. This will provide baseline information for the status of the G. kimorum as it pertains to predictions for biological control success.

#### Material and methods

#### Rearing of Ganaspis kimorum

Two colonies of *G. kimorum* were maintained at the University of California Kearney Agricultural Research and Extension Center in California. The first colony was established from material originally collected in Tokyo, Japan, in 2015 (Girod et al. 2018b; released in the USA and Italy as a biological control agent: 'rel'), the second was collected in Washington, USA, in 2020 (Beers et al. 2022; adventive North American population: 'adv'). Both colonies were maintained at  $25 \pm 5$  °C,  $35 \pm 5$ % relative humidity and 16:8 L:D photoperiod and rearing protocols were similar. Following Rossi-Stacconi et al. (2022), 10–15 fresh, rinsed blueberries were placed on paper towels in plastic containers (80 mm high, 90.5 mm diameter) with mesh lids and exposed to around 50 D. suzukii (50:50 sex ratio) for 24–72 h. Cotton wicks soaked in sugar water served as nutrition for the adult flies. Then, the eggs and the hatched D. suzukii larvae were exposed to the parasitoids by adding around 12 G. kimorum (50:50 sex ratio) to each container for 72 h. Cotton wicks soaked in honey water and honey droplets on the mesh lid replaced every second day served as nutrition for the adult parasitoids. After the parasitoids were removed, the paper towels were kept moist until G. kimorum offspring emerged and adult G. kimorum were then collected daily by aspiration and immediately used for the colony. The rearing containers described above were placed in mesh cages ('BugDorm-4090 Insect Rearing Cage 47.5 × 47.5 × 47.5 cm', MegaView Science Co. Ltd., Taichung, Taiwan) as an additional barrier to separate the two colonies. All cages were inspected before opening and if there were any stray wasps that had escaped a container they were removed. We had separate handling cages for transferring G. kimorum individuals from the two colonies to prevent escapees and contamination and transferred them with mouth aspirators only used for the specific colony. Whenever possible, one person worked on one colony, and afterwards a second person on the other.

#### Cross-breeding experiment

The two G. kimorum populations were cross-bred in 2022–2023 with the following treatments: 'rel' female × 'adv' male, and 'adv' female × 'rel' male. To establish what proportion of G. kimorum females produces female offspring under the experimental conditions and also possible cytoplasmic incompatibility, the controls 'rel' female × 'rel' male, and 'adv' female × 'adv' male were added. If cytoplasmic incompatibility occurs, cross-breedings between infected males with uninfected females can result in reproductive incompatibility. Unmated individuals of G. kimorum were collected the day they emerged and placed with a mate for 1 h inside a plastic vial (70 mm high, 20.5 mm diameter) with a sponge lid that was coated in a thin layer of honey. They were observed for the first 10 min, and once every 10 min after that within the hour. The occurrence of mating behavior was recorded when mating was observed. After 1 h, the couple was placed into a rearing container, as previously described, that contained blueberries with 0-24 h old D. suzukii eggs and larvae. After 72 h, the parasitoids were removed and placed into 1.5 ml Eppendorf tubes filled with 90% ethanol to be stored at -80 °C. Emerged offspring was sexed and counted. Since G. kimorum is haplodiploid, meaning that males emerge from unfertilized eggs and females from fertilized eggs, the presence of daughters indicates successful mating. To confirm the viability of emerged daughters, replicates with both female and male offspring were used for a secondary experiment. Offspring were collected and stored in vials with honey until females and males had had at least 24 h of time to mate before one female and one male from each vial were placed onto new blueberries with D. suzukii immatures, as described previously. Only a maximum of three daughters per replicate was used to establish F1 viability. Afterwards, all F1 offspring were similarly stored in 90% ethanol.

#### Statistical analyses of cross-breeding experiment

The proportion of female *G. kimorum* producing daughters was compared between treatments and controls with a generalized linear model (GLM) with a binomial error distribution. Only cross-breedings that produced offspring were included. The relationship between observed mating and the occurrence of female offspring was investigated with a Pearson's product-moment correlation. All statistics were conducted in R version 3.6.2 (R Core Team 2020) and RStudio version 1.2.5033 (RStudio Team 2016) as well as package 'car' (Fox et al. 2016).

#### Barcoding

A total of 127 adult parasitoids were used for DNA barcoding. DNA was extracted from the whole body of each specimen using the FastDNA<sup>\*</sup> kit and the FastPrep<sup>\*</sup> Instrument (MP Biomedicals, Santa Ana, California, USA), according to the manufacturer's instructions, with minor modifications. Extracted DNA was quantified using a Nanodrop 2000c spectrophotometer (Thermo Fischer Scientific, USA), diluted to approximately 50 ng/ $\mu$ L and stored at -20 °C.

The barcode region of the mitochondrial coding gene Cytochrome Oxidase subunit 1 (*COI*) was amplified with the universal primer pairs LCO/HCO (LCO: 5'- GGT-CAACAAATCATAAAGATATTGG – 3' and HCO: 5' – TAAACTTCAGGGTGAC-CAAAAAATCA - 3', 440–688 bp) (Folmer et al. 1994). Polymerase chain reaction (PCR) was conducted in a 20  $\mu$ l mixture containing 10  $\mu$ l of GoTaq<sup>\*</sup> Green Master Mix (Promega, Madison, Wisconsin, USA), 2  $\mu$ l of extracted DNA, 0.5  $\mu$ l of each primer and ultrapure water up to the final volume.

The *COI* target region was amplified by setting the following profile of the T100 Thermal Cycler (Bio-Rad): 94 °C for 10 min, 35 cycles of 94 °C for 1 min, 50 °C for 1 min and 72 °C for 1.5 min, followed by final extension at 72 °C for 1.5 min. PCR products were sent to the University of California, Berkeley DNA sequencing facility for direct sequencing of both strands using the ABI Big Dye V3.1 terminator sequencing reaction kit (Perkin-Elmer/ABI, Weiterstadt, Germany) on an ABI 3707xl DNA Analyzer (Perkin-Elmer) with POP 7 and a 50 cm array. A Basic Local Alignment Search Tool (BLAST) comparison of amplified *COI* sequences was performed using the NCBI database.

Sequences were trimmed using FinchTV (Geospiza, Inc., Seattle, Washington, USA) software by removing terminal ambiguous regions and a multiple sequence alignment was performed using the MUSCLE algorithm (Edgar 2004) in MEGA (version 11) (Tamura et al. 2021). Forty-two available *COI* sequences of *G*. cf. *brasiliensis* were downloaded from the NCBI database in March 2023, including those originating from Nomano et al. (2017), Giorgini et al. (2019) and Abram et al. (2020), and then added to the dataset before analysis.

A neighbor-joining tree (Saitou and Nei 1987) was constructed using the Maximum Composite Likelihood method with 1000 bootstrap replicates in MEGA (version 11) (Tamura et al. 2021). A *G. xanthopoda* (Ashmead, 1896) sequence was included in the analysis as the outgroup.

#### Results

#### Cross-breeding experiment

All four cross-breedings yielded *G. kimorum* offspring (Table 1). The production of daughters suggests that successful mating had occurred. There were no significant differences between the cross-breedings in the proportion of females that produced daughters (GLM, DF = 3, 55,  $\chi^2 = 0.74$ , p = 0.864).

Sixty-three percent of the females producing offspring were observed to have mated with their male during the first hour. There was no correlation between observed mating and the occurrence of female offspring (Pearson's correlation, t = -0.41, DF = 57, p = 0.684); some females that had not been observed mating produced daughters and vice versa.

The majority of the F1 generation did not produce offspring. The one daughter from the 'rel' female × 'adv' male cross-breeding that did produce offspring, also produced female offspring. Similarly, the two cross-breedings between 'adv' females x 'rel' males F1 generation producing offspring included daughters, indicating viable original cross-breedingss.

#### Barcoding

The molecular characterization based on the mitochondrial *COI* gene confirmed that generated high quality reads from specimens showed 99–100% sequence similarity with *G. brasiliensis* isolate USNMENTO (accession number: MT559420.1), *G. xan-thopoda* isolate suz21 (accession number: LC122451.1) and isolate suzukii type 3 (accession number: AB678736.1), and sequences were submitted to GenBank (accession number: PP980973 and PQ493166–PQ493291). Moreover, both the parental 'rel' and 'adv' *G. kimorum* used in the cross-breeding experiment matched with the same accession numbers showing a high sequence similarity (99–100%).

The phylogenetic tree showed two main clusters with an extended group referring to the *G. kimorum* samples (Fig. 1, blue). The *G. kimorum* cluster included the crossbreedings of the 'rel' and 'adv' *G. kimorum* in this work, as well as samples of *G.* cf. *brasiliensis* collected both in Japan and China and reported in Nomano et al. (2017) and Giorgini at al. (2019). The second extended cluster showed a substructure consisting of a clade made of the *G.* cf. *brasiliensis* G2 sequences (LC122441.1 and LC122440.1; Fig. 1, red) and another clade incorporating sequences of *G. lupini*, *G.* cf. *brasiliensis* G4, and *G. brasiliensis* s. str. (Fig. 1, yellow, orange, green).

**Table 1.** Females producing daughters after cross-breedings. 'rel' = released population, 'adv' = adventive population, 'WA' = Washington State, USA.

Cross-	Origin	Origin	Parental	Total progeny	Females producing	Females producing	Females producing
breeding	of female	of male	females (n)	(n)	offspring (n)	daughters (n)	daughters (%)
ʻrel' × ʻadv'	Tokyo	WA	68	143	25	18	72.0
ʻrel' × ʻadv'	WA	Tokyo	28	29	9	7	77.8
ʻrel' × ʻrel'	Tokyo	Tokyo	36	125	17	11	64.7
ʻadv' × ʻadv'	WA	WA	22	29	8	5	62.5



**Figure 1.** Neighbor-joining tree; Neighbor-joining tree based on *COI* sequences for *G. kimorum* specimens used in the cross-breeding experiment (arrows) and on sequences retrieved from NCBI. The accession number, collection locality and host are also reported for each sequence. *Ganaspis xanthopoda* AB624299 was used as outgroup. Bootstrap values are indicated on the branches (values < 50% are not shown).

#### Discussion

Our results confirm that the *G. kimorum* currently being released in the framework of the classical biological control program against *D. suzukii* is reproductively compatible with the adventive population of *G. kimorum* reported in North America. This was confirmed by cross-breeding of the adventive and the imported *G. kimorum* populations producing female progeny providing evidence for reproductive compatibility, and with the clustering of the *COI* barcoding region.

Taxonomic status and reproductive compatibility of introduced parasitoids and previously released, adventive or native parasitoids can be crucial for the outcome of biological control programs (Vallina et al. 2020). For example, the presence of incompatible populations of biological control agents inhabiting the same ecological niche can lead to competition (Paterson et al. 2016). On the other hand, admixture between different populations can introduce new genetic variations and potentially enhance their adaptability to diverse environments (Chapple et al. 2013; Dlugosch et al. 2015). The majority of the F1 generation in our study did not produce offspring. Since this occurred in both controls, we attribute this to the rearing conditions but with the cross-bred F1 generations producing some offspring a change through admixture could be at play. However, the benefits of admixture are not guaranteed and can be limited by factors such as genetic divergence and the timing of admixture (Rincon et al. 2006; Havill et al. 2012). For example, while admixture can introduce beneficial alleles, it can also lead to outbreeding depression or the dilution of local adaptations (Barker et al. 2018). If the introduced population has low genetic diversity to begin with, admixture may not provide significant benefits as there are fewer beneficial alleles to mix (Dlugosch et al. 2015; Barker et al. 2018).

Given the wide distribution of G. kimorum in East Asia (Daane et al. 2016; Girod et al. 2018b; Giorgini et al. 2019), understanding its genetic diversity and reproductive compatibilities among geographical populations is crucial for effective biological control of D. suzukii. The Asian origin of the adventive G. kimorum populations in Pacific Northwest is unclear, as is whether they originated from multiple sources. A recent genomic analysis showed a high similarity of the currently released Tokyo strain and individuals collected from the British Colombian population and Wolbachia sequences were found in the genomic sequencing of different populations (Hopper et al. 2024). Our results provide evidence that the currently released and adventive populations are not only genetically identical but also reproductive compatible. In our crossbreedings between the released and the adventive populations, combinations of both sexes were prepared, and for both combinations ('rel' female × 'adv' male as well as 'adv' female × 'rel' male) proof of successful mating could be obtained, suggesting reproductive compatibility. Our results also ruled out potential cytoplasmic incompatibility between populations caused by a symbiotic Wolbachia. A previous test with the Tokyo G. kimorum females also revealed that unmated females produced male offspring only, i.e., ruling out the possibility of thelytoky due to Wolbachia infection in this species (Hopper et al. 2024). We can therefore expect interactions between released and adventive G. kimorum in North America might occur. Future studies should investigate the origin of adventive G. kimorum populations in the Pacific Northwest and the potential effects of admixture on their fitness and effectiveness as biological control agents. By carefully considering the genetic diversity and ecological characteristics of different G. kimorum populations, we can optimize the introduction of biological control agents and improve their long-term success.

This study has practical implications for the classical biological control program of *D. suzukii*. Since the laboratory colony descends from only a small subset of the adventive population, our results cannot eliminate the possibility of additional species within the *G. brasiliensis* species group being present in the adventive range, which might have less or no compatibility with the released material. However, aligning with Beers et al. (2022), this study is further evidence of adventive *G. kimorum*, the specific agent with government approval for release in Italy and the USA. Having successfully established in North America, the adventive *G. kimorum* population will likely be welladapted to climate conditions in the adventive range. This creates an opportunity for re-distribution from the adventive range to other locations within the administrative region (depending on the legislation of the relevant state, province, or country), as has been considered or realized for other biological control agents (Braman et al. 2021; Bergh et al. 2023).

# Conclusion

Our results settle potential concerns about mating incompatibility and pave the way for re-distribution in the USA of the adventive *G. kimorum* population and imported *G. kimorum* from Tokyo. Overall, this study contributes to a better understanding of the reproductive status of two *G. kimorum* populations being used for classical biological control and improves predictions of the outcome of field releases for classical biological control against *D. suzukii* in North America. Still there is the possibility of viability or phenotypic effects resulting from the admixture of the two populations that has yet to be determined.

# Acknowledgements

We thank Jeanne Gourlaouen, Emily Henry, Gadiel Leon, Michael Lopez, and Thomas Bultez for their technical assistance and fly and parasitoid colony maintenance. The authors are grateful to Paul Abram for his helpful comments on an earlier version of this manuscript. This project received funding from USDA NIFA SCRI 2020-51181-32140, USDA-NIFA OREI 2022-51300-37890, USDA APHIS Farm Bill Fund (60-8010-4-001), and USDA ARS Areawide Pest Management Program (administered by Stephen Young, National Program leader). Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the USDA. USDA is an equal opportunity provider and employer.

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RESEARCH ARTICLE



# A new species and new records of Hoplitis Klug (Hymenoptera, Megachilidae) from Russia

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Academic editor: Michael Ohl | Received 18 October 2024 | Accepted 30 November 2024 | Published 20 December 2024

https://zoobank.org/3B4F61BA-8D5D-41C0-BAD7-E748C82C503F

**Citation:** Fateryga AV, Proshchalykin MYu, Abakumov EV (2024) A new species and new records of *Hoplitis* Klug (Hymenoptera, Megachilidae) from Russia. Journal of Hymenoptera Research 97: 1417–1433. https://doi.org/10.3897/jhr.97.139623

#### Abstract

*Hoplitis* (*Hoplitis*) andreasmuelleri **sp. nov.**, a member of the *H. adunca* species group, is described from the vicinity of Kurush (Samurskiy National Park, Dagestan, Russia). The new species is closely related to *H. dagestanica* Fateryga, Müller & Proshchalykin, 2023. Females of *H. andreasmuelleri* can be easily distinguished from those of *H. dagestanica* by a black antenna, a small impunctate triangular area at the base of the clypeus, ferruginous tarsi, sparse and often interrupted apical band of hairs on terga 1–5, and a whitish scopa. Males of *H. andreasmuelleri* can be easily distinguished from those of *H. andreasmuelleri* can be easily distinguished from those of *H. andreasmuelleri* can be easily distinguished from those of *H. adgestanica* by a black antenna, the last antennal article not tapering towards the apex, antennal articles 5–12 not modified, ferruginous tarsi, and the lateral lobes of the bilobed membranous appendage at the apical margin of sternum 6 laterally elongated into a rounded tip and medially not separated from each other by an emargination. Females of *H. andreasmuelleri* (Morawitz, 1875) is reported from Russia (Altai Republic) for the first time. New distributional records are reported for *H. (Alcidamea) fulva* (Eversmann, 1852) and *H. (Anthocopa) perezi* (Ferton, 1894). *Hoplitis (Anthocopa) papaveris* (Latreille, 1799) is excluded from the fauna of Crimea and the south of European Russia from where it was previously reported based on a misidentification of *H. perezi*. The biology of *H. perezi* in Crimea is briefly discussed. An updated distributional list of all 39 species of *Hoplitis* known from Russia is provided.

#### **Keywords**

Altai, Caucasus, Crimea, megachilid bees, osmiine bees, Palaearctic region, taxonomy

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# Introduction

With 391 species described so far, *Hoplitis* Klug is the largest genus of osmiine bees (Hymenoptera, Megachilidae, Osmiini) (Müller 2024). The genus is distributed in the Palaearctic, Nearctic, and Afrotropical regions; a few species also occur in the Oriental region (Michener 2007). The genus *Hoplitis* is especially diverse in the Palaearctic region, where 14 subgenera and 315 species occur (Praz et al. 2008; Ungricht et al. 2008; Sedivy et al. 2012a; Müller 2024). At least 64 Palaearctic species are still undescribed, of which at least 50 species belong to the largest subgenus *Hoplitis* (*Hoplitis*) (Aubert et al. 2024; Müller 2024). This subgenus comprises several species groups, the largest of which is the *H. adunca* species group, one of the taxonomically most challenging osmiine bee taxa due to the high morphological uniformity among its species, especially in the female sex (Müller 2016, 2024). The nesting biology of *Hoplitis* is extremely diverse and encompasses the whole diversity observed across the osmiine bees (Müller 2024).

Twenty-eight species of *Hoplitis* were reported from Russia in the "Annotated catalogue of the Hymenoptera of Russia" (Proshchalykin and Fateryga 2017). Subsequently published updates excluded five of them and added 14 other species (Fateryga et al. 2019, 2023; Proshchalykin and Müller 2019; Fateryga and Proshchalykin 2020, 2024; Fateryga and Ivanov 2023; Proshchalykin et al. 2023), including two new species of *Hoplitis* (*Hoplitis*) (Fateryga et al. 2023). The purpose of the present contribution is to report new data on the genus *Hoplitis* from Russia. One species is described as new to science and one species is reported from Russia for the first time; new distributional records of two other species are also reported.

# **Material and methods**

The acronyms for the institutions where the studied specimens are deposited are as follows:

- CAFK Research collection of A.V. Fateryga, Feodosiya, Russia;
- CFUS V.I. Vernadsky Crimean Federal University, Simferopol, Russia;
- ETHZ Entomological Collection of ETH Zurich, Switzerland;
- **FSCV** Federal Scientific Center of the East Asia Terrestrial Biodiversity of the Far Eastern Branch of the Russian Academy of Sciences, Vladivostok, Russia;
- **ZISP** Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

Morphological terminology and definitions for body measurements follow Michener (2007) with the following specifications: i) the distance between lateral ocellus and preoccipital margin was measured in top view rather than in lateral view; ii) the diameter of an ocellus includes the ocellar border, which is often of the same color as the surrounding cuticle thereby differing from the usually light color of the central part of the ocellus; iii) the length of a segment of the labial palpus was measured from its sclerotized base to the sclerotized base of the subsequent segment; iv) the length of an antennal article was measured along its ventral margin, while its width corresponds to the maximal width of the article; v) numbering of antennal articles starts from the scapus, which is antennal article 1, and ends with the last flagellomere, which is antennal article 12 (females) or 13 (males). Measurements to the nearest 0.1 mm or 0.5 mm (for body length) were taken using an ocular micrometer of an MBS-9 stereomicroscope.

Photographs of the specimens were taken with a Canon EOS 550D digital camera and a Yongnuo YN-14EX macro flash attached to an Olympus SZX16 stereomicroscope, except the photographs of the habitus, which were taken with a Canon EOS RP digital camera with a Sigma AF 105 mm f/2.8 macro lens and a Yongnuo YN-14EX macro flash. The final illustrations were processed for sharpness, contrast, and brightness with Adobe Photoshop CS2 software.

The distribution of species in Russia is based on Proshchalykin and Fateryga (2017) and subsequently published updates (Byvaltsev and Proshchalykin 2019; Fateryga et al. 2019, 2023; Proshchalykin and Müller 2019; Fateryga and Proshchalykin 2020, 2024; Levchenko 2020, 2023; Fateryga and Ivanov 2023; Proshchalykin et al. 2023). The distribution outside Russia is based on Müller (2024). New distributional records (both national and provincial) are marked in the text with an asterisk (\*).

#### **Results and discussion**

#### Hoplitis (Alcidamea) fulva (Eversmann, 1852)

- Osmia fulva Eversmann, 1852: 63, ♂ (type locality: "in prov. Orenburg. australi, in prov. Saratov. et Astrachanensi, et in terris transuralensibus" [Russia: Southern Urals and Lower Volga Region]), syntypes, ♂♂, Institute of Systematic and Experimental Zoology of the Polish Academy of Sciences, Krakow, Poland.
- *Osmia grandis* Morawitz, 1872: 54, ♀♂ (type locality: "Sarepta" [Russia: Volgograd], according to the lectotype designation by Proshchalykin et al. 2017: 25), lectotype, ♂, ZISP. Synonymized by Ducke 1900: 202.

**Material examined (new records).** RUSSIA. • Astrakhan Province: Ryn-Peski,  $1 \Leftrightarrow$  [ZISP]. • Volgograd Province: 18 km NNE Kalach-na-Donu, 10–13.VII.2015,  $4 \Leftrightarrow$ , leg. M. Proshchalykin, V. Loktionov, M. Mokrousov, S. Belokobylskij [FSCV].

**Distribution.** Russia: European part (East, \*South, Crimea), Urals. – Eastern Europe, Armenia, Azerbaijan, Turkey, Syria, Jordan, Kazakhstan, Mongolia, China.

# Hoplitis (Anthocopa) perezi (Ferton, 1894)

Fig. 1

*Osmia perezi* Ferton, 1894: 207, ♀ (type locality: "Miramas" [France], according to the lectotype designation by Tkalců 1969: 330), lectotype, ♀, Muséum National d'Histoire Naturelle, Paris, France.

*Osmia papaveris convolvuli* Ducke, 1899: 214, ♀♂ (type locality: "Triest" [Italy], "Fiume" [Croatia], "Sicilien" [Italy], "Spanien" [Spain]), syntypes, ♀♀, ♂♂, Natural History Museum, Vienna, Austria and other collections not indicated. Synonymized by Tkalců 1969: 330.

Material examined (new records). RUSSIA. • Astrakhan Province: 8 km SE Promyslovka, 45°40'23"N, 47°14'26"E, 21.V.2019, 1 ♀, leg. M. Proshchalykin, V. Loktionov [FSCV]. • Krasnodar Territory: Temryuk District, Taman Peninsula, vicinity of Priazovskiy, 25.VI.2012, 1 2, leg. I. Popov [CAFK]. • Crimea: Tarkhankut Peninsula, Kipchak Bay, 28.V.2004, 1 3, leg. S. Ivanov [CFUS]; • ibid., 23.VI.2007, 1 ♀, leg. A. Fateryga [CFUS]; • ibid., 27.VI.2007, 1 ♀, at nest, leg. A. Fateryga [CAFK]; • ibid., 1.VI.2012, 1 3, leg. V. Zhidkov [CFUS]; • ibid., 14.VI.2012, 1 ♂, leg. V. Zhidkov [CFUS]; • ibid., 12.VI.2013, 1 ♀, leg. V. Zhidkov [CFUS]; • ibid., 26–27.VI.2013, 1 2, leg. V. Zhidkov [CFUS]; • ibid., 14.VI.2014, 1 2, leg. V. Zhidkov [CFUS]; • Tarkhankut Peninsula, Bolshov Kastel Bay, 31.V.2014, 1 9, leg. V. Zhidkov [CFUS]; • ibid., 31.V.2014, 1 d, leg. V. Zhidkov [CAFK]; • Adym-Chokrak Valley, 9.VII.2011, 1 3, leg. V. Zhidkov [CFUS]; • Yalta, 21.VI.1999, 1  $\bigcirc$ , leg. S. Ivanov [CFUS]; • ibid., 17.VII.2004, 1  $\bigcirc$ , leg. A. Fateryga [CFUS]; • Yalta, Seaport, 8.VI.2011, 1 &, on Malva sylvestris, 1 &, on Convolvulus arvensis, leg. A. Fateryga [CFUS]; • Yalta, Sovetskoye, 5.VI.2010, 1 2, 1 3, leg. S. Ivanov [CFUS]; • ibid., 6.VI.2010, 1 3, on Echium vulgare, leg. S. Ivanov [CFUS]; • Yalta Reserve, below Mt. Aypetri, 6.VI.2010, 2 3, leg. V. Zhidkov [CFUS]; • Mt. Demerdzhi, Angarskiy Pass, 15.VI.2002, 1 &, leg. S. Ivanov [CFUS]; • Kanaka Valley, 27–28.V.2000, 2 ♀, leg. S. Ivanov [CFUS]; • Karadag Reserve, 24.V.2000, 1 ♀, leg. Yu. Budashkin [CFUS]; • ibid., 20–21.VI.2004, 1 2, leg. Yu. Budashkin [CFUS]; • ibid., 15.VI.2008, 1 2, leg. V. Zhidkov [CFUS]; • Opuk Reserve, 1.VI.2002, 1 3, leg. S. Ivanov [CFUS].

**Distribution.** Russia: European part (\*South, North Caucasus, \*Crimea). – Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkmenistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan.

**Remarks.** All previous reports of *Hoplitis papaveris* (Latreille, 1799) from Crimea (Fateryga et al. 2018 and references therein; Fateryga and Ivanov 2023), as well as the report from the south of European Russia (Fateryga and Proshchalykin 2020), were based on a misidentification of *H. perezi*. Therefore, *H. papaveris* should be excluded from the fauna of these regions. *Hoplitis perezi* is confined in Crimea to open land-scapes with a steppe vegetation (Fig. 1A). Females nest in the ground, on horizontal surfaces. The nest hole and its entrance are lined with fragments of petals of *Convol-vulus cantabrica* L. (Convolvulaceae) (Fig. 1C, D). Females use flowers of the same plant species as the source of pollen and nectar (Fig. 1B). Following nest construction, the female dismantles the entrance collar of petals and fills the nest entrance with earth. Females of *H. perezi* often use abandoned nest holes of other hymenopterans for nesting, e.g., burrows of *Tropidodynerus interruptus* (Brullé, 1832) (Hymenoptera:



**Figure 1.** *Hoplitis perezi* (Ferton, 1894) in Crimea **A** habitat in Bolshoy Kastel Bay, Tarkhankut Peninsula **B** female on a flower of *Convolvulus cantabrica* L., Yalta **C** flower of *C. cantabrica* with cuts made by *H. perezi*, Yalta **D** entrance of a freshly constructed nest, Lisya Bay **E** old nest in the entrance turret of an abandoned nest of *Paragymnomerus signaticollis tauricus* (Kostylev, 1940), Bolshoy Kastel Bay, Tarkhankut Peninsula.

Vespidae) (Fateryga 2009, the bee reported as *H. papaveris*) or even entrance turrets of *Paragymnomerus signaticollis tauricus* (Kostylev, 1940) (Hymenoptera: Vespidae) (Fateryga 2018, the bee also reported as *H. papaveris*). In the latter case, the nest entrance of *H. perezi* can be situated aboveground (Fig. 1E). According to the previously published data on the biology of this species, mainly from France and Italy (Ferton 1894, 1895, 1897, 1901; Ducke 1899, 1900; Benoist 1931; Müller 2024), females of *H. perezi* excavate burrows in hard and generally horizontal soil (ca. 2–3 cm deep) and construct 1–3 linearly arranged cells entirely built of several layers of petals of *Convol-vulus* spp., particularly *C. cantabrica*; petals are also used to build partitions between adjacent cells and to line the entrance burrow. Thus, we confirm the close relationship of *H. perezi* with flowers of *C. cantabrica* but cannot confirm that the nest burrow is excavated. At least in Crimea, this species is confirmed to use pre-existing burrows, at least in some cases.

*Hoplitis (Hoplitis) andreasmuelleri* Fateryga & Proshchalykin, sp. nov. https://zoobank.org/0CC62277-14AA-43E4-BEB5-C2C6F4F3EBB4 Figs 2, 3

Diagnosis. Among the western Palaearctic Hoplitis species of the subgenus Hoplitis s. str., the female of *H. andreasmuelleri* (Fig. 2A) is unequivocally characterised by the following combination of characters: i) sternum 6 lateroapically with distinct submarginal carina and medioapically elongated into a very short triangular tooth; ii) proboscis not reaching to trochanter of hind leg in repose and second segment of labial palpus distinctly shorter than maximal length of mesosoma measured in lateral view (Fig. 2A); iii) clypeus and galea of proboscis normally haired, without apically curved or wavy pollen-collecting bristles; iv) lateral lobes of pronotum not inflated; v) apex of inner tibial spur of hind leg strongly curved at an angle of 30 to 40 degrees, spur yellowish (Fig. 2C); vi) clypeus medially without uninterrupted sharp and narrow longitudinal carina, basally with a small impunctate triangular area (Fig. 2B); vii) disc of tergum 5 covered with moderately dense and appressed whitish pilosity (Fig. 2E); viii) when seen from behind, longest erect hairs on median half of tergum 1 only about 1/7 to 1/8 as long as maximal length of lateral hair tuft; ix) punctation of lateroapical part of scutum with interspaces reaching the diameter of one puncture; x) metasomal scopa whitish (Fig. 2A); xi) tarsi of all legs predominately ferruginous (Fig. 2A); xii) antenna completely black (Fig. 2B); xiii) marginal zone of terga 1-5 with sparse and often interrupted band of whitish hairs (Fig. 2D). The male of H. andreasmuelleri (Fig. 3A) is easily diagnosed by the following combination of characters: i) apical margin of tergum 7 medially rounded (Fig. 3D); ii) second segment of labial palpus longer than compound eye (Fig. 3A); iii) antenna black (Fig. 3B, C); iv) last article of antenna about 1.7× as long as basally wide (Fig. 3B); v) in dorsal view, posterior side of the last article of antenna strongly widened towards apex (Fig. 3C); vi) antennal article 3 about 1.3× as long as apically wide and longer than article 4 (Fig. 3B, C); vii) ventral margin of antennal articles 3-4 distinctly widened distally (Fig. 3B); viii) antennal articles 4-5 as wide as article 3 apically and in dorsal view wider than articles 6–12 (Fig. 3C); ix) lateral lobes of bilobed membranous appendage at apical margin of sternum 6 moderately haired, distinctly wider than long, laterally elongated into a distinct rounded tip and medially not separated from each other by an emargination (Fig. 3E); x) apical margin of the sclerotised base of sternum 6 with two very narrow and diverging median tufts of few long hairs, which surpass the centre of the membranous appendage of sternum 6; xi) marginal zone of sterna 4–5 reddish and very densely punctured with interspaces much narrower than the diameter of one puncture (Fig. 3E).

**Differential diagnosis.** Among other species of *Hoplitis* (*Hoplitis*) known from Dagestan, viz. *H.* (*H*). *adunca* (Panzer, 1798), *H.* (*H*). *anthocopoides* (Schenck, 1853), *H.* (*H*). *dagestanica* Fateryga, Müller & Proshchalykin, 2023, *H.* (*H*). *linguaria* (Morawitz, 1875), and *H.* (*H*). *manicata* Morice, 1901 from the *H. adunca* species group and *H.* (*H*). *astragali* Fateryga, Müller & Proshchalykin, 2023 from the *H. monstrabilis* 



**Figure 2.** *Hoplitis andreasmuelleri* Fateryga & Proshchalykin, sp. nov.,  $\bigcirc$ , paratype **A** habitus in lateral view **B** head in front view **C** part of hind leg with inner tibial spur **D** terga 1–2 in dorsal view **E** terga 5–6 in dorsal view. Scale bars: 1 mm.

species group (Fateryga and Proshchalykin 2024), the new species is the most closely related to H. dagestanica. Females of H. andreasmuelleri can be easily distinguished from those of *H. dagestanica* by black antenna (flagellum partly dark reddish-brown anteriorly in *H. dagestanica*), a small impunctate triangular area at the base of clypeus (absent in *H. dagestanica*), ferruginous tarsi (brown in *H. dagestanica*), sparse and often interrupted apical band of hairs on terga 1-5 (denser uninterrupted band in H. dagestanica), and whitish scopa (yellowish in H. dagestanica). Males of H. andreasmuelleri can be easily distinguished from those of H. dagestanica by black antenna (flagellum predominantly dark reddish-brown in H. dagestanica), last antennal article not tapering towards apex (tapering towards apex with ventral margin slightly concave in H. dagestanica), antennal articles 5-12 not modified (with roundish bump or small pointed tubercle near distal end of posterior side in H. dagestanica), ferruginous tarsi (brown in *H. dagestanica*), and lateral lobes of bilobed membranous appendage at apical margin of sternum 6 laterally elongated into a rounded tip and medially not separated from each other by an emargination (laterally elongated into a more or less acute tip and separated from each other by a shallow median emargination in *H. dagestanica*).



**Figure 3.** *Hoplitis andreasmuelleri* Fateryga & Proshchalykin, sp. nov., ♂, holotype (**A**) and paratype (**B–F**) **A** habitus in lateral view **B** antenna in front view **C** antenna in dorsal view **D** terga 4–6 in dorsal view **E** sterna 5–6 and tergum 7 in ventral view **F** genitalia in dorsal view. Scale bars 1 mm.

**Assignment to species group.** Due to the presence of a submarginal carina on female sternum 6 and the apically rounded male tergum 7, *H. andreasmuelleri* is clearly a member of the *H. adunca* species group.

**Description.** Due to the uniform morphology of the numerous species of *Hoplitis* (*Hoplitis*), the following description is restricted to characters, that are relevant for the recognition of the new species.

**Female.** Body length 9–10 mm. *Head*: Head about  $0.9 \times$  as long as wide (Fig. 2B). Distance between lateral ocellus and preoccipital margin about  $1.6 \times$  as long as ocellar diameter. Second segment of labial palpus about  $2.3 \times$  as long as first segment and about  $1.4 \times$  as long as compound eye (Fig. 2A). Proboscis reaching coxa of mid leg when folded. Mandible three-toothed, its preapical zone weakly reddish. Clypeus densely punctured with interspaces rarely surpassing the diameter of half a puncture, basally with a small impunctate triangular area continuing to a short and indistinct polished midline (Fig. 2B).

Antennal article 3 almost  $1.5 \times$  as long as apically wide and about  $1.5 \times$  as long as article 4. Antenna completely black (Fig. 2B). *Mesosoma*: Tegula dark brown except for black anterior third and black inner margin. Scutum and scutellum densely punctured with interspaces rarely surpassing the diameter of one puncture except lateroapically on scutum, where interspaces reach the diameter of one puncture. Basal area of propodeum shagreened throughout. Posterior surface of propodeum shagreened with scattered indistinct punctures. Propodeal pit polished. Tibial spur of fore leg elongated into tip, which is slightly longer than basally wide and angularly stepped from more basal part of spur. Tibial spurs of hind leg yellowish; inner spur slightly tapering towards apex, which is strongly curved at an angle of 30 to 40 degrees (Fig. 2C); outer spur slightly shorter than inner spur, its apex curved at an angle of about 45 degrees. Tarsi of all legs ferruginous except basal black parts on outer sides of basitarsi (Fig. 2A). Metasoma: Punctation of tergal discs moderately dense with interspaces reaching the diameter of two to four punctures on discs 1-3 (Fig. 2D). Marginal zone of terga 1-5 covered with sparse band of whitish hairs, which may be interrupted medially in worn specimens (Fig. 2D). Tergal discs 1-4 with sparse short erect pilosity of whitish hairs, which are shorter than antennal article 2. When seen from behind, longest erect hairs on median half of tergum 1 only about 1/7 to 1/8 as long as maximal length of lateral hair tuft. Disc of terga 5–6 covered with moderately dense and appressed whitish pilosity (Fig. 2E). Sternum 6 lateroapically with distinct submarginal carina and medioapically with a very short triangular tooth. Scopa whitish.

Male. Body length 9.5–10.5 mm. Head: Head about 0.8× as long as wide. Distance between lateral ocellus and preoccipital margin about 1.3× as long as ocellar diameter. Second segment of labial palpus about 2.15× as long as first segment and 1.2× as long as compound eye (Fig. 3A). Proboscis reaching coxa of mid leg when folded. Mandible twotoothed and predominantly black, sometimes with dark reddish-brown preapical zone. Clypeus rather strongly convex in profile, its punctation very fine and dense without polished interspaces. Apical margin of clypeus shallowly emarginate and crenulate. Antennal article 1 about 2.2× as long as maximally wide (Fig. 3B). Antennal article 3 about 1.3× as long as apically wide and almost 1.6× as long as article 4; antennal articles 3–4 with ventral margin distinctly widened distally (Fig. 3B). Antennal articles 4-5 as wide as article 3 apically and in dorsal view wider than articles 6–12 (Fig. 3C). Last article of antenna about 1.7× as long as basally wide (Fig. 3B); in dorsal view, its posterior side strongly widened towards apex (Fig. 3C). Antenna black (Fig. 3B, C). Mesosoma: Tegula brownish-red except for black anterior third and black inner margin. Scutum and scutellum densely punctured with interspaces rarely surpassing the diameter of one puncture except laterally on scutum, where interspaces may reach the diameter of one and a half punctures. Basal area of propodeum shagreened throughout. Posterior surface of propodeum shagreened with scattered punctures. Propodeal pit polished. Tibial spur of fore leg elongated into tip, which is as long as basally wide and angularly stepped from more basal part of spur. Tibial spurs of hind leg yellowish, tapering towards apex and apically curved. Tarsi of all legs ferruginous (Fig. 3A). Metasoma: Punctation of tergal discs moderately dense with interspaces reaching the diameter of one to three punctures on discs 1-4. Marginal zone of terga 1-5 covered with rather dense band of whitish to yellowish-white hairs (Fig. 3D), which may be interrupted on terga 1-3 in worn specimens. Tergum 6 laterally toothed, its marginal zone reddish,

ciliated with yellowish hairs, apically crenulate and medially very slightly emarginate to straight (Fig. 3D). Apical margin of tergum 7 medially rounded (Fig. 3D). Marginal zone of sterna 2-5 reddish and very densely punctured with interspaces much narrower than the diameter of one puncture (Fig. 3E). Apical margin of sterna 1-4 almost straight and of sternum 5 weakly rounded and medially shallowly emarginate (Fig. 3E). Marginal zone of sterna 2-4 with loose whitish to yellowish hair band (Fig. 3E). Sterna 2-5 with preapical transverse swelling, which is sparsely punctured and medioapically emarginate (Fig. 3E). Sternum 6 basally with pair of membranous flaps. Lobes of bilobed membranous appendage at apical margin of sternum 6 moderately haired, distinctly wider than long, laterally elongated into a distinct rounded tip and medially not separated from each other, forming an entire structure (Fig. 3E). Apical margin of the sclerotised base of sternum 6 with two very narrow and diverging median tufts of few long hairs, which surpass the centre of the membranous appendage of sternum 6. Gonoforceps very narrow, slightly bent inwards and downwards in its apical third and apically with dense and short tuft of yellowish-white hairs (Fig. 3F). Outer margin of penis valve ciliated with yellowish-white bristles, of which the longest are one and a half times longer than the maximal valve width (Fig. 3F).

**Material examined.** *Holotype*: RUSSIA. • Dagestan: vicinity of Kurush, 41°15'59"N, 47°49'33"E, 26.VI.2023,  $\eth$ , leg. A. Fateryga [ZISP]. *Paratypes*: RUSSIA. • Dagestan: vicinity of Kurush, 41°15'59"N, 47°49'33"E, 26.VI.2023, 1  $\heartsuit$ , on *Vicia alpestris*, leg. A. Fateryga [ZISP]; • ibid., 26.VI.2023, 3  $\circlearrowright$ , leg. A. Fateryga [CAFK, ETHZ, FSCV]; ibid., 26.VI.2023, 3  $\heartsuit$ , leg. M. Proshchalykin [CAFK, ETHZ, FSCV].

**Etymology.** It is a pleasure to name this species after our colleague Andreas Müller (Zurich, Switzerland), the leading expert on osmiine bees.

**Distribution.** Russia: European part (North Caucasus). The species is currently known only from the type locality in Dagestan.

**Remarks.** The species was collected in Samurskiy National Park, on alpine meadow slopes of the Chekhychay River valley (Samur River basin) below the village of Kurush (Dokuzparinskiy District of the Republic of Dagestan), about 2330 m a.s.l. (Fig. 4A). One female was collected visiting flowers of *Vicia alpestris* Steven



Figure 4. Habitat of *Hoplitis andreasmuelleri* Fateryga & Proshchalykin, sp. nov. in Chekhychay River valley, Samurskiy National Park, Dagestan **A** overview **B** slope with flowering *Vicia alpestris* Steven.

(Fig. 4B), while three other females were collected by sweeping patches of another species, *Vicia sosnowskyi* Ekutim. (Fabaceae). Males were collected on the ground between patches of both plant species. These data suggest a preference for the genus *Vicia* L. by *H. andreasmuelleri*, perhaps representing narrow oligolecty on a single plant genus (Müller and Kuhlmann 2008). However, more flower visitation data including microscopical analysis of pollen contained in the female scopae are needed to clarify the species' degree of host plant specialization, although many members of the *H. adunca* species group exclusively or predominantly exploit Fabaceae for pollen (Müller 2016, 2024; Sedivy et al. 2012b).

# Hoplitis (Kumobia) abbreviata (Morawitz, 1875)

Fig. 5

*Osmia abbreviata* Morawitz, 1875: 96, ♀ (type locality: "Prope Syr-darjam" [Central Asia]), holotype, ♀, type depository not indicated, probably Zoological Museum of the M.V. Lomonosov Moscow State University, Moscow, Russia.

**Material examined (new record).** RUSSIA. • Altai Republic: "Mars", 50°03'50"N, 88°18'45"E, 25.VI.2022, 1  $\bigcirc$ , leg. M. Proshchalykin [CAFK].

**Distribution.** Russia: Western Siberia (\*Altai Republic). – Kyrgyzstan, Kazakhstan, Mongolia.

**Remarks.** The species was collected in a mountain semi-desert with sparse shrubs of *Caragana bungei* Ledeb. (Fabaceae) (Fig. 5A) at an elevation of about 1800 m a.s.l.

### Conclusions

A total of 39 species of *Hoplitis* is known from Russia to date (Table 1). Among them, *H. daurica* (Radoszkowski, 1887), *H. dagestanica*, and *H. andreasmuelleri* are known only from Russia. Most other species are distributed from the Mediterranean to the Middle East and the Caucasus or to Central Asia; some species have broad distribution in the whole Palaearctic or even Holarctic (*H. robusta* (Nylander, 1848)) region, and some species are restricted to the eastern part of Central Asia and the Far East. One species (*H. scita* (Eversmann, 1852)) has a remarkably disjunctive distribution in the Caucasus and eastern Central Asia to the Far East (despite bee sampling efforts in other regions of Central Asia in the Soviet period). There are also several Caucasian sub-endemics and possibly a narrow endemic (*H. caucasicola* Müller, 2012). The most species-rich part of Russia in a large scale is the European part where 33 species of *Hoplitis* occur and 19 of them occur in Russia only there. Of them, 23 species occur in the North Caucasus (11 only there), which is the most species-reach region in a smaller scale. There are 12 species in the Urals, 12 species in Western Siberia, 13 species in Eastern Siberia and only five species in the Far East (Table 1).



**Figure 5.** *Hoplitis abbreviata* (Morawitz, 1875) in the Altai Republic **A** habitat in the Mars Place, Kosh-Agach District **B** head in front view **C** habitus in dorsal view **D** habitus in lateral view. Scale bars 1 mm.

	Distribution in Presia	Distribution outside Dussie
Species	Distribution in Russia	Distribution outside Russia
Hoplitis (Alcidamea) acuticornis	European part (East, North Caucasus, Crimea), Urals,	Western, Southern, and Eastern Europe,
(Dufour & Perris, 1840)	Western Siberia (Omsk Province, Tomsk Province,	Armenia, Azerbaijan, Turkey, Cyprus, Syria,
	Novosibirsk Province, Kemerovo Province, Altai	Jordan, Lebanon, Israel, Iran, Turkmenistan,
	Territory), Eastern Siberia (Krasnoyarsk Territory)	Tajikistan, Kyrgyzstan, Kazakhstan
Hoplitis (Alcidamea) beijingensis	Eastern Siberia (Buryatia)	China
Wu, 1987		
Hoplitis (Alcidamea)	European part (North Caucasus)	Southern and Eastern Europe, Northern Africa,
campanularis (Morawitz, 1877)		Georgia, Turkey, Lebanon, Israel
Hoplitis (Alcidamea) caucasica	European part (North Caucasus)	Azerbaijan, Turkey
(Friese, 1920)		
Hoplitis (Alcidamea) claviventris	European part (Central, North Caucasus, Crimea),	Western, Northern, Southern, and Eastern
(Thomson, 1872)	Urals, Western Siberia (Omsk Province, Novosibirsk	Europe, Kazakhstan, Mongolia, China
	Province, Kemerovo Province, Altai Territory, Altai	
	Republic), Eastern Siberia (Khakassia, Tyva, Buryatia)	
Hoplitis (Alcidamea) curvipes	European part (North Caucasus)	Western, Southern, and Eastern Europe,
(Morawitz, 1871)		Azerbaijan, Turkey, Syria, Iran
Hoplitis (Alcidamea) fulva	European part (East, South, Crimea), Urals	Eastern Europe, Armenia, Azerbaijan, Turkey,
(Eversmann, 1852)		Syria, Jordan, Kazakhstan, Mongolia, China

Hopfair (Morth, Cartral, Eax, South, North       Watern, Northern, Southern, and Eastern         Inconneliona (Kirby, 1802)       Cascus, Crimoc), Urak, Western, Shier Morinee,       Kazakhatan, Mongolia, China         Hopfair (Michalman, Province, Toronghen, Yang, Lan, Tajikisan, Yangyatan,       Kazakhatan, Mongolia, China         Hopfair (Michalman, Province, Toronghen, Yang, Lan, Tajikisan, Yangyatan,       Kazakhatan, Mongolia, China         Hopfair (Michalman, Province, Torong)       Farti (Minakasia, Farongang Kirritory, Yinada)       Western, Southern, and Eastern Europe, Armenia, Kazakhatan, Mongolia         Hopfair (Michalman, 1952)       Kinkassia, Karanoyasi Kirritory, Yinadaya Karritory, Yinadaya Kirritory, Yina Karakhatan, Kongolia, China	Species	Distribution in Russia	Distribution outside Russia
leasomedina (Kithy, 1902)     Caucasus, Crimea), Urals, Western Sheria (Omai, Eastern Steria (Khakasis, Tyva, Karayayar Reiritory, Harusk Province, Narol Sheria, Khakasisa, Krancha, Kyrgystan, Kuzakhstan, Mongolia, China     Europe, Northern Africa, Corgin, Amerila, Kyrgystan, Kazakhstan, Mongolia, China       Haphitis (Alcidemea) mititi (Narokasis, Kranoynak, Territory, Haphitis (Alcidemea) mititi (Khakasis, Kranoynak, Territory, Yakuria)     Western, Southern, and Eastern Europe, Armenia, Kazakhstan, Mongolia, China       Haphitis (Alcidemea) mititi (Khakasis, Kranoynak, Territory, Yakasis, Kranoynak, Territory, Yakuria)     Eastern Europe, Acatabian, Kazakhstan, Jordan, Uzbekistan, Kyrgystan, Kazakhstan       Haphitis (Alcidemea) multiti (Khakasis, Kranoynak, Territory, Yakuria)     Eastern Europe, Acatabian, Turkey, Syria, Jordan, Uzbekistan, Kyrgystan, Kazakhstan       Haphitis (Alcidemea) multiti (Khakasis, Kranoynak, Territory, Yakuria)     Eastern Europe, Acatabian, Turkey, Syria, Jordan, Uzbekistan, Kazakhstan       Haphitis (Alcidemea) prineteri (Khakasis, Territory, Primookiy Territory)     European part (South, Crimea), Urak, Western, Sheria (Mai, Istapona, Iarae, Sheria, Mai, Istapona, Iarae, Sheria (Mai, Kasathstan, Mongolia, China       Haphitis (Alcidemea) prineteri (Khakarovak, Territory)     European part (South, Crimea), Urak, Western, Sheria (Mai, Republic), Eastern Sheria (Onakasis, Tyva, Iatura), Faster (Shuthey, Primookiy Territory)     Eastern Europe, Kazakhstan, Mongolia, China       Haphitis (Alcidemea) prineteri (Khakarovak, Territory, Altai Republic), Katabarovak, Territory, Haina Republic)     Kyrgystan, Kazakhstan, Mongolia, China       Haphitis (Auroboxpa) prineteri (Pahitis (Auroboxpa) prineteri (Radox	Hoplitis (Alcidamea)	European part (North, Central, East, South, North	Western, Northern, Southern, and Eastern
Province, Toronk Province, Novosibink Province, Kenerovo Dovince, Marabilan, Turkey, Ina, Tajikiana, Kyrgyzan, Kazakhsan, Mongolia, China     Azerbajan, Turkey, Ina, Tajikiana, Kyrgyzan, Kazakhsan, Mongolia, China       Hapitis (Mickidamed) milit (Nylander, 1852)     Territory, Harnia, Vakin, Zashilakhy Territory, Hanoshy Territory, Kinkakasi, Kanoyank, Territory, Natnia)     Western, Southern, and Eastern Europe, Armenia, Kazakhsan, Mongolia       Hapitis (Mickidamed) milit (Khakasia, Kanoyank, Territory, Natnia)     European part (South, Crimea)     Eastern Europe, Arerbajan, Turkey, Yini, Jordan, Ubeksan, Mygyasan, Kazakhsan       Hapitis (Mickidamed) melati (Khakasia, Kazakhsan, Mongolia, China)     European part (South, Crimea)     Eastern Europe, Arerbajan, Turkey, Yini, Jordan, Ubeksan, Mygyasan, Kazakhsan       Hapitis (Mickidamed) melatin (Marawitz, 1873)     European part (South, North Caucasus, Crimea)     Western, Southern, and Eastern Europe, Northern Africa, Turkey, Yini, Jordan, Ubakhsan, Mongolia, China       Hapitis (Mickidamed) principi (Marawitz, 1872)     European part (South, Crimea), Urals, Western Siberia (Altai Republic), Eastern Siberia (Tysa, Itaria (Munuslappa Powince, Kabalistan), Taria (Munuslappa Powince, Kabalistan)     Kyrgyzstan, Mongolia, China       Hapitis (Mickidamed) principi (Morawitz, 1872)     European part (North Caucasus), Western Siberia (Altai Republic), Eastern Siberia (Muas Republic), Eastern Siberia (Muaskasi, Tyva, Istusk Province, Bayyatia), Yakita, Zashidakity Territory)     Kyrgyzstan, Kazakhstan       Hapitis (Mickidamed) rideratata (Dylain (Mickidamed) rideratata Republic), Chernel, Taria, Sun, Mickasha, Tyva, Istusk Province, Bayyatia), Karakhstan     Western, South	leucomelana (Kirby, 1802)	Caucasus, Crimea), Urals, Western Siberia (Omsk	Europe, Northern Africa, Georgia, Armenia,
Kernerov Droinez, Alui Territory, Mai Republic, Eastern Siberia (Musaksi, Tyva, Kazayanski Territory, Harusk Province, Buryatia, Yakutia, Zabaikakky Territory). Ear East (Annuskaya Province, Khabarovsk Territory). Ear East (Annuskaya Province, Khabarovsk Tartikov, 2000     Western, Southern, and Eastern Europe, Armenia, Kazakhstan, Mongolia, China       Hopfait (Middamat) multis (Khakasai, Krazoyara). Territory, Yakutia)     Eastern Europe, Aerzhajan, Turkey, Syria, Jordan, Uzbekisan, Krygozatan, Kazakhstan       Hopfait (Middamat) multis (Makasai, Krazoyara). Territory, Yakutia)     Eastern Europe, Aerzhajan, Turkey, Syria, Jordan, Uzbekisan, Krygozatan, Kazakhstan       Hopfait (Middamat) multis (Moravire, 1872)     European part (South, North Caucasus, Crimea)     Western, Southern, and Eastern Europe, Northern Afric, Turkey, Syria, Jordan, Lobanon, Iarak, Eastern, Kazakhstan       Hopfait (Middamed) prinety (Moravire, 1872)     European part (South, Crimea), Urals, Western Siberia (Mara Republic), Lastern Siberia (Mauska Province, Kazakhstan, Mongolia, China     Kyrgozatan, Mongolia, China       Hopfait (Middamed) prinety (Moravire, 1872)     European part (Central, East, South, North Caucasus, Crimea), Urals, Western Siberia (Chausa, Province, Crimea), Urals, Western Siberia (Chausakay Province, Crimea), Urals, Western Siberia (Chausakay Province, Crimea), Urals, Western, Siberia (Chausakay Province, Crimea), Urals, Western, Siberia (Chausakay, Province, Rovashian, Torvince, Torvinke, Territory)     Western, Southern, and Eastern Europe, Mongolia, China       Hopfaiti (Middamed) phoretau (Nadoskovski, 1877)     Euro		Province, Tomsk Province, Novosibirsk Province,	Azerbaijan, Turkey, Iran, Tajikistan, Kyrgyzstan,
Eastern Siberia (Khakasia, Tyo, Kranoyark Territory, Hindra Province, Rabaidakiy Territory, Pinnokky Territory)     Western, Southern, and Eastern Europe, Armenia, Kazakistan, Mongolia       Hophia (Alcidamea) milit (Nakasia, Kazakyanyark, Territory, Ninonky Territory)     European part (Crimea), Urak, Western Siberia (Keneroro Province, Alai Kepublic), Eastern Siberia (Khakasia, Kazakyanyark, Territory, Nikatia)     Western, Southern, and Eastern Europe, Armenia, Kazakistan, Mongolia       Hophia (Alcidamea) moliti Lacio, 2000     European part (North Caucasus)     Eastern Europe, Aerobajia, Titrkey, Syria, Joach, Wygrastan, Kazakistan       Hophia (Alcidamea) moliti Lacio, 2000     European part (South, North Caucasus, Crimea)     Western, Southern, and Eastern Europe, Northern Africa, Titrkey, Syria, Joachan, Kazakistan       Hophia (Alcidamea) princept (Morawitz, 1872)     European part (South, Crimea), Urak, Western Siberia (Altai Republic), Eastern Siberia (Tyra, Intask Province, Buryatia), Jacatern Siberia (Matai Republic), Eastern Siberia (Tyra, Intask Province, Buryatia), Kazakistan Province, Kabalashiy Territory)     Western, Southern, and Eastern Europe, Northern Africa, Congla, Amenia, Acerbajian, Turkey, Syria, Intask Province, Buryatia, Yakatia, Zashigan Province, Kabalashiy Province, Comask Province, Crimea), Urak, Western Siberia (Oluski Province, Crimea), Urak, Western Siberia (Onusk Province, Crimea)     Western, Southern, and Eastern Europe, Northern Africa, Gongia, Amenia, Acerbajian, Turkey, Syria, Intas, Couth, North Caucasus)       Hophia (Alcidamea) moleculati (Unitary, Province, Novasibink Province, Crimeak, Province, Crimea), Urak, Western Siberia (Oluski Province, Crimeak, Province, Novasibink Province, Crimak, Province, Crimeak, Province, Novasibink Province, Crimeak, Pr		Kemerovo Province, Altai Territory, Altai Republic),	Kazakhstan, Mongolia, China
Hotask Province, Buryatia, Yakutia, Zabalidakky     Territory, Pinnosky Printory, Kabatovsk       Hopliti (Midamea) mitä     European part (Crimea), Urals, Western, Siberia     Western, Southern, and Eastern Europe, Arcebaijan, Turkey, Syria, Jordan, Uzbekistan, Krazahtsan, Mongolia       Hopliti (Midamea) malis     European part (South, Crimea)     Eastern Europe, Acerbaijan, Turkey, Syria, Jordan, Uzbekistan, Krazahtsan, Mongolia       Hopliti (Midamea) malis     European part (South, Crimea)     Eastern Europe, Acerbaijan, Turkey, Syria, Jordan, Uzbekistan, Krazahtsan, Kazahtsan, Mongolia       Hopliti (Midamea) metern     European part (South, North Caucasus)     Georgia, Turkey, Syria, Jordan, Lebanon, Iarael, Ian, Tajikistan, Ucbekistan, Krage Status, Kazahtsan, Mongolia, China       Hopliti (Midamea) princeps     European part (South, Crimea), Unals, Western, Sberia (Van, Hukasht Porvince, Baryatia, Zabailadakiy Territory)     Western, Southern, and Eastern Europe, Kazaktsan, Mongolia, China       Hopliti (Midamea) princeps     European part (Corttel, Crimea), Unals, Western, Siberia (Matia Republic), Eastern Siberia (		Eastern Siberia (Khakassia, Tyva, Krasnoyarsk Territory,	
Territory, Piar East (Anunskaya Province, Khalarovsk. Territory, Pimosky Territory)       Western, Southern, and Eastern Europe, Armenia, Kzaddstan, Mongolia         Hophiti (Alcidamaa) mulits (Khalasais, Krassovark Territory, Yakutia)       Western, Southern, and Eastern Europe, Armenia, Kzaddstan, Mongolia         Hophiti (Alcidamaa) mulits (Khalasais, Krassovark Territory, Yakutia)       Eastern Europe, Azerbaijan, Turkey, Syria, Jordan, Uzbekisan, Kyrgyzstan, Kazakbstan         Hophiti (Alcidamaa) molits (Holaidamaa) ackeki       European part (South, North Caucasus, Crimea)       Eastern Europe, Azerbaijan, Turkey, Syria, Jordan, Uzbekisan, Kyrgyzstan, Kazakbstan         Hophiti (Alcidamaa) princeps (Morawitz, 1892)       European part (South, Crimea), Urals, Western Sheria (Tyra, Izbekistan, Uzbekistan, Kyrgyzstan, Kazakbstan, Mongolia, China         Hophiti (Alcidamaa) scint (Persmann, 1852)       European part (Certral, East, South, North Caucasus, Crimos, Buryatia, Zabailakky Territory)         Hophiti (Alcidamaa) scint (Portore, Buryatia, Far East (Munuskaya Province, Khabarovsk Territory, Primonsky Territory)       Kyrgyzstan, Kazakbstan         Hophiti (Alcidamaa) ridentuat       European part (Cortral, East, South, North Caucasus, Crimos, Ural, Western Sheria (Tyra, Ichausk Province, Khabarovsk Territory, Primonsky Territory)       Kestern, Southern, and Eastern Europe, Khabarovsk Territory, Primonsky Territory)         Hophiti (Alcidamaa) nuberudua       European part (Cortral, East, South, North Caucasus, Province, Novasibink Province, Konnova Province, Novasibink Province, Konnova Province, Novasibink Province, Konnova Province, Novasibink Province, Konnova Provin		Irkutsk Province, Buryatia, Yakutia, Zabaikalskiy	
Territory, Primorsky Territory)         Western, Southern, and Eastern Europe, (Nylander, 1852)         Western, Southern, and Eastern Europe, (Krakassia, Krasnoyarsk Territory, Yakutia)         Armenia, Kazakhstan, Mongolia           Haplitis (Alcidamoa) mollis         European part (North Caucasus)         Eastern Europe, Azerbaijan, Turkey, Syria, Jordan, Uzbekisan, Kryzyastan, Kazakhstan           Haplitis (Alcidamoa) mollis         European part (North Caucasus)         Eastern Europe, Azerbaijan, Turkey, Syria, Jordan, Uzbekisan, Kryzyastan, Kazakhstan           Haplitis (Alcidamoa) motors         European part (North Caucasus, Crimea)         Western, Southern, and Eastern Europe, (Krawkiz, 1872)           (Korawkiz, 1872)         European part (South, Crimea), Urals, Western Sheria (Narawkiz, 1872)         European part (South, Crimea), Urals, Western Sheria (Mataskis), Territory, Haplitis (Alcidamoa) scita         European part (Corth, Caucasus), Western Sheria (Narawkiz, 1872)         European part (Corth, Caucasis), Western Sheria (Alciakhy), Far East (Amundsky), Territory)           Haplitis (Alcidamoa) scita         European part (Corth, Caucasis), Western Sheria (Nataskis), Territory, Hinaisky Territory)         Kyrgyzsan, Kazakhstan           (Dufour & Perris, 1840)         European part (Corth, Caucasis, Surya, Ikuusk Province, Nowoibink Province, Kenerovo Province, Altai Territory, Altaia Republic), Eastern Siberia (Thuskasis, Tyva, Ikuusk Province, Nowoibink Province, Kenerovo Province, Altai Republic), Eastern Siberia (Thuskasis, Tyva, Ikuusk Province, Nowoibink Province, Cornak, Province, Cornak, Province, Norothern, Stuhetern, Suthern, and Eastern Europe, Nagadan Province,		Territory), Far East (Amurskaya Province, Khabarovsk	
Flapfiti (Alidamaa) mitii (Nylander, 1852)         European part (Critnea), Urals, Western Shieria (Khakassia, Krasnoyarak Territory, Yakutia)         Western, Southern, and Eastern Europe, Armenia, Kzzakhstan, Mongolia           Hapfiti (Alidamaa) molli (Khakassia, Krasnoyarak Territory, Yakutia)         Eastern Europe, Azerbaijan, Turkey, Syria, Jacka, 2000           Hapfiti (Alidamaa) moleki Taalci, 2000         European part (North Caucasus)         Eastern Europe, Azerbaijan, Turkey, Syria, Jacka, 2000           Hapfiti (Alidamaa) moleki Taalci, 2000         European part (South, North Caucasus, Crimea)         Western, Southern, and Eastern Europe, Northern Africa, Turkey, Syria, Jordan.           Hapfiti (Alidamaa) princepi (Morawitz, 1872)         European part (South, Crimea), Unls, Western Sheria (Alrai Republic), Eastern Sheria (Gypa, Jikuusk Province, Buryatia, Zabaikalsky Territory)         Western, Southern, and Eastern Europe, Northern Africa, Turkey, Syria, Jordan.           Hapfiti (Alidamaa) princepi (Morawitz, 1872)         European part (North Caucasus), Western Sheria (Alrai Republic), Eastern Sheria (Chinakasya Province, Khabarovak Territory, Phinosky Territory)         Kyrgyztan, Kazakhstan           Hapfiti (Alidamaa) princepi (Norince, Buryatia, Zabaikalsky Territory)         Kyrgyztan, Kazakhstan         Kurkasaa           Hapfiti (Alidamaa) princepati (Crimea), Lask, South, North Caucasus, Khabarovak Territory, Hait Republic)         Kyrgyztan, Kazakhstan         Kurkasaa           Hapfiti (Alidamaa) notorala         European part (Central, East, South, North Caucasus, Crimea), Urak, Western, Southern, and Eastern <td></td> <td>Territory, Primorskiy Territory)</td> <td></td>		Territory, Primorskiy Territory)	
(Nylander, 1852)       (Kemerovo Province, Alai Republic), Eastern Siberia (Khalassia, Krasnoyarak Terrinoy, Yakuria)       Armenia, Kazakhstan, Mongolia         Hoplitis (Alcidamaa) mollis Taaleč, 2000       European part (South, Crimea)       Eastern Europe, Azerbaijan, Turkey, Syria, Jordan, Uzbekisan, Krgyzana, Kazakhstan         Hoplitis (Alcidamaa) prinorpi (Morawitz, 1893)       European part (North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern Africa, Turkey, Syria, Jordan, Lebnon, Israel, Iran, Tajikisan, Uzbekisan, Krygyzstan, Kazakhstan         Hoplitis (Alcidamaa) prinorpi (Morawitz, 1872)       European part (South, Crimea), Unals, Western Siberia (Alcia Republic), Eastern Siberia (Tiya, Icluark Province, Buryatia, Zabaikakhy Territory)       Eastern Europe, Kazakhstan, Mongolia, China (Kusawata, 1872)         Hoplitis (Alcidamaa) prinorpi (Morawitz, 1872)       European part (North Caucasus), Western Siberia (Alcia Republic), Eastern Siberia (Tiya, Icluark Province, Buryatia, Jara Last, South, North Caucasus), Western, Southern, and Eastern Europe, Crimea), Urals, Western Siberia (Toluaras, Tya, Irkurk Province, Novabihas Province, Tomsk Crimea), Urals, Western Siberia (Toluaras, Tya, Irkurk Province, Novabihas Province, Tomsk Province, Novabihas Province, State Province, Jased Lana, Magdan Province, Province, Novabihas Province, State	Hoplitis (Alcidamea) mitis	European part (Crimea), Urals, Western Siberia	Western, Southern, and Eastern Europe,
(Khlakssia, Kramoynsk Territory, Yakutia)         Heplitis (Midiama) mollis       European part (South, Crimea)       Eastern Europe, Azerbaijan, Turkey, Syria, Jordan, Uzbekisan, Kyrgyzan, Kazakhstan         Heplitis (Midiamaa) mashesi       European part (North Caucasus)       Georgia, Turkey         Hoplitis (Midiamaa) mashesi       European part (South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern Africa, Turkey, Syria, Jordan, Uzbekisan, Kyrgyzatan, Kazakhstan         Hoplitis (Midiamaa) princeps       European part (South, Crimea), Unals, Western Sheria (Iriya, Irkusk Province, Buryatia, Zabailadky Territory)         Hoplitis (Midiamaa) scint       European part (Contral, East, South, North Caucasus, Crimea)       Kyrgyzatan, Kazakhstan         (Dufusi & Chinama) scint       European part (Contral, East, South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Kababaroski Territory, Primosky Territory         Hoplitis (Midiamaa) ridemaat       European part (Contral, East, South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern, Southern, and Eastern Europe, Northen, Northern, Northern, Southern, and Eastern Europe, Northen, Northern, Northern, Southern, and Eastern Europe, Northen, Northern, Southern, and Eastern Europe, Northen, Southern, and Eastern Europe, Northen, Southern, and Eastern Europe, Northern, Southern, and Eastern Europe, Northen, Northern, Southern, Southern, and Eastern Europe, Northen, Southern, and Eastern Europe, Mongolia, China         (Puptitis (Advidence) indeviced       European part (North, Caucasus)       Western, Southern, and East	(Nylander, 1852)	(Kemerovo Province, Altai Republic), Eastern Siberia	Armenia, Kazakhstan, Mongolia
Hephtis (Akidamaa) mellis         European part (South, Crimea)         Eastern Europe, Areptisian, Turkey, Syria, Jordan, Uzbekisan, Kyrgyzstan, Kazdkhstan Ipolitis (Akidamaa) naeketi         European part (North Caucasus)         Georgia, Turkey           Taalci, 2000         Fulpitis (Akidamaa) naeketi         European part (South, North Caucasus, Crimea)         Western, Southern, and Eastern Europe, Morthern Africa, Turkey, Syria, Jordan, Lebanon, Israel, Iran, Tajjkistan, Uzbekistan, Kyrgyzstan, Kazakhstan           Hoplitis (Akidamaa) princeys         European part (South, Crimea), Urals, Western Siberia         Eastern Europe, Kazakhstan           Hoplitis (Akidamaa) princeys         European part (South, Caucasus), Western Siberia         Kstern Europe, Kazakhstan           Korawitz, 1872)         Feynbilic), Eastern Siberia (Chausasia), Tyva, Irkusk         Kyrgyzstan, Kazakhstan           Hoplitis (Akidamaa) ridua         European part (Central, East, South, North Caucasus, Crimes, Durine, Northern Africa, Carakhstan         Kyrgyzstan, Kazakhstan           Hoplitis (Akidamaa) riduatata         European part (Central, East, South, North Caucasus, Crimes, Durine, Northern Africa, Carakhstan         Western, Southern, and Eastern Europe, Altai Republic), Eastern Siberia (Chausasia, Tyva, Irkusk           Hoplitis (Akidamaa) nidematat         European part (North, Central, East, South, North Caucasus, Crimes), Turkey, Syria, Israel, Iran, Uzbekistan, Kyrgyzstan, Kazakhstan           Hoplitis (Akidamaa) nidematat         European part (North, Central, East, South, North Caucasus)         Western, Sout		(Khakassia, Krasnoyarsk Territory, Yakutia)	
Tkalci, 2000     Jordan, Uźbekisan, Kyrgyzatan, Kazakhstan       Inplitis (Alcidamaa) neketai     European part (North Caucasus)     Georgia, Turkey       Tkalci, 2000     Western, Southern, and Eastern Europe, (Morawitz, 1893)     European part (South, North Caucasus, Crimea)     Western, Southern, and Eastern Europe, Northern Africa, Turkey, Syria, Jordan, Lebanon, Israel, Iran, Tajikistan, Użbekistan, Kyrguzstan, Kazakhstan       Hoplitis (Alcidamaa) princeps     European part (South, Crimea), Urals, Western Siberia     Eastern Europe, Kazakhstan, Mongolia, China       Hoplitis (Alcidamaa) tridentatai     European part (North Caucasus), Western Siberia (Altai     Kyrguzstan, Kazakhstan       Hoplitis (Alcidamaa) tridentatai     European part (North Caucasus), Western Siberia (Altai     Kyrguzstan, Kazakhstan       Province, Buryania, Far East (Manuskaya Province, Khabarovsk Territory)     Northern Africa, Georgia, Armenia, Azerbajan, Province, Novosibirsk Province, Comsk Province, Comsk     Northern Africa, Georgia, Armenia, Azerbajan, Province, Ornak Province, Comsk       Inglitis (Alcidamaa) tuderculatat     European part (North, Central, East, Urals, Western     Northern Africa, Georgia, Armenia, Azerbajan, Province, Ornak Province, Comsk       Inglitis (Alcidamaa) tuderculatat     European part (North, Central, East, Youth, North Caucasus)     Western, Southern, and Eastern Europe, Mongolia, China       Hoplitis (Alcidamaa) tuderculatat     European part (North, Central, East), You, Ikursk     Western, Southern, and Eastern       Hoplitis (Autosopa) dauricat     European part (South, No	Hoplitis (Alcidamea) mollis	European part (South, Crimea)	Eastern Europe, Azerbaijan, Turkey, Syria,
Hepfits (Alcidamea) ackeki         European part (North Caucasus)         Georgia, Turkey           Tkalců, 2000         European part (South, North Caucasus, Crimea)         Western, Southern, and Eastern Europe, Northern Africi, Turkey, Syria, Jordan, Lebanon, Isnel, Iran, Tajikism, Uzekšisan, Kyrgzzstan, Kazakhstan           Haplitis (Alcidamea) princejs         European part (South, Crimea), Urals, Western Siberia (Alcia Republic), Eastern Siberia (Tyva, Irkusk Province, Norawirz, 1872)         Eastern Europe, Kazakhstan, Mongolia, China           Hoplitis (Alcidamea) reidentari (Eversmann, 1852)         European part (North Caucasus), Western Siberia (Alcia Republic), Eastern Siberia (Tyva, Irkusk Province, Khabarosk Territory, Primosky Territory)         Kyrgzstan, Mongolia, China           Hoplitis (Alcidamea) reidentari (Dufour & Perris, 1840)         European part (Central, East, South, North Caucasus, Province, Novosibinsk Province, Knenerovo Province, Altai Territory, Altai Republic), Eastern Siberia (Othakasai, Tyva, Irkunsk Province, Novosibinsk Province, Knenerovo Province, Altai Republic), Eastern Siberia (Makasai, Tyva, Irkunsk Province, Novosibinsk Province, Kanerovo Province, Altai Republic), Eastern Siberia (Makasai, Tyva, Irkunsk Province, Novosibinsk Province, Kanerovo Province, Altai Republic), Eastern Siberia (Tyva, Buryatia)         -           Hoplitis (Anthocopa) adueted Radozkovski, 1887)         European part (Central, Azab, Lask, Urals, Western Northern, Africa, Armenia, Azetbaijan, Turkey, Stria, Jarat         -           Hoplitis (Anthocopa) dueurica (Radozkovski, 1874)         European part (Central, North Caucasus, Crimea)         Western, Southern, and Eastern Europe, Itarkey, I	Tkalců, 2000		Jordan, Uzbekistan, Kyrgyzstan, Kazakhstan
Tkalsča, 2000         Hoplini (Akidaman) praetanu (Morawitz, 1873)       European part (South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern Africa, Turkey, Syria, Jordan, Lebanon, Israel, Iran, Tighistan, Uzbekistan, Kyrgystan, Kazakhstan         Hoplitis (Akidama) princeps (Morawitz, 1872)       European part (South, Crimea), Urals, Western Siberia (Mai Kepublic), Eastern Siberia (Tya, Iktusk Province, Buryaria, Zabilakki); Triritory)       Eastern Europe, Kazakhstan, Mongolia, China         Hoplitis (Akidama0) scita (Eversmann, 1852)       European part (North Caucasus), Western Siberia (Alai (Eversmann, 1852)       Kyrgyzstan, Kazakhstan         Pholitis (Akidama0) ridentan (Dufour & Perris, 1840)       European part (North Caucasus), Western Siberia (Nausskapa Province, Khabaroosk Territory, Primorsky Territory)       Western, Southern, and Eastern Europe, Crimea), Urals, Western Siberia (Omsk Province, Tomsk Province, Norosibirsk Province, Kemetoro Province, Altai Republic)       Western, Northern, Southern, and Eastern European part (North, Caucasus)         Hoplitis (Akidama0 inducedata (Nylander, 1848)       European part (North, Caucasus, Province, Novsibirsk Province, Kametoro Province, Altai Republic), Eastern Siberia (Khakassia, Tyva, Iktusk Province, Novsibirsk Province, Kametoro Province, Altai Republic), Eastern Siberia (Nakassia, Tyva, Iktusk Province, Novsibirsk Province, Kametoro Province, Altai Republic), Eastern Siberia (Nakassia, Tyva, Iktusk Province, Novsibirsk Province, Kametoro Province, Altai Republic), Eastern Siberia (Nakassia, Tyva, Iktusk Province, Novsibirsk Province, Kametoro Province, Altai Republic), Eastern Siberia (Nakassia, Tyva, Iktusk Province, Ruyasita, Statusi, Zabilakki, Territory), Magadan	Hoplitis (Alcidamea) ozbeki	European part (North Caucasus)	Georgia, Turkey
Hophiti (Alcidamea) praestaur (Morawitz, 1893)       European part (South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern Africa, Turkey, Syria, Jordan, Lebanon, Israel, Iran, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Polpitis (Alcidamea) princept (Morawitz, 1872)       European part (South, Crimea), Urals, Western Siberia (Alai Republic), Eastern Siberia (Iya, Irkutsk Province, Buryata, Zabalialskiy Territory)       Eastern Europe, Kazakhstan         Polpitis (Alcidamea) ricitar (Eversmann, 1852)       European part (North Caucasus), Western Siberia (Alai Republic), Eastern Siberia (Makasia, Tya, Irkutsk Province, Buryata), Zabalialskiy Territory)       Kyrgyzstan, Mongolia, China         Phopitis (Alcidamea) ricitant (Eversmann, 1852)       European part (Central, East, South, North Caucasus, Crimea), Urals, Western Siberia (Maskasia, Tya, Irkutsk Province, Novosibitsk Province, Kemerovo Province, Altai Territory, Altai Republic)       Western, Northern, and Eastern Europe, Kygnater, Northern, Southern, and Eastern Kygnater, 1848)         Polpitis (Authocopal) caucaitedat (Nylander, 1848)       European part (Central, East), Urals, Western Siberia (Tyumen Province, Komsk Province, Tomsk Province, Novosibitsk Province, Komservo Province, Altai Republic), Eastern Siberia (Makasia, Tyva, Irkutsk Province, Buryata, Yakuta, Zabailalsky Territory), Far East (Amurskaya Province)       Western, Northern, Southern, and Eastern European part (South, North Caucasus)       Georgia         Hoplitis (Anthocopa) datacidati (Radoszkowski, 1874)       European part (Central, North Caucasus, Crimea)       -         Hoplitis (Anthocopa) paparerit (Price, 1895)       European pa	Tkalců, 2000		
(Morawitz, 1893)     Northern Africa, Turkley, Syria, Jordan, Lebanon, Israel, Iran, Tajkistan, Uzbekistan, Kyrgyzstan, Kazakhstan       Hopliti (Alcidamei) princeps (Morawitz, 1872)     European part (South, Crimea), Urals, Western Siberia (Altai Republic), Eastern Siberia (Tyva, Irkursk Province, Buryzatia, Zabulalaky Territory)     Eastern Europe, Kazakhstan, Mongolia, China       Hopliti (Alcidamea) sciat (Eversmann, 1852)     European part (North Caucasus), Western Siberia (Altai (Eversmann, 1852)     Kyrgyzstan, Mongolia, China       (Paptitis (Alcidamea) tridemtatz (Dufour & Perris, 1840)     European part (Cornta, East, South, North Caucasus, Province, Novosibitsk Province, Comsk Province, Crimea), Urals, Western Siberia (Omsk Province, Tomsk Province, Novosibitsk Province, Kemerovo Province, Altai Territory, Altai Republic)     Western, Northern, and Eastern Europe, Northern Africa, Georgia, Armenia, Azerbaijan, Turkey, Syria, Israel, Iran, Uzbekistan, Kyrgyzstan, Kazakhstan       Hoplitis (Alcidamea) tuberculatat (Nylander, 1848)     European part (North, Central, East), Urals, Western Siberia (Tyunen Province, Chabarovsk Territory), Far East (Anuuskaya Province, Khabarovsk Territory), Far East (Buropean part (Central, North Caucasus, Crimea), Urals (Radoszkowski, 1874)     Georgia <t< td=""><td>Hoplitis (Alcidamea) praestans</td><td>European part (South, North Caucasus, Crimea)</td><td>Western, Southern, and Eastern Europe,</td></t<>	Hoplitis (Alcidamea) praestans	European part (South, North Caucasus, Crimea)	Western, Southern, and Eastern Europe,
Hoplitis (Alcidameal) princeps (Morawitz, 1872)     European part (South, Crimeal), Urals, Western Siberia (Altai Republic), Eastern Siberia (Tyva, Iktusk Province, Buryata, Zabailalskiy Territory)     Eastern Europe, Kazakhstan, Mongolia, China       Hoplitis (Alcidameal) scitat (Eversmann, 1852)     European part (North Caucasus), Western Siberia (Altai Republic), Eastern Siberia (Khakasia, Tyva, Iktusk Province, Buryata), Far East (Munuskya Province, Khabarovsk Territory)     Kyrgyzatan, Mongolia, China       Hoplitis (Alcidameal) tridentatat (Dufour & Perris, 1840)     European part (Central, East, South, North Caucasus, Province, Novssibirsk Province, Kemerovo Province, Altai Territory, Altai Republic)     Western, Southern, and Eastern European part (North, Central, East), Urals (Western Siberia (Tyumen Province, Omsk Province, Tomsk Province, Novssibirsk Province, Kemerovo Province, Altai Republic), Eastern Siberia (Khakasia, Tyva, Irkutsk Province, Buryatia, Yakutia, Zabailalskiy Territory), Far East (Amuskya Province, Khabarovsk Territory, Magadan Province)     Western, Northern, Southern, and Eastern European part (Central, Khabarosk Territory, Magadan Province)       Hoplitis (Anthocopa) dustricat (Radozskowski, 1874)     European part (Central, North Caucasus)     Georgia       Hoplitis (Anthocopa) dustricat (Radozskowski, 1874)     European part (Central, North Caucasus, Crimea), Urals (European part (Central, North Caucasus, Crimea)     Western, Southern and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkernistan, Tajikistan, Kazakhstan, China       Hoplitis (Anthocopa) mocaryi (Friese, 1895)     European part (Central, North Caucasus, Crimea)     Western, Southern, and Eastern Europe, Northern, Mirka, Armenia, Azerbaijan, Turkey, Ir	(Morawitz, 1893)		Northern Africa, Turkey, Syria, Jordan,
Kyrgystan, Kazakhstan           Hopliti (Alcidamea) princeps (Morawirz, 1872)         European part (South, Crimea), Urals, Western Siberia (Tyva, Irkutsk Province, Buryatia, Zabaikalsky Territory)         Eastern Europe, Kazakhstan, Mongolia, China           Hopliti (Alcidamea) scita         European part (North Caucasus), Western Siberia (Altai         Kyrgystan, Margolia, China           (Eversmann, 1852)         European part (Central, East, South, North Caucasus, Chabarowsk Territory, Primorskiy Territory)         Western, Southern, and Eastern Europe, Altai Territory, Altai Republic), Eastern Siberia (Altai         Western, Southern, and Eastern Europe, Altai Territory, Altai Republic)           Hopliti (Alcidamea) nuberculata         European part (North, Central, East, Urals, Western Siberia (Tyune, Novašbinsk Province, Tomsk Province, Novosibinsk Province, Kamerovo Province, Altai Republic), Eastern Siberia (Khakasia, Tyu, Irkutsk Province, Novosibinsk Province, Kamerovo Province, Altai Republic), Eastern Siberia (Khakasia, Tyu, Irkutsk Province, Novosibinsk Province, Kamerovo Province, Altai Republic), Eastern Siberia (Tyva, Buryatia)         -           Hopliti (Anthocopa) dutorica (Radoszkowski, 1877)         Eastern Siberia (Tyva, Buryatia)         -           Hopliti (Anthocopa) jukovlevi         European part (Central, North Caucasus, Crimea), Urals         Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkey, Iran, Turkey, Iran, Turkey, Iran,			Lebanon, Israel, Iran, Tajikistan, Uzbekistan,
Haplitis (Alcidamea) princeps (Morawiz, 1872)       European part (South, Crimea), Urals, Western Siberia (Altai Republic), Eastern Siberia (Tyva, Iktursk Province, Buryaria, Zabialakisky Territory)       Eastern Europe, Kazakhstan, Mongolia, China         Haplitis (Alcidamea) scita (Eversmann, 1852)       European part (North Caucasus), Western Siberia (Altai Republic), Eastern Siberia (Munkskay Province, Khabarowsk Territory, Primorskiy Territory)       Western, Southern, and Eastern Europe, Crimea), Urals, Western Siberia (Omsk Province, Tomsk Province, Novosibiisk Province, Kanerovo Province, Altai Territory, Alai Republic)       Western, Southern, and Eastern Europe, Kazakhstan         Hoplitis (Alcidamea) ridematat (Dufour & Perris, 1840)       European part (Contr.al, East), Cuils, Western Siberia (Tyumen Province, Comsk Province, Novosibiisk Province, Kemerovo Province, Altai Territory, Alai Republic)       Western, Northern, Aouthern, and Eastern Europe, Mongolia, China         Hoplitis (Alcidamea) nuberculata (Nylander, 1848)       Floropean part (North, Carula, East), Urals, Western Siberia (Tyumen Province, Khabarovsk Territory), Far East (Amurskaya Province, Khabarovsk Territory), Far East (Amurskaya Province, Khabarovsk Territory), Far East (Amurskaya Province)       Western and Southern, and Eastern Altai Republic), Eastern Siberia (Tyva, Buryatia)       –         Haplitis (Anthocopa) aluancia (Radoszkowski, 1887)       European part (Central, North Caucasus, Crimea), Urals (Friese, 1895)       Western, Southern and Eastern Europe, Turkey, Israel, Ian         Haplitis (Anthocopa) appateris (Laterille (Anthocopa) appateris (Laterille, 1799)       European part (Central, North Caucasus, Crimea) (Friese, 1895)       S			Kyrgyzstan, Kazakhstan
(Morawitz, 1872)       (Altai Republic), Eastern Siberia (Tyva, Ikursk Province, Buryatia, Zabaikalsky Territory)         Hoplitis (Alcidamea) scita (Eversmann, 1852)       European part (North Caucasus), Western Siberia (Altai Republic), Eastern Siberia (Khakassia, Tyva, Ikursk Province, Buryatia), Far East (Amuskaga Province, Khabarovsk Territory)       Kyrgyzstan, Mongolia, China         Hoplitis (Alcidamea) scita (Dufour & Perris, 1840)       European part (Central, East, South, North Caucasus, Crimea), Urals, Western Siberia (Maia Republic)       Western, Southern, and Eastern Europe, Northern Africa, Geogia, Armenia, Azerbäjan, Turkey, Syria, Israel, Ian, Uzbekistan, Siberia (Tyumen Province, Comsk Province, Altai Territory, Altai Republic), European part (North, Central, East), Urals, Western       Western, Northern, Southern, and Eastern Europe, Mongolia, China         Hoplitis (Anthocopa) outcoatioda Miller, 2012       European part (North Caucasus)       Georgia         Hoplitis (Anthocopa) outcoatioda Miller, 2012       European part (North Caucasus)       Georgia         Hoplitis (Anthocopa) outcoatioda Miller, 2012       European part (North Caucasus)       Georgia         Hoplitis (Anthocopa) outcoatioda Miller, 2012       European part (Central, North Caucasus, Crimea), (Friese, 1895)       Western and Southern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkenenistan, Tajikistan, Kyrgyzstan, Kazakhstan, China         Hoplitis (Anthocopa) opprezi (Ferton, 1894)       European part (Central, North Caucasus, Crimea) (Friese, 1895)       Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran	Hoplitis (Alcidamea) princeps	European part (South, Crimea), Urals, Western Siberia	Eastern Europe, Kazakhstan, Mongolia, China
Buryatia, Zabaikalskiy Territory)           Hoplitis (Alcidamea) scita (Eversmann, 1852)         European part (North Caucasus), Western Siberia (Altai Province, Buryatia), Far East (Amurskaya Province, Khabarovsk Territory, Primoskiy Territory)         Vestern, Southern, and Eastern Europe, Crimea), Urals, Western Siberia (Omsk Province, Tomsk Province, Novosibirsk Province, Kemerovo Province, Altai Territory, Altai Republic)         Northern Africa, Georgia, Armenia, Azerbaijan, Turkey, Syria, Israel, Iran, Uzbekistan, Kygarder, 1848)           Hoplitis (Alcidamea) tuberculata (Nylander, 1848)         European part (North, Central, East), Urals, Western Siberia (Tyumen Province, Kemerovo Province, Altai Territory, Mai Republic)         Western, Northern, Southern, and Eastern European part (North, Central, East), Urals, Western Siberia (Tyumen Province, Comsk Province, Tomsk Province, Novosibirsk Province, Kemerovo Province, Altai Republic), Eastern Siberia (Khakassia, Tyva, Irkutsk Province, Novosibirsk Province, Kemerovo Province, Altai Republic), Far East (Amurskaya Province, Tomsk Province, Surayatia, Yakutia, Zabaikalskiy Territory), Far East (Amurskaya Province, Khabarovsk Territory, Magadan Province)         Western and Southern, Southern, and Eastern European part (South, North Caucasus, Crimea), Urals         Western and Southern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkew, Isan, Suthern, and Eastern Europe, Turkey, Israel, Iran           Hoplitis (Ambocapa) paparereri (Radoszkowski, 1887)         European part (Central, North Caucasus, Crimea), Urals         Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran           Hoplitis (Ambocapa) paparereri (Ferton, 1894)         European part (Central, North Caucasus, Crimea)	(Morawitz, 1872)	(Altai Republic), Eastern Siberia (Tyva, Irkutsk Province,	
Hoplitis (Alcidamea) scitat       European part (North Caucasus), Western Siberia (Altai (Eversmann, 1852)       Kyrgyzstan, Mongolia, China         (Eversmann, 1852)       Republic), Eastern Siberia (Khakasia, Tyva, Irkusk Province, Ruyatai), Far East (Amurskaya Province, Khabarovsk Territory)       Western, Southern, and Eastern Europe, Crimea), Urals, Western Siberia (Omsk Province, Tomsk Province, Novosibinsk Province, Cemerovo Province, Altai Territory, Altai Republic)       Western, Southern, and Eastern European part (North, Central, East), Urals, Western         Hoplitis (Alcidamea) tubeculata (Nylander, 1848)       European part (North, Central, East), Urals, Western Siberia (Tyume Province, Omsk Province, Tomsk Province, Novosibinsk Province, Comsk Province, Tomsk Province, Novosibinsk Province, Kemerovo Province, Altai Republic), Eastern Siberia (Khakassia, Tyva, Irkutsk Province), Novosibinsk Province, Kemerovo Province, Altai Republic), Eastern Siberia (Nakassia, Tyva, Irkutsk Province)       Western, Northern, Southern, and Eastern Europe, Mongolia, China         Hoplitis (Antbocopa) acucasicola Miller, 2012       European part (North Caucasus)       Georgia         Hoplitis (Antbocopa) acucasicola Miller, 2012       European part (South, North Caucasus, Crimea), Urals       Western, Southern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkes, Stash, China         Hoplitis (Antbocopa) abovlevi (Radoszkowski, 1887)       European part (Central, North Caucasus, Crimea), Urals       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Antbocopa) papaversi (Larrelle, 1799)       European part (Central, North Caucasus, Crimea)       Western, Sout		Buryatia, Zabaikalskiy Territory)	
(Eversmann, 1852)       Republic), Eastern Siberia (Khakasia, Tyva, Irkursk Province, Buryatia), Far East (Amusskapa Province, Khabarovsk Territory)       Western, Southern, and Eastern Europe, Cimica, Dursk Western Siberia (Omsk Province, Tomsk Province, Novosibinsk Province, Komer Sovo Province, Altai Territory, Altai Republic)       Western, Southern, and Eastern Europe, Cimica, Goorgia, Armenia, Azerbaijan, Turkey, Syria, Irszel, Iran, Uzbekistan, Altai Territory, Altai Republic)         Hoplitis (Alcidamea) tuberculatu (Nylander, 1848)       European part (North, Central, East, Jurals, Western Siberia (Tyumen Province, Komerovo Province, Province, Novosibinsk Province, Komerovo Province, Altai Republic), Eastern Siberia (Khakassia, Tyva, Irkursk Province, Novosibinsk Province, Kemerovo Province, Altai Republic), Eastern Siberia (Khakassia, Tyva, Irkursk Province, Novosibinsk Province, Khabarovsk Territory), Far East (Amusskaya Province, Khabarovsk Territory)       Western, Northern, Southern, and Eastern Europe, Mongolia, China         Hoplitis (Anthocopa) duuricat (Radoszkowski, 1887)       European part (North Caucasus)       Georgia         Hoplitis (Anthocopa) duuricat (Radoszkowski, 1887)       European part (Central, North Caucasus, Crimea), Urals       Western, and Southern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkempiatan, Turkempiatan, China         Hoplitis (Anthocopa) abaveris (Latrelle, 1799)       European part (Central, North Caucasus, Crimea), Urals (Friese, 1895)       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) apareris (Latrelle, 1799)       European part (Central, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern, Africa	Hoplitis (Alcidamea) scita	European part (North Caucasus), Western Siberia (Altai	Kyrgyzstan, Mongolia, China
Province, Buryatia), Far East (Amurskaya Province, Khabarovsk Territory, Primorskiy Territory)Hoplitis (Alcidamea) tridentata (Dufour & Perris, 1840)European part (Central, East, South, North Caucasus, Province, Novosibisk Province, Kemerovo Province, Altai Territory, Altai Republic)Western, Southern, and Eastern Europe, Northern Africa, Georgia, Armenia, Azerbaijan, Turkey, Syria, Israel, Iran, Uzbekistan, Kyrgzstan, KazakhstanHoplitis (Alcidamea) tuberculata (Nylander, 1848)European part (North, Central, East), Urals, Western Siberia (ITyumen Province, Omsk Province, Tomsk Province, Novosibisk Province, Tomsk Province, Buryatia, Yakutia, Zabaikalskiy Territory), Far East (Amurskaya Province, Kababrovsk Territory, Magadan Province)Western, Northern, Southern, and Eastern European part (North Caucasus)Hoplitis (Anthocopa) caucasicola Müller, 2012European part (North Caucasus, Crimea), Urals (Radoszkowski, 1887)Western and Southern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkey, Isara, Iran, Uzbekistan, Kyrgyzstan, Kazakhstan, ChinaHoplitis (Anthocopa) mocsaryi (Friese, 1895)European part (Central, North Caucasus, Crimea), Urals (Lareille, 1799)Western, Southern, and Eastern Europe, Surthern, Suthern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkey, Isaral, IranHoplitis (Anthocopa) pateveris (Lareille, 1799)European part (Central, North Caucasus), Urals (Lareille, 1799)Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran (Kazakhstan, ChinaHoplitis (Anthocopa) sexialitis (Granaden, 1994)European part (North Caucasus), Urals (Lareille, 1799)Western, S	(Eversmann, 1852)	Republic), Eastern Siberia (Khakassia, Tyva, Irkutsk	
Khabarovsk Territory, Primorskiy Territory)Hoplitis (Alcidamea) tridentata (Dufour & Perris, 1840)European part (Central, East, South, North Caucasus, Province, Nowsbirsk Province, Komerovo Province, Altai Territory, Altai Republic)Northern Africa, Georgia, Armenia, Azerbaijan, Turkey, Syria, Israel, Iran, Uzbekistan, Kyrgyzstan, KazakhstanHoplitis (Alcidamea) tuberculata (Nylander, 1848)European part (North, Central, East), Urals, Western Siberia (Tyunen Province, Omsk Province, Tomsk Province, Novsbirsk Province, Comsk Province, Tomsk Province, Novsbirsk Province, Comsk Province, Tomsk Province, Northern, and Eastern European part (North Caucasus)Western, Northern, Southern, and Eastern European part (North Caucasus)Hoplitis (Anthocopa) caucaticola Miller, 2012European part (North Caucasus)GeorgiaHoplitis (Anthocopa) jakovlevi (Radoszkowski, 1887)European part (South, North Caucasus, Crimea), Urals (Suestern, Suthern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkenenisan, Tajikistan, Kyrgyzstan, Kazakhstan, China-Hoplitis (Anthocopa) jakovlevi (Radoszkowski, 1874)European part (Central, North Caucasus, Crimea), Urals (European part (Central, North Caucasus), Urals (Latreille, 1799)Western, Southern, and Eastern Europe, Turkey, Israel, IranHoplitis (Anthocopa) papaveris (Latreille, 1799)European part (Central, North Caucasus), Urals (European part (Central, North Caucasus), Urals (Latreille, 1799)Western, Southern, and Eastern Europe, Northern, Arteisan, Turkey, Iran, Turkey, Iran, Turkey, Iran, Turkey, Iran, Tajikistan, Uxpezijan, Turkey, Israel, IranHoplitis (Anthocopa) papaveris (Latreille, 179		Province, Buryatia), Far East (Amurskaya Province,	
Hoplitis (Alcidamea) tridentatat       European part (Central, East, South, North Caucasus, (Dufour & Perris, 1840)       Western, Southern, and Eastern Europe, (Crimea), Urals, Western Siberia (Omsk Province, Altai Territory, Altai Republic)       Northern Africa, Georgia, Armenia, Azerbaijan, Turkey, Syria, Isnel, Fran, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Alcidamea) nuberculata (Nylander, 1848)       European part (North, Central, East), Urals, Western Siberia (Tyumen Province, Omsk Province, Formsk Province, Novosibinsk Province, Kemerovo Province, Altai Republic), Eastern Siberia (Khakassia, Tyva, Irkutsk Province, Buryatia, Yakutia, Zabaikalskiy Territory, Far East (Amurskaya Province, Khabarovsk Territory, Magadan Province)       Western, Northern, Southern, and Eastern Europe, Mongolia, China         Hoplitis (Anthocopa) caucasicola Miller, 2012       European part (North Caucasus)       Georgia         Hoplitis (Anthocopa) jabonlevi (Radoszkowski, 1887)       European part (South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkensistan, Taijkistan, Kyrgyzstan, Kazakhstan, China         Hoplitis (Anthocopa) papaveris (Latreille, 1799)       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Kazakhstan, China         Hoplitis (Anthocopa) papaveris (Latreille, 1799)       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Kazakhstan, China         Hoplitis (Anthocopa) papaveris (Latreille, 1799)       European part (Central, North Caucasus), Urals       Western, S		Khabarovsk Territory, Primorskiy Territory)	
(Dufour & Perris, 1840)       Crimea), Urals, Western Siberia (Omsk Province, Tomsk Province, Novosibirsk Province, Kemerovo Province, Altai Territory, Altai Republic)       Northern Africa, Georgia, Armenia, Azerbaijan, Turkey, Syria, Istael, Iran, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Alcidamea) nuberculata       European part (North, Central, East), Urals, Western Siberia (Tyumen Province, Omsk Province, Tomsk Province, Novosibirsk Province, Kemerovo Province, Altai Republic), Eastern Siberia (Alkassia, Tyva, Iktursk Province, Buryatia, Yakutia, Zabaikalskiy Territory), Far East (Amuskaya Province, Khabarovsk Territory), Far East (Amuskaya Province, Khabarovsk Territory), Magadan Province)       Western, Northern, Southern, and Eastern Europe, Northern Altai Republic), Eastern Siberia (Ifyva, Buryatia)         Hoplitis (Anthocopa) daurica (Radoszkowski, 1877)       European part (South, North Caucasus, Crimea), Urals       Western and Southern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkmenistan, Tajikistan, Kyrgyzstan, Kazakhstan, China         Hoplitis (Anthocopa) mocaryi (Frices, 1895)       European part (Central, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Turkey, Kazakhstan, China         Hoplitis (Anthocopa) papaveris (Latreille, 1799)       European part (Central, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Turkey, Kazakhstan, China         Hoplitis (Anthocopa) papaveris (rated, 1794)       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Kazakhstan, China         Hoplitis (Anthocopa) papaveris (rated, 1799)       European part (North Caucasus), Crimea)	Hoplitis (Alcidamea) tridentata	European part (Central, East, South, North Caucasus,	Western, Southern, and Eastern Europe,
Province, Novosibirsk Province, Kemerovo Province, Altai Territory, Altai Republic)Turkey, Syria, Israel, Iran, Uzbekistan, Kyrgzstan, KazakhstanHoplitis (Alcidamea) nuberculatat (Nylander, 1848)European part (North, Central, East), Urals, Western Siberia (Tyumen Province, Omsk Province, Tomsk Province, Novosibirsk Province, Kemerovo Province, Altai Republic), Eastern Siberia (Khakasia, Tyva, Irkutsk Province, Buryatia, Yakutia, Zabaikalskiy Territory, Far East (Amurskaya Province, Khabarovsk Territory, Magadan Province)Western, Northern, Southern, and Eastern Europe, Mongolia, ChinaHoplitis (Anthocopa) caucasicola Müller, 2012European part (North Caucasus)GeorgiaHoplitis (Anthocopa) daurica (Radoszkowski, 1887)European part (South, North Caucasus, Crimea), Urals (Triese, 1895)Western and Southern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkey, Iran, Turkey, Iran, Turkey, Iran, Turkey, Iran, Turkey, Iran, Hoplitis (Anthocopa) papaveris (European part (Central, North Caucasus, Crimea)Western, Southern, and Eastern Europe, Turkey, Iran, Turkey, Iran, Turkey, Iran, Turkey, Iran, Turkey, Iran, Turkey, Iran, Tajikistan, Kyrgyzstan, Kazakhstan, ChinaHoplitis (Anthocopa) papaveris (European part (Central, North Caucasus, Crimea)Western, Southern, and Eastern Europe, Turkey, Iran, Turkey, Kazakhstan, ChinaHoplitis (Anthocopa) papaveris (Ferton, 1894)European part (Central, North Caucasus, Crimea)Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, IranHoplitis (Anthocopa) viellosa (van der Zanden, 1994)European part (North Caucasus, Crimea)Western, Southern, and Eastern Europe, Nort	(Dufour & Perris, 1840)	Crimea), Urals, Western Siberia (Omsk Province, Tomsk	Northern Africa, Georgia, Armenia, Azerbaijan,
Altai Territory, Altai Republic)Kyrgyzstan, KazakhstanHoplitis (Alcidamea) tuberculata (Nylander, 1848)European part (North, Central, East), Urals, Western Siberia (Tyumen Province, Omsk Province, Tomsk Province, Novoshishk Province, Kemerovo Province, Altai Republic), Eastern Siberia (Khakassia, Tyva, Irkutsk Province, Buryatia, Yakutia, Zabaikalskiy Territory), Far East (Amurskaya Province, Khabarovsk Territory, Magadan Province)Western, Northern, Southern, and Eastern Europe, Mongolia, ChinaHoplitis (Anthocopa) caucasicola Müller, 2012European part (North Caucasus)GeorgiaHoplitis (Anthocopa) daurica (Radoszkowski, 1887)European part (South, North Caucasus, Crimea), Urals (Radoszkowski, 1874)Western and Southern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkmenistan, Tajikistan, Kyrgyzstan, Kazakhstan, ChinaHoplitis (Anthocopa) papaveris (Friese, 1895)European part (Central, North Caucasus, Crimea) European part (Central, North Caucasus, Crimea)Western, Southern, and Eastern Europe, Turkey, Kazakhstan, ChinaHoplitis (Anthocopa) papaveris (Larerille, 1799)European part (South, North Caucasus, Crimea)Western, Southern, and Eastern Europe, Turkey, Kazakhstan, ChinaHoplitis (Anthocopa) sozialis (rerton, 1894)European part (North Caucasus, Crimea)Western, Southern, and Eastern Europe, Northern, 1894)Hoplitis (Anthocopa) sozialis (ran der Zanden, 1994)European part (North Caucasus)Southern, and Eastern Europe, Northern, Tajikistan, Kyr		Province, Novosibirsk Province, Kemerovo Province,	Turkey, Syria, Israel, Iran, Uzbekistan,
Hoplitis (Alcidamea) tuberculata (Nylander, 1848)       European part (North, Central, East), Urals, Western, Siberia (Tyumen Province, Omsk Province, Tomsk Province, Novosibirsk Province, Kemerovo Province, Altai Republic), Eastern Siberia (Khakassia, Tyva, Irkutsk Province, Buryatia, Yakutia, Zabaikalskiy Territory), Far East (Amurskaya Province, Khabarovsk Territory, Magadan Province)       Western, Northern, Southern, and Eastern Europe, Mongolia, China         Hoplitis (Anthocopa) caucasicola Müller, 2012       European part (North Caucasus)       Georgia         Hoplitis (Anthocopa) daucica (Radoszkowski, 1887)       Eastern Siberia (Tyva, Buryatia)       –         Hoplitis (Anthocopa) jakovlevi (Radoszkowski, 1887)       European part (South, North Caucasus, Crimea), Urals (Paitis (Anthocopa) jakovlevi (Radoszkowski, 1874)       Western and Southern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkmenistan, Tajikistan, Kyrgyzstan, Kazakhstan, China         Hoplitis (Anthocopa) papaveris (Friese, 1895)       European part (Central, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) papaveris (Friese, 1894)       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkmenistan, Tajikistan, Uzbekistan, China         Hoplitis (Anthocopa) secialis (van der Zanden, 1994)       European part (North Caucasus)       Southern Europe, Turkey, Iran, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Inthocopa) villosa (Scheneck, 1853)       European part (North Caucasu		Altai Territory, Altai Republic)	Kyrgyzstan, Kazakhstan
(Nylander, 1848)       Siberia (Tyumen Province, Omsk Province, Tomsk Province, Novosibirsk Province, Kemerovo Province, Altai Republic), Eastern Siberia (Khakassia, Tyva, Irkutsk Province, Buryatia, Yakutia, Zabaikalskiy Territory), Far East (Amurskaya Province, Khabarovsk Territory), Far East (Amurskaya Province, Khabarovsk Territory), Far East (Amurskaya Province, Khabarovsk Territory), Far East (Amurskaya Province)       Georgia         Müller, 2012       European part (North Caucasus)       Georgia         Hoplitis (Anthocopa) jakovlevi (Radoszkowski, 1887)       European part (South, North Caucasus, Crimea), Urals       Western and Southern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkmenistan, Tajikistan, Kyrgyzstan, Kazakhstan, China         Hoplitis (Anthocopa) mocsaryi (Prices, 1895)       European part (Central, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) papaveris (Latreille, 1799)       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) perezi (Ferton, 1894)       European part (South, North Caucasus), Urals       Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkey, Israel, Iran, Afghanistan, Turkey, Isran, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Anthocopa) perezi (Ferton, 1894)       European part (North Caucasus), Crimea)       Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkey, Isran, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan	Hoplitis (Alcidamea) tuberculata	European part (North, Central, East), Urals, Western	Western, Northern, Southern, and Eastern
Province, Novosibirsk Province, Kemerovo Province, Altai Republic), Eastern Siberia (Khakassia, Tyva, Irkutsk Province, Buryatia, Yakutia, Zabaikalskij Territory), Far East (Amurskaya Province) Hoplitis (Anthocopa) caucasicola Müller, 2012 Hoplitis (Anthocopa) caucasicola Miguer, 2012 Hoplitis (Anthocopa) daurica (Radoszkowski, 1887) Hoplitis (Anthocopa) jakovlevi (Radoszkowski, 1874) European part (South, North Caucasus, Crimea), Urals Hoplitis (Anthocopa) mocaryi (Priese, 1895) European part (Central, North Caucasus, Crimea) Hoplitis (Anthocopa) papaveris European part (Central, North Caucasus, Crimea) Hoplitis (Anthocopa) papaveris European part (Central, North Caucasus), Urals Hoplitis (Anthocopa) papaveris (Larreille, 1799) European part (Central, North Caucasus), Urals Hoplitis (Anthocopa) perezi (Ferton, 1894) Hoplitis (Anthocopa) saxialis Furopean part (North Caucasus, Crimea) (Ferton, 1894) Hoplitis (Anthocopa) saxialis Furopean part (North Caucasus) Furopean part (North Caucasus) Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkmenistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan Hoplitis (Anthocopa) saxialis Furopean part (North Caucasus) Southern Europe, Turkey, Iran (van der Zanden, 1994) Hoplitis (Inthocopa) saxialis (Parting (Formicapi)) maritima (Eastern Siberia (Buryatia), Far East (Primorskiy Mongolia (Romankova, 1985)	(Nylander, 1848)	Siberia (Tyumen Province, Omsk Province, Tomsk	Europe, Mongolia, China
Altai Republic), Eastern Siberia (Khakassia, Tyva, Irkursk Province, Buryatia, Yakutia, Zabaikalskiy Territory), Far East (Amurskaya Province, Magadan Province)         Hoplitis (Anthocopa) caucasicola Müller, 2012       European part (North Caucasus)       Georgia         Hoplitis (Anthocopa) daurica (Radoszkowski, 1887)       Estern Siberia (Tyva, Buryatia)       -         Hoplitis (Anthocopa) jakovlevi (Radoszkowski, 1887)       European part (South, North Caucasus, Crimea), Urals       Western and Southern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkemenistan, Tajikistan, Kyrgyzstan, Kazakhstan, China         Hoplitis (Anthocopa) jakovlevi (Radoszkowski, 1874)       European part (Central, North Caucasus, Crimea), Urals       Western and Southern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkemenistan, Tajikistan, Kyrgyzstan, Kazakhstan, China         Hoplitis (Anthocopa) papaveris (Latreille, 1799)       European part (Central, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) papaveris (Latreille, 1799)       European part (Central, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Turkey, Israel, Iran, Afghanistan, Turkey, Israel, Iran, Afghanistan, Urkey, Israel, Iran, Afghanistan, Urkey, Israel, Iran, Afghanistan, Turkey, Israel, Iran, Afghanistan, Turkey, Israel, Iran, Afghanistan, Turkey, Israel, Iran, Afghanistan, Turkey, Israel, Iran, Afghanistan, Turkey, Iran (van der Zanden, 1994)       Southern Europe, Turkey, Iran (van der Zanden, 1994)         Hoplitis (Anthocopa) saxialis (van der Zanden, 1994)       European part (North Caucasus)		Province, Novosibirsk Province, Kemerovo Province,	
Province, Buryatia, Yakutia, Zabaikalskiy Territory), Far East (Amurskaya Province, Khabarovsk Territory, Magadan Province) Hoplitis (Anthocopa) caucasicola Müller, 2012 Hoplitis (Anthocopa) jakovlevi (Radoszkowski, 1887) Hoplitis (Anthocopa) jakovlevi (Radoszkowski, 1887) Hoplitis (Anthocopa) jakovlevi (Radoszkowski, 1874) European part (South, North Caucasus, Crimea), Urals Hoplitis (Anthocopa) jakovlevi (Friese, 1895) Hoplitis (Anthocopa) papaveris (Latreille, 1799) Hoplitis (Anthocopa) perezi (Ferton, 1894) Hoplitis (Anthocopa) saxialis (van der Zanden, 1994) Hoplitis (Anthocopa) saxialis (van der Zanden, 1994) Hoplitis (Formicapis) maritima Komankova, 1985) Hoplitis (Formicapis) maritima Kamathana Kastern Siberia (Buryatia), Far East (Primorskiy Kongolia (Borgia		Altai Republic), Eastern Siberia (Khakassia, Tyva, Irkutsk	
Far East (Amurskaya Province, Khabarovsk Territory, Magadan Province)         Hoplitis (Anthocopa) caucasicola Müller, 2012       European part (North Caucasus)       Georgia         Hoplitis (Anthocopa) daurica (Radoszkowski, 1887)       Eastern Siberia (Tyva, Buryatia)       –         Hoplitis (Anthocopa) jakovlevi (Radoszkowski, 1887)       European part (South, North Caucasus, Crimea), Urals (Radoszkowski, 1874)       Western and Southern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkmenistan, Tajikistan, Kyrgyzstan, Kazakhstan, China         Hoplitis (Anthocopa) mocsaryi (Friese, 1895)       European part (Central, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) papaveris (Latreille, 1799)       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) papaveris (Iatreille, 1799)       European part (South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkey, Iran         Hoplitis (Anthocopa) socialis (van der Zanden, 1994)       European part (North Caucasus)       Southern Europe, Turkey, Iran         Hoplitis ( <i>Inthocopal</i> ) villosa (Schenck, 1853)       Puropean		Province, Buryatia, Yakutia, Zabaikalskiy Territory),	
Magadan Province)         Hoplitis (Anthocopa) caucasicola       European part (North Caucasus)       Georgia         Müller, 2012       -         Hoplitis (Anthocopa) daurica (Radoszkowski, 1887)       Eastern Siberia (Tyva, Buryatia)       -         Hoplitis (Anthocopa) jakovlevi (Radoszkowski, 1887)       European part (South, North Caucasus, Crimea), Urals (Radoszkowski, 1874)       Western and Southern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkmenistan, Tajikistan, Kyrgyzstan, Kazakhstan, China         Hoplitis (Anthocopa) mocsaryi (Friese, 1895)       European part (Central, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) papaveris (Latreille, 1799)       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) perezi (Ferton, 1894)       European part (South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkey, Israel, Iran, Afghanistan, Turkey, Israel, Iran, Afghanistan, Turkey, Israel, Iran, Afghanistan, Turkey, Israel, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkey, Iran         Hoplitis (Anthocopa) sexialis (van der Zanden, 1994)       European part       Western, Southern, and Eastern Europe (Schenck, 1853)         Hoplitis (Formicapis) maritima       Eastern Siberia (Buryatia), Far East (Primorskiy       Mongolia (Romankova, 1985)		Far East (Amurskaya Province, Khabarovsk Territory,	
Hoplitis (Anthocopa) caucasicola       European part (North Caucasus)       Georgia         Müller, 2012       -         Hoplitis (Anthocopa) daurica (Radoszkowski, 1887)       Eastern Siberia (Tyva, Buryatia)       -         Hoplitis (Anthocopa) jakovlevi (Radoszkowski, 1887)       European part (South, North Caucasus, Crimea), Urals       Western and Southern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkmenistan, Tajikistan, Kyrgyzstan, Kazakhstan, China         Hoplitis (Anthocopa) mocsaryi (Friese, 1895)       European part (Central, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) papaveris (Latreille, 1799)       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) papaveris (Latreille, 1799)       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Israel, Iran, Afghanistan, China         Hoplitis (Anthocopa) perezi (Yerton, 1894)       European part (North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkmenistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Anthocopa) saxialis (van der Zanden, 1994)       European part (North Caucasus)       Southern Europe, Turkey, Iran         Hoplitis (Southocopa) saxialis (Van der Zanden, 1994)       European part (North Caucasus)       Southern and Eastern Europe         Hoplitis		Magadan Province)	
Müller, 2012         Hoplitis (Anthocopa) daurica (Radoszkowski, 1887)       Eastern Siberia (Tyva, Buryatia)       –         Hoplitis (Anthocopa) jakovlevi (Radoszkowski, 1887)       European part (South, North Caucasus, Crimea), Urals       Western and Southern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkmenistan, Tajikistan, Kyrgyzstan, Kazakhstan, China         Hoplitis (Anthocopa) mocsaryi (Friese, 1895)       European part (Central, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) papaveris (Latreille, 1799)       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Kazakhstan, China         Hoplitis (Anthocopa) papaveris (Latreille, 1799)       European part (South, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Kazakhstan, China         Hoplitis (Anthocopa) papaveris (Certon, 1894)       European part (South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkmenistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Anthocopa) saxialis (van der Zanden, 1994)       European part (North Caucasus)       Southern Europe, Turkey, Iran         Hoplitis (Formicapis) maritima (Schenck, 1853)       Eastern Siberia (Buryatia), Far East (Primorskiy       Mongolia         Hoplitis (Romankova, 1985)       Territory)       Mongolia	Hoplitis (Anthocopa) caucasicola	European part (North Caucasus)	Georgia
Hoplitis (Anthocopa) daurica (Radoszkowski, 1887)       Eastern Siberia (Tyva, Buryatia)       –         Hoplitis (Anthocopa) jakoulevi (Radoszkowski, 1887)       European part (South, North Caucasus, Crimea), Urals       Western and Southern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkmenistan, Tajikistan, Kyrgyzstan, Kazakhstan, China         Hoplitis (Anthocopa) mocsaryi (Friese, 1895)       European part (Central, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) papaveris (Latreille, 1799)       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) papaveris (Latreille, 1799)       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Israel, Iran, Afghanistan, China         Hoplitis (Anthocopa) papaveris (Ferton, 1894)       European part (South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkmenistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Anthocopa) saxialis (van der Zanden, 1994)       European part (North Caucasus)       Southern Europe, Turkey, Iran         Hoplitis (Sonthocopa) villosa (Schenck, 1853)       European part       Western, Southern, and Eastern Europe         Hoplitis (Formicapis) maritima (Romankova, 1985)       Eastern Siberia (Buryatia), Far East (Primorskiy       Mongolia	Müller, 2012		
(Kadoszkowski, 1887)       European part (South, North Caucasus, Crimea), Urals       Western and Southern Europe, Northern         (Radoszkowski, 1874)       European part (South, North Caucasus, Crimea), Urals       Western and Southern Europe, Northern         Africa, Armenia, Azerbaijan, Turkey, Iran, Turkmenistan, Tajikistan, Kyrgyzstan, Kazakhstan, China       Kazakhstan, China         Hoplitis (Anthocopa) mocsaryi       European part (Central, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) papaveris       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Kazakhstan, China         Hoplitis (Anthocopa) papaveris       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Kazakhstan, China         Hoplitis (Anthocopa) perezi       European part (South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkmenistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Anthocopa) saxialis       European part (North Caucasus)       Southern Europe, Turkey, Israel, Iran, Afghanistan, Turkmenistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Anthocopa) saxialis       European part (North Caucasus)       Southern Europe, Turkey, Iran         (van der Zanden, 1994)       European part       Western, Southern, and Eastern Europe         Hoplitis	Hoplitis (Anthocopa) daurica	Eastern Siberia (Tyva, Buryatia)	-
Haplitis (Anthocopa) jakoulevi (Radoszkowski, 1874)       European part (South, North Caucasus, Crimea), Urals       Western and Southern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Iran, Turkmenistan, Tajikistan, Kyrgyzstan, Kazakhstan, China         Hoplitis (Anthocopa) mocsaryi (Friese, 1895)       European part (Central, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) papaveris (Latreille, 1799)       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Kazakhstan, China         Hoplitis (Anthocopa) perezi (Ferton, 1894)       European part (South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkmenistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Anthocopa) saxialis (van der Zanden, 1994)       European part (North Caucasus)       Southern Europe, Turkey, Iran         Hoplitis (Grmicopis) maritima (Schenck, 1853)       Eastern Siberia (Buryatia), Far East (Primorskiy Mongolia       Southern, and Eastern Europe	(Radoszkowski, 188/)		
(Radoszkowski, 1874)       Africa, Armenia, Azerbaijan, Turkey, Iran, Turkmenistan, Tajikistan, Kyrgyzstan, Kazakhstan, China         Hoplitis (Anthocopa) mocsaryi (Friese, 1895)       European part (Central, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) papaveris (Latreille, 1799)       European part (Central, North Caucasus, Urals       Western, Southern, and Eastern Europe, Turkey, Kazakhstan, China         Hoplitis (Anthocopa) perezi (Ferton, 1894)       European part (South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkmenistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Anthocopa) saxialis (van der Zanden, 1994)       European part (North Caucasus)       Southern Europe, Turkey, Iran         Hoplitis (Anthocopa) villosa (Schenck, 1853)       European part (North Caucasus)       Southern, and Eastern Europe         Hoplitis (Formicapis) maritima (Romankova, 1985)       Eastern Siberia (Buryatia), Far East (Primorskiy       Mongolia	Hoplitis (Anthocopa) jakovlevi	European part (South, North Caucasus, Crimea), Urals	Western and Southern Europe, Northern
Haplitis (Anthocopa) mocsaryi       European part (Central, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) papaveris       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) papaveris       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Kazakhstan, China         Hoplitis (Anthocopa) perezi       European part (South, North Caucasus), Urals       Western, Southern, and Eastern Europe, Northern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkey, Israel, Iran, Afghanistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Anthocopa) saxialis       European part (North Caucasus)       Southern Europe, Turkey, Iran         (van der Zanden, 1994)       European part       Western, Southern, and Eastern Europe         Hoplitis (Anthocopa) villosa       ?European part       Western, Southern, and Eastern Europe         (Schenck, 1853)       Eastern Siberia (Buryatia), Far East (Primorskiy       Mongolia         Hoplitis (Formicapis) maritima       Eastern Siberia (Buryatia), Far East (Primorskiy       Mongolia	(Radoszkowski, 1874)		Africa, Armenia, Azerbaijan, Turkey, Iran,
Kazakhstan, China         Haplitis (Anthocopa) mocsaryi         European part (Central, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Turkey, Israel, Iran         Hoplitis (Anthocopa) papaveris       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Kazakhstan, China         Hoplitis (Anthocopa) papaveris       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Kazakhstan, China         Hoplitis (Anthocopa) prezi       European part (South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern, Afghanistan, Turkey, Israel, Iran, Afghanistan, Turkey, Israel, Iran, Afghanistan, Turkey, Israel, Iran, Afghanistan, Turkey, Israel, Iran, Afghanistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Anthocopa) saxialis       European part (North Caucasus)       Southern Europe, Turkey, Iran         (van der Zanden, 1994)       European part       Western, Southern, and Eastern Europe         Hoplitis (Anthocopa) villosa       European part       Western, Southern, and Eastern Europe         (Schenck, 1853)       Eastern Siberia (Buryatia), Far East (Primorskiy       Mongolia         Hoplitis (Formicapis) maritima       Eastern Siberia (Buryatia), Far East (Primorskiy       Mongolia			lurkmenistan, lajikistan, Kyrgyzstan,
Haplitis (Anthocopa) mocsaryi       European part (Central, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Iurkey, Israel, Iran         Hoplitis (Anthocopa) papaveris       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Kazakhstan, China         Hoplitis (Anthocopa) perezi       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Kazakhstan, China         Hoplitis (Anthocopa) perezi       European part (South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern, Afghanistan, Turkey, Israel, Iran, Afghanistan, Turkey, Israel, Iran, Afghanistan, Turkey, Israel, Iran, Afghanistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Anthocopa) saxialis       European part (North Caucasus)       Southern Europe, Turkey, Iran         (van der Zanden, 1994)       European part       Western, Southern, and Eastern Europe         Hoplitis (Anthocopa) villosa       European part (North Caucasus)       Southern Europe, Turkey, Iran         (Schenck, 1853)       Eastern Siberia (Buryatia), Far East (Primorskiy       Mongolia         Hoplitis (Formicapis) maritima       Eastern Siberia (Buryatia), Far East (Primorskiy       Mongolia         (Romankova, 1985)       Territory)       Mongolia			Kazakhstan, China
(friese, 1895)       Israel, Iran         Hoplitis (Anthocopa) papaveris (Latreille, 1799)       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Turkey, Kazakhstan, China         Hoplitis (Anthocopa) prezi (Ferton, 1894)       European part (South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkmenistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Anthocopa) saxialis (van der Zanden, 1994)       European part (North Caucasus)       Southern Europe, Turkey, Iran         Hoplitis (Anthocopa) villosa (Schenck, 1853)       European part       Western, Southern, and Eastern Europe         Hoplitis (Formicapis) maritima (Romankova, 1985)       Eastern Siberia (Buryatia), Far East (Primorskiy       Mongolia	Hoplitis (Anthocopa) mocsaryi	European part (Central, North Caucasus, Crimea)	Western, Southern, and Eastern Europe, Turkey,
Hoplitis (Anthocopa) papaveris       European part (Central, North Caucasus), Urals       Western, Southern, and Eastern Europe, Iurkey, Kazakhstan, China         Hoplitis (Anthocopa) perezi       European part (South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkmenistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Anthocopa) saxialis       European part (North Caucasus)       Southern Europe, Turkey, Iran         (van der Zanden, 1994)       European part       Western, Southern, and Eastern Europe         Hoplitis (Anthocopa) villosa       European part (North Caucasus)       Southern Europe, Turkey, Iran         (Schenck, 1853)       Eastern Siberia (Buryatia), Far East (Primorskiy       Mongolia         Hoplitis (Formicapis) maritima       Eastern Siberia (Buryatia), Far East (Primorskiy       Mongolia	(Friese, 1895)		Israel, Iran
Itarrenie, 1799)       Razakństan, China         Hoplitis (Anthocopa) perezi (Ferton, 1894)       European part (South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkmenistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Anthocopa) saxialis (van der Zanden, 1994)       European part (North Caucasus)       Southern Europe, Turkey, Iran         Hoplitis (Anthocopa) villosa (Schenck, 1853)       European part       Western, Southern, and Eastern Europe         Hoplitis (Formicapis) maritima (Romankova, 1985)       Eastern Siberia (Buryatia), Far East (Primorskiy       Mongolia	Hoplitis (Anthocopa) papaveris	European part (Central, North Caucasus), Urals	Western, Southern, and Eastern Europe, Turkey,
Hoplitis (Anthocopa) perezi       European part (South, North Caucasus, Crimea)       Western, Southern, and Eastern Europe, Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkmenistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Anthocopa) saxialis       European part (North Caucasus)       Southern Europe, Turkey, Iran         (van der Zanden, 1994)       European part (North Caucasus)       Southern Europe, Turkey, Iran         Hoplitis (Anthocopa) villosa       European part       Western, Southern, and Eastern Europe         (Schenck, 1853)       Eastern Siberia (Buryatia), Far East (Primorskiy       Mongolia         (Romankova, 1985)       Territory)       Mongolia	(Latreille, 1/99)		Kazaknstan, China
(rerton, 1894)       Northern Africa, Armenia, Azerbaijan, Turkey, Israel, Iran, Afghanistan, Turkmenistan, Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Anthocopa) saxialis (van der Zanden, 1994)       European part (North Caucasus)       Southern Europe, Turkey, Iran         Hoplitis (Anthocopa) villosa (Schenck, 1853)       European part       Western, Southern, and Eastern Europe         Hoplitis (Formicapis) maritima (Romankova, 1985)       Eastern Siberia (Buryatia), Far East (Primorskiy       Mongolia	Hoplitis (Anthocopa) perezi	European part (South, North Caucasus, Crimea)	Western, Southern, and Eastern Europe,
Israel, Iran, Afghanistan, Iurkmenistan, Tajikistan, Vzbekistan, Kyrgyzstan, Kazakhstan       Hoplitis (Anthocopa) saxialis     European part (North Caucasus)     Southern Europe, Turkey, Iran       (van der Zanden, 1994)     *     *     *       Hoplitis (Anthocopa) villosa     *     European part     Western, Southern, and Eastern Europe       (Schenck, 1853)     *     *     *     *       Hoplitis (Formicapis) maritima     Eastern Siberia (Buryatia), Far East (Primorskiy     Mongolia       (Romankova, 1985)     Territory)     *     *	(rerton, 1894)		Nortnern Africa, Armenia, Azerbaijan, Turkey,
Tajikistan, Uzbekistan, Kyrgyzstan, Kazakhstan         Hoplitis (Anthocopa) saxialis       European part (North Caucasus)       Southern Europe, Turkey, Iran         (van der Zanden, 1994)       *       European part       Western, Southern, and Eastern Europe         Hoplitis (Anthocopa) villosa       *       European part       Western, Southern, and Eastern Europe         Kohenck, 1853)       *       *       Mongolia         Hoplitis (Formicapis) maritima       Eastern Siberia (Buryatia), Far East (Primorskiy       Mongolia         (Romankova, 1985)       Territory)       *			Israel, Iran, Argnanistan, Turkmenistan,
Impute (Introduction) statuts     European part (INORTH Caucasus)     Southern Europe, Turkey, Iran       (van der Zanden, 1994)	Haplitia (Anthones )	European part (NI)	Southorn Europe Tenlere Jack
Hoplitis (Anthocopa) villosa     ?European part     Western, Southern, and Eastern Europe       (Schenck, 1853)     Eastern Siberia (Buryatia), Far East (Primorskiy     Mongolia       (Romankova, 1985)     Territory)	(van der Zanden, 1994)	European part (North Caucasus)	Soutnern Europe, Turkey, Iran
Hoppitis (Formicapis) maritima     Eastern Siberia (Buryatia), Far East (Primorskiy     Mongolia       (Romankova, 1985)     Territory)	Hotlitic (Anthoest a) willow	Furance	Wastern Southern and Eastern Europe
Hoplitis (Formicapis) maritima     Eastern Siberia (Buryatia), Far East (Primorskiy     Mongolia       (Romankova, 1985)     Territory)	(Schenck, 1853)	:European part	western, southern, and Eastern Europe
(Romankova, 1985) Territory)	Hoplitis (Formicabis) maritima	Fastern Siberia (Burvatia) Far Fast (Primorskiv	Mongolia
	(Romankova, 1985)	Territory)	Bound

Species	Distribution in Russia	Distribution outside Russia
Hoplitis (Formicapis) robusta (Nylander, 1848)	European part (Central), Western Siberia (Tomsk Province, Altai Republic), Eastern Siberia (Irkutsk Province, Buryatia, Yakutia, Zabaikalskiy Territory), Far East (Amurskaya Province, Magadan Province, Chukotka Autonomous Area)	Western, Northern, Southern, and Eastern Europe, Mongolia, China, North America
Hoplitis (Hoplitis) adunca (Panzer, 1798)	European part (Central, South, North Caucasus), Urals	Western, Northern, Southern, and Eastern Europe, Northern Africa, Georgia, Armenia, Azerbaijan, Turkey, Turkmenistan, Kyrgyzstan, Kazakhstan
Hoplitis (Hoplitis) andreasmuelleri Fateryga & Proshchalykin, <b>sp. nov.</b>	European part (North Caucasus)	_
Hoplitis (Hoplitis) anthocopoides (Schenck, 1853)	European part (South, North Caucasus, Crimea)	Western, Northern, Southern, and Eastern Europe, Northern Africa, Armenia, North America (introduced)
Hoplitis (Hoplitis) astragali Fateryga, Müller & Proshchalykin, 2023	European part (North Caucasus)	Azerbaijan, Turkmenistan
Hoplitis (Hoplitis) carinata (Stanek, 1969)	European part (Crimea)	Southern and Eastern Europe, Armenia, Azerbaijan, Turkey, Syria, Jordan, Iran
Hoplitis (Hoplitis) dagestanica Fateryga, Müller & Proshchalykin, 2023	European part (North Caucasus)	_
Hoplitis (Hoplitis) kaszabi Tkalců, 2000	Western Siberia (Altai Republic), Eastern Siberia (Buryatia)	Tajikistan, Kazakhstan, Mongolia, China
Hoplitis (Hoplitis) linguaria (Morawitz, 1875)	European part (North Caucasus)	Georgia, Turkey
<i>Hoplitis (Hoplitis) manicata</i> Morice, 1901	European part (South, North Caucasus, Crimea)	Western, Southern, and Eastern Europe, ?Northern Africa, Armenia, Azerbaijan, Turkey
Hoplitis (Kumobia) abbreviata (Morawitz, 1875)	Western Siberia (Altai Republic)	Kyrgyzstan, Kazakhstan, Mongolia
Hoplitis (Pentadentosmia) laevifrons (Morawitz, 1872)	?European part, Urals	Western, Southern, and Eastern Europe, Armenia, Azerbaijan, Turkey, Pakistan, India
Hoplitis (Pentadentosmia) tringa (Warncke, 1991)	European part (North Caucasus)	Azerbaijan, Turkey, Iran
Hoplitis (Platosmia) inconspicua Tkalců, 1995	Western Siberia (Altai Republic), Eastern Siberia (Khakassia, Tyva)	Mongolia

# Acknowledgements

We thank Ramazan Murtazaliev (Caspian Institute of Biological Resources of the Dagestan Federal Research Center of RAS, Makhachkala, Russia) for organizing our visit to the Samurskiy National Park, where the specimens of *H. andreasmuelleri* were collected. We thank also Andreas Müller (ETH Zurich, Institute of Agricultural Sciences, Biocommunication and Entomology, Zurich, Switzerland), who confirmed that this species is indeed new and recommended to describe it. Two anonymous reviewers provided some suggestions to improve the text.

This work was supported by the Ministry of Science and Higher Education of the Russian Federation in accordance with agreement No. 075-15-2022-322, date 22 April 2022, on providing a grant in the form of subsidies from the Federal budget of the Russian Federation. The grant was provided for state support for the creation and development of a World-class Scientific Center "Agrotechnologies for the Future".

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