CHECKLIST



An updated checklist of the bees (Hymenoptera, Apoidea, Anthophila) of Pennsylvania, United States of America

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Abstract

Checklists provide information about the species found in a defined region and serve as baselines for detecting species range expansions, contractions, or introductions. Bees are a diverse and important group of insect pollinators. Although some bee populations are declining, these patterns are difficult to document and generalize due to a lack of long-term studies for most localities. Documenting the diversity of wild bee communities is critical for assessing pollination services, community ecology, and geographical and temporal changes in distribution and density. Here, an updated checklist of the bees of the Commonwealth of Pennsylvania, USA, is presented. Since the first checklist was published (2010; 372 species), thousands of additional specimens from the state have been collected and databased, new species have been described in the region, and the taxonomic status of some species have changed. Specimen data from insect collections, databases, scientific literature, and unpublished records were compared to the original checklist. Seventy-nine new state species records – including 49 first-time reports – representing five of the six bee families in North America, were documented resulting in a total of at least 437 bee

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species reported from Pennsylvania. We highlight new county records and species persistence details. Our list includes a total of 23 exotic species and at least five species of conservation concern. Lists of species excluded from the state checklist and species anticipated to occur in Pennsylvania are also included. This checklist provides baseline data for researchers and the public. The benefits of insect collections, specimen databases, determination and voucher labels, and georeferencing to biodiversity studies and other aspects of biological research are also discussed.

Keywords

Aculeata, adventive species, Andrenidae, Apidae, biodiversity, check list, Colletidae, conservation, distribution, faunal records, Halictidae, new records, Megachilidae, Melittidae, persistence, phenology, pollinators

Introduction

Bees (Hymenoptera: Apoidea: Anthophila) represent a fascinating and diverse group of insects. World-wide, there are at least 20,473 species of bees and, of these, 5,227 species are recorded from North America (Ascher and Pickering 2020). The majority of these bee species are native, but at least 45 species have been introduced to the continent since 1620 (Russo 2016; Gibbs and Dathe 2017; Martins et al. 2017; Normandin et al. 2017; USGS Native Bee Laboratory 2019). Because of their ecologically important role as pollinators of flowering plants in natural ecosystems and agricultural areas, maintaining wild bee species diversity is critical for crop pollination and ecosystem function (Genung et al. 2017; Winfree et al. 2008; Winfree et al. 2018; Grab et al. 2019).

Overwhelming evidence of declines in managed and wild bee populations has emphasized the need for a better understanding of bee diversity across different geographic areas (e.g., Potts et al. 2010b; Colla et al. 2012; Bartomeus et al. 2013). Despite extensive research efforts, our understanding of the status of most native bee species remains deficient (Cane and Tepedino 2001; Potts et al. 2010a; Koh et al. 2016; Meiners et al. 2019). It is challenging to assess the status of many species due to a lack of comparable historical and long-term datasets. In the past 140 years, non-*Apis* and non-*Bombus* bee species richness declines measured 15% in the northeastern United States (Bartomeus et al. 2013). Recent surveys revealed that ~5% of the eastern North American species had not been documented between 1990 and 2009, though the exact reason(s) for their absence in collections remains unconfirmed (Colla et al. 2012). These findings in bees reflect the larger issue of global insect decline, most recently reviewed by Montgomery et al. (2019).

Checklists serve as baselines, helping fill the lack of knowledge of species' distributions, taxonomic classifications, and biodiversity of a region. They may also contribute details on the phenology, persistence, and other biological aspects of species. Checklists can be used to detect range shifts in both native and non-native species over time, and to identify under-surveyed localities and seasonalities (e.g., Dibble et al. 2017; Gibbs et al. 2017a). This information can contribute to establishing long-term monitoring programs (Berenbaum et al. 2007; LeBuhn et al. 2013). Repeated surveys, coupled with long-term monitoring of bee biodiversity, community composition, and population dynamics over time, can provide data to establish conservation strategies and priorities (Berenbaum et al. 2007; LeBuhn et al. 2013; Koh et al. 2016).

Taxonomic studies of bees in the eastern United States have documented some of the biodiversity in the Commonwealth of Pennsylvania (PA), USA (Cockerell 1908; Stephen 1954; Mitchell 1960, 1962; Ordway 1966; Shinn 1967; Roberts 1972; Daly 1973; LaBerge 1969, 1971, 1973, 1977, 1980, 1985, 1987, 1989; LaBerge and Bouseman 1970; LaBerge and Ribble 1972, 1975; Milliron 1973a; Baker 1975; Timberlake 1975; Svensson et al. 1977; Bouseman and LaBerge 1978; McGinley 1986, 2003; Broemeling 1988). Donovall and vanEngelsdorp (2010) published the first checklist of bees in Pennsylvania, reporting 372 species from 13,076 specimens located in 20 collections. Since then, a number of crop pollination studies and citizen science projects have been done in the state (e.g., DeBarros 2010; Sidhu 2013; studies cited in Table 1). In addition, the Pennsylvania Department of Agriculture (PDA) has surveyed bees nearly annually since 2005 (Donovall and vanEngelsdorp 2010; Karen Roccasecca, pers. comm.) and bycatch from PDA invasive pest insect monitoring traps also commonly includes bees (Mikulas and Barringer 2018). As a result, thousands of bee specimens from across the state have been collected, identified, and documented in collection databases and research publications.

This study updates the taxonomy of species listed in Donovall and vanEngelsdorp (2010), resolves dubious records reported in Donovall and vanEngelsdorp (2010), and reports additional Pennsylvanian bee species data. We present new records at state and county levels, distribution data at the county level, collection date ranges, and the most recent year of collection or observation for each species. Additionally, we discuss the natural history of Pennsylvania's bee biodiversity, the value of checklists, and the importance of repeatable taxonomy, collections, and voucher material to faunistic studies and knowledge.

Methods

Baseline Pennsylvania bee checklist data

We transcribed the list of Pennsylvanian bee species and their county, dates of collection, most recent year of collection records, and all other information from Donovall and vanEngelsdorp (2010) (Suppl. material 1). In addition, species' taxonomy was updated as necessary following recent revisions. This document provided a baseline to which new data could be compared to information reported in the previous checklist.

The individual specimens examined for the previous checklist were not traceable due to a lack of voucher/accession numbers or another way to reliably identify the physical material that was deposited/returned to the collections after their study. A spreadsheet that Donovall and vanEngelsdorp had used to record some of the data for their checklist was obtained via personal communications with both authors and Emily Agar (University of Guelph, Ontario, Canada). A subset of the bee species records within the spreadsheet, using their specimen data in place of voucher identifiers, were targeted for verification based on the proximity and accessibility of collections they were housed at. This included material in the following collections: Department of Entomology, Academy of Natural Sciences, Philadelphia, PA (ANSP), Section of Insects and Spiders, Carnegie Museum of Natural History, Pittsburg, PA (CMNH = ICCM), and the Pennsylvania Department of Agriculture Arthropod Collection, Bureau of Plant Industry, Pennsylvania Department of Agriculture, Harrisburg, PA (PADA). Specimens at the PADA collection were also examined for new records. As not all of the PADA specimens listed in the spreadsheet were present in the PADA collection and material at the other collections was difficult to trace, we used new data to verify previously reported species records. Furthermore, the full details for two records were not available in the spreadsheet: "USNM 1" for Colletes americanus Cresson, 1868 and "PADA 15" for Osmia cornifrons (Radoszkowski, 1887). Specifically, Pennsylvanian C. americanus specimens from the collection suggested by the codon and number was not present and, in the case of O. cornifrons, the species was absent from the spreadsheet. Thus, the full specimen records indicated by these codes could not be verified and the data was removed from the checklist. All other data published in Donovall and vanEngelsdorp (2010) was unable to be fully verified and is reprinted here with this caveat.

Specimen database review

Databases of bee specimens collected in Pennsylvania and identified by experts were primarily obtained via personal communications from eight sources between Summer 2017 and Fall 2019 (Table 1). Only species identified to a single species-level name were used; specimen records with no names and no data, identified to more than one species name (e.g., Ceratina dupla sensu lato, Hylaeus affinis/modestus), or with taxonomic uncertainty (containing terms such as "maybe", "like", "close to", "cf" in their name or a notes section), were excluded. We also excluded 17 specimen records that were identified to species-level. These records warrented verification of the specimens' identities, but we were unable to examine them of as part of this study. County-record data for specimens with no county given in the database were confirmed via personal communications with the database manager(s) or georeferenced using Google Earth Pro (version 7.3.2.5776 (64-bit); Table 1). Julian dates in Bartomeus et al. (2013) were converted to calendar dates using the DATE function in Microsoft Excel (version 16.16.15; Table 1). Individual specimen records in each database were compared to the previously published data for bee species recorded in Pennsylvania (Donovall and vanEngelsdorp 2010). For specimens without a determiner listed in the database, we treated them as if they were identified by at least one of the other experts associated with the collection's material, but that these specimens did not have determinationlabels applied as is sometimes common when specimens are identified; not all specimens may bear determination labels by the end of the process and are thus databased without a determiner listed.

Table 1. Information about the bee specimen databases examined for this study. Database names, locations of the specimen material, the total numbers of records used, the names of people who identified material, and the names of people who provided database files/access are presented.

Database Name	Location(s) of	Total # of	Primary Identifiers	Obtained	Supplemental
	Specimen Material	specimen		from	material #
	_	records used			
Bartomeus et al. 2013	American Museum	537	J.S. Ascher, R.W.	Bartomeus	2
	of Natural History,		Brooks, E.L. Bzdyk,	et al.	
	University of		B. Coelho, Daly, L.	(2013)	
	Connecticut,		Day, N.B. DeBarros,		
	Cornell University,		S. Droege, G.C.		
	Rutgers University,		Eickwort, J. Gibbs,		
	Connecticut		R.S. Jacobson,		
	Agricultural Station,		Bouseman &		
	University of		LaBerge, W.E.		
	New Hampshire,		LaBerge, R.B. Miller,		
	University of		T.B. Mitchell,		
	Massachusetts,		D.W. Ribble,		
	Vermont State Bee		L. Richardson,		
	Database, New		M.G. Rightmyer,		
	York State Museum,		R.B. Roberts, G.		
	Bohart Museum		Sandhouse, R.R.		
	of Entomology		Snelling, R.W.		
	(University of		Thorp, Viereck		
	California, Davis)				
Biddinger Laboratory	Penn State University	96,382	D. Biddinger, J.	Kathryn	3
Database [includes data	Fruit Research		Gibbs, R. Jean, K.	Wholaver,	
from Shugrue (2016)	and Extension		Wright	pers.	
and Gibbs et al. (2017b)]	Center, Biglerville,			comm.	
	PA (PSUB); Frost				
	Entomological				
	Museum, Department				
	of Entomology,				
	Pennsylvania State				
	University, University				
	Park, PA (PSUC)				
Droege Database	United State	1,139	J. Ascher, S. Droege,	Sam	4
	Geological Survey		S. Rehan	Droege,	
	(USGS) Patuxent			pers.	
	Wildlife Research			comm.	
	Center, Laurel, MD				
Integrated Crop	Frost Entomological	1,176	S. Droege, J. Gibbs,	N/A	5
Pollination (ICP)	Museum, Department		R. Jean, D. Roberts,		
Project: Fleischer	of Entomology,		K. Watrous		
Laboratory Database	Pennsylvania State				
lincludes data from	University, University				
McGrady et al. (2019)]	Park, PA (PSUC)				
López-Uribe Laboratory	López-Uribe	3,417	N.D. Amon, J.	N/A	6
Database [includes	Laboratory,		Baker, S. Burrows,		
2008 Pennsylvania	Department of		L.R. Donovall, S.		
Department of	Entomology,		Droege, K.E. Ellis,		
Agriculture survey	Pennsylvania State		S.K. Kilpatrick,		
material]	University, University		M.M. Mikulas, R.		
	Park, PA		Snyder		

Database Name	Location(s) of	Total # of	Primary Identifiers	Obtained	Supplemental
	Specimen Material	specimen		from	material #
		records used			
Winfree Laboratory	Winfree Laboratory,	17,804	J. Ascher, S.	Rachel	7
Database [includes data	Department of		Droege, J. Gibbs,	Winfree,	
from Winfree et al.	Ecology, Evolution		T. Griswold, T.	pers.	
2008]	and Natural		Harrison, M.	comm.	
	Resources, Rutgers		Rightmyer		
	University, New				
	Brunswick, NJ				
Mahan et al., in prep	Frost Entomological	2,614	S. Droege, D.	Carolyn	8
[Utility Rights-of-way	Museum, Department		Roberts, L. Russo,	Mahan and	
at State Game Lands 33	of Entomology,		H. Stout	Hannah	
and Green Lane Research	Pennsylvania State			Stout, pers.	
& Demonstration Areas;	University, University			comm.	
https://sites.psu.edu/	Park, PA (PSUC)				
transmissionlineecology/]					
Choate et al. 2018	Choate Laboratory,	1,520	S. Droege, P.L.	Beth	9
[includes full data from	Department of		Hickman, E.A.	Choate,	
Choate et al. (2018)]	Environmental		Moretti	pers.	
	Science &			comm.	
	Sustainability,				
	Allegheny College,				
	Meadville, PA				

It is noted that Donovall and vanEngelsdorp (2010) used material deposited at the Penn State University Fruit Research and Extension Center, Biglerville, PA (PSUB) in their manuscript. However, as it was impossible to determine specifically what specimen records they reviewed/reported, we used all of the specimen records available. Additionally, some of the specimen records in PSUB were also part of the Integrated Crop Pollination (ICP) Project database (Table 1). To avoid duplication of records, only non-PSUB data from the ICP database was reported while the PSUB database was used in full. A total of 124,589 specimen records from databases were used (Table 1).

Literature review

We examined several literature sources that contributed to the first list of species in Pennsylvania: Mitchell (1960, 1962), LaBerge (1985), Timberlake (1975), and McGinley (2003). Other literature cited by Donovall and vanEngelsdorp (2010) as treating Pennsylvanian bee fauna was also examined to verify record information (Ord-way 1966; Shinn 1967; LaBerge and Bouseman 1970; LaBerge and Ribble 1972; Roberts 1972; Daly 1973; Milliron 1973a; Baker 1975; LaBerge 1973, 1977, 1980, 1987; Bouseman and LaBerge 1978; McGinley 1986; Broemeling 1988). We also reviewed other scientific literature, with a focus on bee studies performed in Pennsylvania, the northeastern United States, or on Pennsylvanian taxa since 2010, for new species and details for inclusion in our updated checklist (Cockerell 1908; Swenk 1915; Stephen 1954; LaBerge 1969, 1971, 1989; LaBerge and Ribble 1975; Svensson et al. 1977;

Schwarz and Gusenleitner 2004; Matteson et al. 2008; Rightmyer 2008; Gibbs 2009, 2010, 2011, 2012; DeBarros 2010; Droege et al. 2010; Rehan and Sheffield 2011; Gibbs et al. 2013; Sidhu 2013; Gibbs and Dathe 2017; Onuferko 2017, 2018; Mikulas and Barringer 2018). We compiled 1,283 specimen records from these sources (Suppl. material 10). County geography was verified for records as feasible using Google Earth Pro (version 7.3.2.5776 (64-bit)). There were only six cases in which a specific locality name was available, but county-level geography was impossible to assign with certainty (see comments in Suppl. material 10). Dates ranges were inferred from methods sections as feasible, though these are not included in the checklist if they did not represent a single collecting event (as in DeBarros 2010; Suppl. material 10). Furthermore, year of collection ranges from Sidhu (2013) are only reported in our checklist if they represented either the most recent year(s) of collection (n = 1) or the only known year(s) of collection for a species (n = 2) (Suppl. material 1, 10). Specimen data from Winfree et al. (2008), Shruge (2016), Gibbs et al. (2017b), Choate et al. (2018), and McGrady et al. (2019) were not included in the literature review as their data were reviewed in databases (Table 1). Reports of species or specimens inferred from range maps without data points, generalized distribution statements, tentative identifications, and observation-based records in the reviewed literature were not compiled and are thus not presented; they are considered unverifiable until either a specimen from Pennsylvania is confirmed to exist or specimens' identities are fully confirmed.

Several of the papers reviewed did not provide full data for the specimens examined or collected. The full data for some of these (Daly 1973; McGinley 1986; DeBarros 2010; Sidhu 2013) was either stated or seemed likely to be available based on the text. The appropriate personnel at the institutions as assumed or indicated by each author were contacted in an attempt to verify complete collecting events. The availability of Daly's (1973) and DeBarros's (2010) data remains unknown. McGinley's (1986) specimen data was not available from the Smithsonian Institution Archives (Ellen Alers, pers. comm.) or U.S. National Entomological Collection (USNM) / Department of Entomology (Floyd Shockley, pers. comm.). McGinley is in the process of locating these records to resolve the discrepancy (Ron McGinley, pers. comm.). In the case of Sidhu (2010), the records that were expected to be in the Frost Entomological Museum's holdings were not available, but an additional data sheet was (Andy Deans, pers. comm.).

Additional records

State and county records were haphazardly added to the checklist as we became aware of them and they were verified. A total of four specimens, from PSUB, Rosemary Malfi Insect Collection, and Emily Erickson [now deposited in the Bee Inventory and Monitoring Lab (BIML)], were examined and their identities confirmed for inclusion in the checklist (Suppl. material 11). Other specimen records came from the Department of Entomology Collection, American Museum of Natural History, New York, New York (AMNH) available on Discover Life (http://discoverlife.org) and reliable

records on BugGuide, typically identified by J.S. Ascher (http://bugguide.net) – based either on a specimen deposited in a collection or with clear archived images accompanying the occurrence record. We also systematically retrieved records from both Bug-Guide and iNaturalist (https://www.inaturalist.org/) on 10 November 2019 to ensure no species were missing from our checklist, and present these as supplemental records (Suppl. materials 12–17). Specimen data available on GBIF.org were retrieved on 07 January 2020 (GBIF Occurrence Download https://doi.org/10.15468/dl.wghcks) and reviewed for records identified by known bee experts. The BugGuide, iNaturalist, and GBIF records that are not presented within the checklist are not included in the species data for the state, and are not represented in the tables and figures.

Taxonomy

We updated species names applied in earlier records to match modern taxonomic understanding, agree with the gender of their genus name (e.g., some *Melissodes* Latreille), and reflect their status as nouns (e.g., some *Lasioglossum* Curtis). We follow Michener (2007) with exceptions based on more recent studies. For *Lasioglossum* subgenera we followed Gibbs et al. (2013), and we used an inclusive *Eucera* Scopoli based on Dorchin et al. (2018) that treats *Cemolobus* Robertson and *Peponapis* Robertson as subgenera. For clarity, we also present a list of species names included in the previous checklist, which are not included in our results due to recent taxonomic changes or verification of Donovall and vanEngelsdorp's (2010) original intent:

- *Anthophora plumipes* (Pallas, 1772): Černá et al. (2017) provide evidence that *A. plumipes* and *A. villosula* Smith, 1854 are distinct species, and that *A. villosula* was the species introduced to North America.
- *Epeolus lanhami* Mitchell, 1962: Onuferko (2017) synonomized this name with *Epeolus americanus* (Cresson, 1878).
- *Nomada 077ensis* Cockerell: This entry was intended to be *Nomada lehighensis* Cockerell, 1903 based on Donovall and vanEngelsdorp's (2010) original notes.
- *Nomada bishoppi* (Cockerell, 1911): Schwarz and Gusenleitner (2004) synonomized this name with *Nomada imbricata* Smith, 1854.
- *Nomada inepta* Mitchell, 1962: This name is a synonym of *Nomada gracilis* Cresson, 1863 based on Sheffield et al. (2009).
- *Andrena irana* Cockerell, 1929: LaBerge and Bouseman (1977) synonomized this name with *Andrena (Scaphandrena) nigerrima* Casad, 1896. Note that this record is well outside the known range of the species, but could not be verified and has been removed from the state checklist.
- *Lasioglossum (Dialictus) rohweri (Ellis, 1915):* Gibbs (2010) synonomized this name with *Lasioglossum (Dialictus) versatum* (Robertson, 1902).
- *Lasioglossum (Evylaeus) divergens (Lovell, 1905):* Gibbs et al. (2013) synonymized this name with *Lasioglossum (Hemihalictus) macoupinense* (Robertson, 1895).

- *Lasioglossum (Dialictus) apertum (Sandhouse, 1924):* Gibbs (2010) synonymized this name with *Lasioglossum (Dialictus) versatum* (Robertson, 1902).
- *Lasioglossum* (*Dialictus*) *atlanticum* (Mitchell, 1960): Gibbs (2012) replaced this name with *Lasioglossum* (*Dialictus*) *hitchensi* Gibbs, 2012 to resolve a case of secondary homonymy.
- *Lasioglossum (Dialictus) nymphaearum (Robertson, 1895):* This name is a junior synonym of *L. albipenne* (see Gibbs et al. 2017a). *Lasioglossum (Dialictus) oceanicum* (Cockerell, 1916) is the valid name for the species typically referred to as *L. nymphaearum*.
- *Lasioglossum (Evylaeus) macoupinense* (Robertson, 1895): Although *L. macoupinense* is retained on the list, it is used for a different species. The earlier use of this name and most applications of it prior to Gibbs et al (2013) refer to *Lasioglossum* (*Hemihalictus*) *birkmanni* (Crawford, 1906).
- Lasioglossum (Dialictus) perspicuum (Knerer & Atwood, 1966): Gibbs (2010) synonomized this name with Lasioglossum (Dialictus) admirandum (Sandhouse, 1924).
- *Lasioglossum (Paralictus) asteris (Mitchell, 1960):* Gibbs (2011) synonomized this name with *Lasioglossum (Dialictus) lionotus* (Sandhouse, 1923).
- *Megachile (Eutricharaea) concinna* Smith, 1879: considered a synonym of *Megachile (Eutricharaea) pusilla* by Soltani et al. (2017).
- *Stelis (Microstelis) vernalis* Mitchell, 1962: synonymized with *Stelis (Stelis) coarctatus* Crawford, 1916 by Parker and Griswold, in Gibbs et al. (2017).

When available, the year of determination was used to update the taxonomy of specimen records in the databases we reviewed. Otherwise, specimen data was presented for the species it was recorded as. Notes are included within the checklist for species of *Andrena* F., *Ceratina* Latreille, and *Lasioglossum* that may have records attributable to different species reported under their name. For the purpose of species counts at the state and county levels, and figure data, occurrence records for *Augochloropsis metallica* sensu lato F., 1793 and *A. metallica fulgida* Smith, 1853 were combined.

Figures

Figures were created in Microsoft Excel (version 16.16.17), Adobe Illustrator (version 23.1.1), and R 3.4.1 in RStudio (R Core Team 2017; RStudio Team 2015), using the following packages: *dunn.test* (Dinno 2017), *ggmap* (Kahle and Wickham 2013) *ggplot2* (Wickham 2016), *grid* (R Core Team 2017), *mapdata* (Becker et al. 2016), *mapproj* (McIlroy 2017), *maps* (Becker et al. 2017), *plyr* (Wickham 2011), and *raster* (Hijmans 2017).

Results and discussion

We record 437 species of bees in Pennsylvania by adding 79 new species from our review, removing eight species based on unverifiable records, and accounting for six



Figure 1. The numbers of bee species by family and per checklist study in Pennsylvania. Blue portions of bars represent the number of species reported in the previous checklist (Donovall and vanEngelsdorp 2010); orange portions of bars denote data from our study. The number inside the blue portion of each bar represents the number of species retained from the previous checklist. Numbers with "-" and enclosed in parentheses indicate taxa removed from the state checklist due either to unverifiable records or synonymy. The numbers with "+", either inside the orange portion or adjacent to the end of each bar, signify new state species records. The families rank from least to greatest number of species as follows: Melittidae (4 spp.), Colletidae (24 spp.), Megachilidae (81 spp.), Andrenidae (100 spp.), Halictidae (110 spp.), and Apidae (118 spp.).

species removed from the total due to synonymies, compared to those included in the previous state checklist (Donovall and vanEngelsdorp 2010; Fig. 1). We present the first literature reports that we are aware of for 49 species in the state. There are new species records for five of the six North American bee families. Apidae has the most species recorded (118 spp.), followed by Halictidae (110 spp.), Andrenidae (100 spp.), Megachilidae (81 spp.), Colletidae (24 spp.), and Melittidae (4 spp.) (Fig. 1). We newly report the occurrence of three genera in the state (Melecta Latreille, Melitoma Lepeletier and Serville, and *Pseudoanthidium* Friese), for a total of 46 genera. These measures of biodiversity are comparable to that of neighboring jurisdictions including Connecticut (349 spp.; Zarrillo et al. 2016), Maine (278 spp.; Dibble et al. 2017), Maryland (442 spp.; North American Native Bee Collaborative 2017; Sam Droege, pers. comm.), Michigan (467 spp.; Gibbs et al. 2017a; Jamieson et al. 2019), New York (416 spp.; Danforth and van Dyke 2015 / 447 spp.; Ascher et al. 2014), Ontario (427 spp.; Sheffield et al. 2017; Bees of Canada 2020), and West Virginia (301 spp.; McKinney 2016) (Fig. 2). In addition, we provide a list of nine dubious species records and a list of 11 species that potentially occur in Pennsylvania, with notes about their current known distributions. Our checklist contributes to ongoing projects that docu-



Figure 2. Map of northeastern North America with relative bee species richness. The number of bee species reported for Pennsylvania (this study), and neighboring provinces and states, is shown: Connecticut (Zarrillo et al. 2016), Maine (Dibble et al. 2017), Maryland (North American Native Bee Collaborative 2017; Sam Droege, pers. comm.), Michigan (Gibbs et al. 2017a; Jamieson et al. 2019), New York (Danforth and van Dyke 2015; Ascher et al. 2014), Ontario (Sheffield et al. 2017; Bees of Canada 2020), and West Virginia (McKinney 2016).

ment bee biodiversity in North America. In addition to the checklists summarized above, additional checklists now available or in progress include Colorado (Scott et al. 2011), Illinois (Decker et al., in review), Indiana (Jean 2010), Louisiana (Owens et al. 2018), Massachusetts (Goldstein and Ascher 2016), northern Arizona (McCabe et al. 2020), and Wisconsin (Wolf and Ascher 2009; Scott et al. 2011). The bees of the following states are also being surveyed: Montana (Casey Delphia, pers. comm.), New York (New York Natural Heritage Program 2019), Oregon (Andony Melathopoulos, pers. comm.), and Virginia (Ellison Orcutt, pers. comm.).

Sixty-five of 67 counties (all except for Forest and Mifflin) have new species records (Fig. 3; Suppl. material 1). The number of species reports for counties ranges from one (Cameron Co.) to 246 (Adams Co.) (Fig. 3). Even counties that had high species richness reported in the previous checklist had new records. For example, Allegheny, Centre, Cumberland, Dauphin, Delaware, and Philadelphia counties, each had over 100 species listed previously, but all had new records (Donovall and vanEngelsdorp 2010; Fig. 3). Notably, these six counties also have large institutional insect collec-



Figure 3. Choropleth map of Pennsylvania specifying bee species richness by county. The greater number of species recorded for a county, the darker blue the county is on the map; lighter-colored counties have fewer species reported from them. The number of species reports for counties ranges from one (Cameron Co.) to 246 (Adams Co.).

tions located in or near them. Furthermore, Adams and Centre counties have been intensively sampled in the past decade, primarily due to high agroecological and habitat management research activity within their borders, and currently have the highest documented species richness in the state (Fig. 3). However, species expected to be widespread remain undocumented for these seven counties and many parts of the state (Suppl. material 1). Additionally, there are still regions within the state that appear under-surveyed, particularly in the western part of the state (Fig. 3; Suppl. material 1). Sampling of such areas would likely yield additional species records and they should be targeted for future studies to increase information about bee species' distributions across the state (Jamieson et al. 2019). Counties adjacent to neighboring states also have the potential to record new state records as changes in species' distributions occur (i.e., Mikulas and Barringer 2018). By updating the first checklist within a decade of its publication, our work has shown that checklists are not static. Regularly compiling species and specimen data, and adding additional analyses, could allow species' relative abundances to be tracked overtime. Undoubtably, additional specimen material and records will contribute new data for bee species in Pennsylvania in the future.

Our records also include the presence of at least 23 exotic species. This includes three species not previously reported in Pennsylvania to our knowledge: *Coelioxys coturnix* Pérez, 1884, *Hoplitis anthocopoides* (Schenck, 1853), and *Pseudoanthidium nanum* (Mocsáry, 1881). These species were generally expected to reach the state, based on where they were first confirmed in North America, and in some cases, where they have spread since detection (Sheffield et al. 2011a; Russo 2016; Portman et al. 2019; USGS Native Bee Laboratory 2019). We also add distribution data for *Anthophora*

villosula Smith, 1854, which was reported in Donovall and vanEngelsdorp (2010), but not included on the main checklist. *Lasioglossum zonulum* (Smith, 1848) is listed as an exotic species, based on recent evidence (Giles and Ascher 2006; USGS Native Bee Laboratory 2019). Additionally, the earliest verified year of collection for *Osmia cornifrons* (Radoszkowski, 1887) in Pennsylvania is updated to 2002, six years earlier than previously published (Donovall and vanEngelsdorp 2010). Non-native species can potentially out-compete native bees for resources, transmit diseases and parasites, change pollination effectiveness and network structures, and hybridize with local species/populations (Russo 2016; Portman et al. 2019). On the other hand, exotic species may also have positive effects, serving as pollinators of native and agricultural plants, bioindicators and biological control agents, and as study systems for biology and natural history (Russo 2016; Portman et al. 2019). Checklists and monitoring programs that include regular faunistic surveys can be used to readily detect exotic species and identify their effects on local taxa over time.

Our list includes five species of conservation concern. We include one endangered species, Bombus affinis Cresson, 1863, which has been federally listed since 2017 (U.S. Fish and Wildlife Service 2019; Xerces Society for Invertebrate Conservation 2019b). Other currently threatened or declining bumble bee species that occur in Pennsylvania are B. fervidus (F., 1798), B. pensylvanicus (DeGeer, 1773), and B. terricola Kirby, 1837 (Xerces Society for Invertebrate Conservation 2019b). Epeoloides pilosulus (Cresson, 1878) is also considered a species of conservation concern due to extreme rarity within its range since the 1960s (Bartomeus et al. 2013; Wood et al. 2019; Xerces Society for Invertebrate Conservation 2019a); it has not been recovered in Pennsylvania since 1911 according to our data. The population status for many bee species remains unassessed; other taxa may be experiencing declines or other changes, and require further study. In the absence of these data, we present a breakdown of the number of years since collection for all Pennsylvanian taxa (Fig. 4; Suppl. material 1). The majority of bee species in the state have been collected between 2000-2018, but at least 56 species (12.8% of all species in the state) have not been detected within that time frame (Fig. 4; Suppl. material 1). An additional 15 species with no year of collection available are the result of specimens reported in the literature with either no or limited collecting event information. These species' collection years, based on the years of publication which they are referenced in, range from pre-1908 to pre-2011. Of the species that Colla et al. (2012) listed as unrecorded in the eastern North America between 1990-2009, one was also undocumented in Pennsylvania between 1990-2018: Andrena mendica Mitchell, 1960, most recently collected in Pennsylvania in 1937 (Suppl. material 1). Contrastingly, two of the unrecorded species listed by Colla et al. (2012) were collected in Pennsylvania within the same time period: A. daeckei Viereck, 1907 and Sphecodes smilacinae Robertson, 1897, last collected in 2007 and 2011, respectively (Suppl. material 1). It is possible that species which have not been recently collected are still present in Pennsylvania but are not represented in the datasets we analyzed. Expeditions specifically focused on collecting these species based on their historical reports would reveal more information about their present status. However, it is also difficult to assess



Figure 4. The number of bee species by their most recent years of collection/observation in Pennsylvania. The number within each bar represents the total number of species in the specified time period. Of the species in the state, 366 (83.8%) have been detected between 2000–2018, while at least 56 species (12.8%) have not. No date of collection/observation was available for 15 species (3.4%).

the status of species that have just recently been reported in the state and their populations could also be surveyed to provide these data. We update the most recent year of collection/observation in Pennsylvania for 276 species, compared to data presented in Donovall and vanEngelsdorp (2010). For 105 species, the difference between the most recent year of collection, between the previous checklist and our data, was greater than 20 years (ranging from 23–139 years), further showing the importance of regular and widely-ranging surveys (Donovall and vanEngelsdorp 2010; Suppl. material 1).

We contribute floral visitation records with specimen collection data for many species (Suppl. materials 3–6, 11), and increase phenology information. We note that female bees collected on plants may not have been foraging for pollen or nectar, or at all. Furthermore, some records are attributable to male individuals as well; specimens' sexes were not always indicated in databases or the literature. Thus, "host plant" status for plant taxa listed must be interpreted with caution. Biological and ecological information for Pennsylvania bee taxa can be found in Hurd (1979), Michener (2007), Fowler (2016), Gibbs et al. (2017), Danforth et al. (2019), as well as the previouslycited reviews and revisions. As approximately 15% of northeastern United States native bee species are specialists (Fowler 2016), focused collections on plant taxa known to attract oligolectic species may contribute additional bee taxa to the Pennsylvanian checklist. Additionally, of the data used in this study, few specimen records were from early- and late-season collections. These gaps can be filled by additional surveying during these time periods throughout the state.

We included information from eight databases, 39 literature sources, three collections, and three additional datasets, and focused on specimens in Pennsylvania which were identified by experts and deposited in collections, without overlapping material addressed in Donovall and vanEngelsdorp (2010). We acknowledge that the datasets compiled for our study were not exhaustive; additional specimen records exist, which are not reflected in our data. Furthermore, our inclusion of AMNH, BugGuide, iNaturalist, and GBIF records in the checklist was limited to a few specimens with reliable determinations. We include all of the BugGuide and iNaturalist reports we retrieved as supplementary data and the GBIF records are accessible online (Suppl. material 12–17; GBIF Occurrence Download https://doi.org/10.15468/dl.wghcks). Records from other sources were either not retrieved in our process or not included due to difficulties accessing the data contained, validating identifications, and/or the lack of voucher specimens/images that could be examined in the future (Wheeler et al. 2004; Turney et al. 2015; Funk et al. 2018; Packer et al. 2018). Additional data, along with specimens in other collections, could be incorporated into future checklist updates.

Tracking the fate of specimens used for studies, within collections, loans, or deaccessioned material, using barcodes or a similar system, is critical for retrieving or evaluating vouchers' statuses. We follow recommendations for generating reproducible and verifiable specimen-based entomological research (Packer et al. 2018) as closely as possible. Our limitations include not knowing what materials were used to identify specimens and the ability to place accession numbers on individual specimens. The specimens in the datasets we used represent vouchers (Yoshimoto 1978). Lists of specimen records used, associated with species name (used in the respective database; not necessarily the most taxonomically-updated name), and specimen code, identifier, and determination date when available, is included to assist with tracking individual materials within their respective collections (Suppl. material 2–9, 11). Providing this data allows others to more easily locate specimens used as records and verify them, or use them in future studies.

One of the challenges of biodiversity work, which was apparent in our project, was the wide range of formats used to capture specimen data. There was little standardization between the datasets we reviewed as each of them had been created for different purposes. Based on the variety we encountered, we recommend that database columns be clearly labeled and metadata describing the contents of each column should accompany it. This will avoid assumptions about what one header or another means as these may differ between databases. One example of standardized terms for biological data is Darwin Core (https://dwc.tdwg.org/). Additionally, in some cases, readily-available and detailed information about the data contained in the database itself would have been helpful. Examples include knowing if the text in the database was copied verbatim or from the label or if it had been transformed in any way, and if and how specimen localities had been georeferenced. Providing this information will make the data set easier to navigate for use in biodiversity research and other projects. Additionally, it was often unclear who was responsible for identifying individual specimens or when the specimen was identified. This was problematic as there was no credibility directly associated with the specimen record. We were often able to confirm who would have examined the material, though that data had not been entered into the database. A possibility for why the name would have been excluded from the database is that the individual specimen did not have a determination label attached. Therefore, we suggest that determination labels be printed for individual specimens when they are identified, not just the first specimen in a series, so that there is no confusion on who identified the specimen and the credibility of the identification in the future, when it is examined or entered into a database. Determination date should be considered just as important as the determiner field in a database due to changes in taxonomy or nomenclatural usage that can be traced to specific years [e.g., *L. birkmanni* and *L. macoupinense*; Gibbs et al. 2013)].

Updating the checklist of bee species known in Pennsylvania provides baseline data for future research on bee biodiversity, ecology, and conservation in the state. By identifying less-surveyed areas, seasons, and species, targeted collecting can be planned to fill gaps in our knowledge. Our results will inform future updates to the Pennsylvania Pollinator Protection Plan (P4), which provides recommendations for supporting pollinator populations (P4 Task Force 2019). Through open access publishing, we also allow these current data to become more readily accessible to all who are interested in understanding bee biodiversity. This also opens the door to future research projects where connections can be made between academia and interested parties; anyone can contribute data on bee biodiversity and potentially discover something entirely new (e.g., Best et al. 2019). Our checklist provides baseline data for more "boots on the ground" by encouraging people to document the species and their natural histories that may be in their own backyards (Wilson 2017).

Checklist

All records for the bee species reported from Pennsylvania that we examined (new and previously reported) are presented here. Within each bee family, taxa are arranged alphabetically first by subfamily, then tribe, genus, subgenus (when applicable), and finally by species name. Each species record consists of the counties for which a voucher specimen or verifiable record has been confirmed. The earliest and latest dates, or only date(s) of collection in Pennsylvania are presented. The most recent year of collection in Pennsylvania is also shown in parentheses. Exotic species are indicated by an asterisk (*) followed by the earliest verified Pennsylvania collection year in parentheses. Bold text indicates a new Pennsylvanian record, previously unpublished to our knowledge and of any type (state, county, date, or most recent year of collection). The source(s) for each record are indicated with superscript numbers defined in the Legend. The source for statewide distribution records with no further data are presented directly after the species name or the earliest verified Pennsylvania collection year, if the species is exotic. AMNH records included in the checklist are presented with their specimen code; full specimen records can be obtained on Discover Life using the 'Retrieve ID' function

(available at https://www.discoverlife.org/mp/20l?act=enter_id). BugGuide records included in the checklist are shown with their Image IDs; full data is available via links in Suppl. material 12–16. Additional BugGuide and all iNaturalist occurrence records for bees in Pennsylvania that are not included below can be found in the Suppl. material 12–17. GBIF data is available online at https://doi.org/10.15468/dl.wghcks. Notes are also presented for certain species, particularly those whose older records may apply to other species as a result of recent taxonomic treatments. Lists of species excluded and species expected to occur in Pennsylvania are presented following the checklist.

Legend: ¹ = Donovall and vanEngelsdorp (2010); ² = Bartomeus et al. (2013); ³ = Biddinger Laboratory Database; ⁴ = Droege Database; ⁵ = Integrated Crop Pollination (ICP) Project: Fleischer Laboratory Database; ⁶ = López-Uribe Laboratory Database; ⁷ = Mahan et al., in prep; ⁸ = Winfree Laboratory Database; ⁹ = Choate et al. (2018); ¹⁰ = Baker, J.R. (1975); ¹¹ = Bouseman, J.K. and LaBerge, W.E. (1978); ¹² = Broemeling, D.K. (1998); ¹³ = Cockerell, T.D.A. (1908); ¹⁴ = Daly, H.V. (1973); ¹⁵ = DeBarros, N.B. (2010); ¹⁶ = Droege et al. (2010); ¹⁷ = Gibbs (2010); ¹⁸ = Gibbs (2011); ¹⁹ = Gibbs and Dathe (2017); ²⁰ = Gibbs et al. (2013); ²¹ = LaBerge (1969); ²² = LaBerge (1971); ²³ = LaBerge (1973); ²⁴ = LaBerge (1977); ²⁵ = LaBerge (1980); ²⁶ = LaBerge (1985); ²⁷ = LaBerge (1987); ²⁸ = LaBerge (1989); ²⁹ = LaBerge and Bouseman (1970); ³⁰ = LaBerge and Ribble (1972); ³¹ = Matteson et al. (2008); ³² = McGinley (1986); ³³ = McGinley (2003); ³⁴ = Mikulas and Barringer (2018); ³⁵ = Milliron (1973a); ³⁶ = Mitchell (1960); ³⁷ = Mitchell (1962); ³⁸ = Onuferko (2017); ³⁹ = Onuferko (2018); ⁴⁰ = Ordway (1966); ⁴¹ = Rehan and Sheffield (2011); ⁴² = Roberts (1972); ⁴³ = Shinn (1967); ⁴⁴ = Sidhu (2013); ⁴⁵ = Stephen (1954); ⁴⁶ = Svensson et al. (1977); ⁴⁷ = Timberlake (1975); ⁴⁸ = AMNH; ⁴⁹ = BugGuide; ⁵⁰ = Swenk (1915); ⁵¹ = PSUB; ⁵² = Rosemary Malfi Insect Collection; ⁵³ = Emily Erickson/BIML.

Melittidae Melittinae Macropidini

Genus Macropis Panzer

Taxonomy: Michez and Patiny (2005); Mitchell (1960).

Subgenus Macropis Panzer s. s.

- *Macropis* (*Macropis*) *ciliata* Patton, 1880 Bucks¹, **Centre**⁷, Cumberland¹, Dauphin¹, Delaware¹, Lancaster¹, Lehigh¹, Philadelphia²; 12 Jun¹ 9 Jul¹ (**2017**⁷).
- Macropis (Macropis) nuda (Provancher, 1882) Lehigh¹, Pike^{1,2}; 21 Apr¹ 9 Jul¹ (1983¹).
- *Macropis* (*Macropis*) *patellata* Patton, 1880 Bucks¹, Cumberland¹, Dauphin¹, Huntingdon¹, Lehigh¹, Philadelphia^{1,2}; 3 Jun² – 14 Jul¹ (1922¹).

Melittini

Genus Melitta Kirby

Taxonomy: Michez and Eardley (2007); Mitchell (1960).

Subgenus Cilissa Leach

Melitta (Cilissa) melittoides (Viereck, 1909)³⁶ – Centre¹; 16 Jun¹ (1958¹).

Apidae Apinae Anthophorini

Genus Anthophora Latreille

Taxonomy: Mitchell (1962); Brooks (1983); Černá et al. (2017).

Subgenus Anthophora Latreille s. s.

Anthophora (Anthophora) villosula Smith, 1854* (2013^{3,8})¹ – Adams³, Union⁸; 10 Apr³ – 28 Apr⁸ (2013^{3,8}).

Subgenus Clisodon Patton

Anthophora (Clisodon) terminalis Cresson, 1869³⁷ – Adams^{3,8}, Allegheny¹, Blair^{1,2},
 Bradford⁸, Centre¹, Chester¹, Cumberland¹, Dauphin¹, Erie⁹, Fayette¹, Franklin¹,
 Huntingdon^{1,8}, Lycoming⁸, Montgomery¹, Northumberland¹, Perry¹, Philadelphia¹, Susquehanna⁸, Union⁸, York¹; 14 May³ – 23 Oct³ (2018³).

Subgenus Lophanthophora Brooks

Anthophora (Lophanthophora) ursina Cresson, 1869 – Schuylkill^{1,2}; 28 May² – 29 May¹ (1988^{1,2}).

Subgenus Melea Sandhouse

Revision: Brooks (1983).

Anthophora (Melea) abrupta Say, 1837 (bomboides group)³⁷ – Adams³, Allegheny¹, Cumberland¹, Dauphin¹, Lackawanna², Lehigh¹, Montgomery^{1,7}, Tioga¹; 10 Apr³ – 17 Aug³ (2018³).

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Anthophora (Melea) bomboides Kirby, 1837 (bomboides group)³⁷ – Adams³, Allegheny¹, Carbon¹, Centre^{1,15}, Dauphin⁶, Huntingdon⁶, Lehigh¹, Montgomery⁷, Northumberland¹, Union⁸, Washington⁶; 23 Apr⁶ – 16 Aug³ (2018³).

Genus Habropoda Smith

Habropoda laboriosa (Fabricius, 1804) – Adams³, Bucks⁸, Cumberland¹, Dauphin¹, Huntingdon⁸, Lycoming⁸, Philadelphia¹, York⁸; 21 Mar³ – 4 Jun¹ (2015^{3,8}).

Apini

Genus Apis Linnaeus

Apis (Apis) mellifera mellifera Linnaeus, 1758* (1887¹)³⁷ – Adams^{3,6}, Allegheny⁶, Beaver⁴⁴, Bedford⁶, Berks⁶, Bradford^{4,6}, Bucks⁴, Cambria^{4,6}, Carbon⁶, Centre^{5,6,7,15,44}, Clearfield^{4,6}, Clinton⁶, Columbia⁵, Crawford^{4,6}, Cumberland⁶, Dauphin^{4,6}, Delaware⁴, Elk⁶, Erie^{6,9}, Franklin⁶, Fulton⁴⁴, Huntingdon³, Jefferson⁶, Juniata^{6,44}, Lackawanna⁴, Lancaster^{3,5,6,15,44}, Lebanon⁴, Lycoming^{6,44}, McKean⁴, Monroe⁶, Montgomery^{6,7,44}, Montour⁶, Northampton^{5,6}, Perry⁶, Pike⁴, Schuylkill⁴, Snyder⁴, Somerset⁶, Tioga⁴, Warren⁶, Washington⁶, Westmoreland^{4,6}, York^{4,6}; 14 Mar¹ – 17 Nov¹ (2017^{3,7}). Notes. This non-native species, previously reported has having a ubiquitous distribution in Pennsylvania (Donovall and vanEngelsdorp 2010), undoubtedly occurs in all counties due to its status as a managed pollinator.

Bombini

Genus Bombus Latreille

Taxonomy: Milliron (1971, 1973a, b); Mitchell (1962); Laverty and Harder (1988); Williams et al. (2008, 2014).

Subgenus Bombias Robertson

Bombus (Bombias) auricomus (Robertson, 1903) – Adams^{3,8}, Allegheny¹, Bradford¹, Bucks^{1,2}, Centre^{1,44}, Cumberland¹, Dauphin¹, Delaware^{1,4}, Erie¹, Fayette¹, Huntingdon³, Juniata¹, Lancaster³, Lawrence¹, Lebanon¹, Lehigh¹, Montgomery^{1,8}, Northumberland¹, Philadelphia¹, Somerset¹, Tioga¹, Washington¹, Westmoreland¹; 27 Apr¹ – 13 Sep¹ (2017³).

Subgenus Bombus Latreille s. s.

Bombus (Bombus) affinis Cresson, 1863 – Allegheny¹, Bucks², Centre¹, Clinton¹, Columbia², Cumberland¹, Dauphin¹, Delaware^{2,52}, Erie¹, Fayette¹, Forest¹, Fulton¹, Huntingdon¹, Juniata¹, Lackawanna², Lancaster¹, Lawrence¹, Lehigh¹, Luzerne^{1,2}, Lycoming¹, McKean¹, Monroe^{1,2}, Northumberland¹, Perry¹, Philadelphia^{1,2}, Tioga¹, Venango¹, Warren¹, Washington¹, Westmoreland^{1,2}, York¹; 22 Apr¹ – 4 Oct¹ (**2006**⁵²).

Bombus (*Bombus*) *terricola* Kirby, 1837 – Blair¹, Centre^{1,2,6,15}, Clearfield¹, Clinton¹, Columbia¹, Erie¹, Huntingdon¹, Lackawanna², Luzerne^{1,2}, Lycoming¹, McKean¹, Monroe^{1,2}, Pike¹, Sullivan¹, Tioga¹, Warren¹; 29 Apr² – 2 Nov¹ (2009¹⁵).

Subgenus Cullumanobombus Vogt

- Bombus (Cullumanobombus) griseocollis (DeGeer, 1773) (griseocollis group) Adams^{3,6,8}, Allegheny^{1,35}, Berks², Bradford¹, Bucks^{1,2,6,8}, Centre^{1,6,7,15}, Chester^{1,8,44}, Columbia⁵, Cumberland¹, Dauphin^{1,4,6}, Delaware^{1,2,4}, Erie¹, Fayette^{1,35}, Huntingdon^{1,8}, Lancaster^{1,3,4,5,6,15,44}, Lebanon⁴, Lehigh¹, Luzerne², Lycoming⁶, Monroe^{1,2}, Montgomery^{7,8}, Perry^{1,4}, Philadelphia^{1,4}, Pike¹, Snyder⁴, Tioga¹, Union⁸, Washington¹, Westmoreland^{1,35}, York^{4,6,8}; 10 Apr³ 12 Oct³ (2018³).
- Bombus (Cullumanobombus) rufocinctus Cresson, 1863 (rufocinctus group) Erie³⁴; 30 Jul³⁴ (2017³⁴).

Subgenus Psithyrus Lepeletier

- *Bombus (Psithyrus) ashtoni* (Cresson, 1864) (*bohemicus* group) Allegheny¹, Berks², Centre^{1,2,15}, Columbia², Cumberland¹, Dauphin¹, Erie¹, Lackawanna¹, Perry¹, Westmoreland¹; 12 May¹ 26 Sep² (2009¹⁵).
- Bombus (Psithyrus) citrinus (Smith, 1854) (citrinus group) Allegheny¹, Berks¹, Bucks⁸, Centre^{1,15}, Columbia¹, Cumberland¹, Dauphin¹, Erie¹, Fulton¹, Huntingdon¹, Lancaster^{1,3}, Lehigh¹, Lycoming¹, Monroe², Northumberland¹, Perry¹, Philadelphia⁴, Pike¹, Westmoreland¹, York¹; 2 Apr¹ – 14 Nov¹ (2012³).
- Bombus (Psithyrus) fernaldae (Franklin, 1911) (sylvestris group) Adams^{1,3}, Centre^{1,6,7,15}, Erie⁹; **6 May⁶ 15–16 Aug**⁷ (**2016**⁷).
- *Bombus (Psithyrus) insularis* (Smith, 1861) (*citrinus* group) Centre^{1,15}, Cumberland¹, Perry¹; 23 Jun¹ (2009¹⁵).

Subgenus Pyrobombus Dalla Torre

Bombus (Pyrobombus) bimaculatus Cresson, 1863 (lapponicus group) – Adams^{1,3,8}, Allegheny¹, Beaver⁴⁴, Bedford^{1,6}, Blair⁶, Bradford^{6,8}, Bucks^{6,8}, Centre^{1,3,5,6,7,15,44}, Chester⁸, Columbia⁵, Crawford¹, Cumberland¹, Dauphin^{1,6}, Delaware^{1,2,4}, Erie⁹, Fulton¹, Huntingdon^{1,2,3,8}, Jefferson⁶, Juniata¹, Lackawanna^{1,2}, Lancaster^{1,3,5,8}, Lebanon¹, Lehigh^{1,6}, Lycoming^{6,8}, Mifflin¹, Monroe¹, Montgomery^{7,8}, Northampton^{5,6}, Northumberland¹, Perry¹, Philadelphia^{1,2}, Pike^{1,4}, Schuylkill^{2,4}, Somerset^{1,6}, Susquehanna⁸, Union^{1,8}, Washington¹, Westmoreland¹, York^{1,8}; 14 Mar¹ – 12 Nov¹ (2018³).
Bombus (Pyrobombus) impatiens Cresson, 1863 (lapponicus group)³⁷ – Adams^{3,8,44}, Allegheny¹, Beaver⁴⁴, Bedford⁶, Berks⁶, Blair⁶, Bradford^{1,4,6,8}, Bucks^{1,4,6,8}, Butler^{1,44},

Cambria⁶, Carbon^{1,6}, Centre^{1,5,6,7,8,15,44}, Chester^{1,6,8,44}, Clearfield^{1,4}, Clinton^{1,6}, Columbia^{2,5}, Crawford^{1,6}, Cumberland¹, Dauphin^{1,4,6}, Delaware^{1,2,4,6,44}, Erie^{1,6,9}, Fayette¹, Franklin¹, Fulton^{1,3,44}, Huntingdon^{1,3,8}, Indiana¹, Jefferson^{1,6}, Juniata^{1,3,6,44}, Lackawanna^{1,2,4,6}, Lancaster^{1,2,3,4,5,6,8,15,44}, Lebanon^{1,4,6}, Lehigh^{1,6}, Luzerne^{1,2}, Lycoming^{1,6,8,44}, McKean^{1,4}, Mifflin¹, Monroe^{1,2,6}, Montgomery^{1,2,6,7,8,44}, **Northampton^{5,6}**, Northumberland^{1,6}, Perry^{1,4}, Philadelphia^{1,2,4,6}, **Schuylkill^{4,6}**, **Snyder⁴**, **Somerset⁶**, Sullivan¹, **Susquehanna**⁸, Union^{1,8}, Washington¹, Wayne¹, Westmoreland^{1,6}, **Wyoming⁴**, York^{1,4,6,8,44}; **31 Mar³** – 12 Nov¹ (**2018**³).

- Bombus (Pyrobombus) perplexus Cresson, 1863 (hypnorum group) Adams^{1,3,8}, Beaver⁴⁴,
 Bradford^{4,6,8}, Bucks^{2,8}, Centre^{1,3,6,7,15,44}, Columbia^{2,5}, Dauphin⁶, Delaware², Erie⁹,
 Huntingdon^{3,8}, Juniata³, Lackawanna^{2,4}, Lancaster^{1,3,4,6}, Lebanon⁶, Lycoming⁸,
 McKean⁴, Monroe⁴, Montgomery⁷, Northampton⁴, Philadelphia², Schuylkill²,
 Union⁸, York^{6,8}; 12 Apr³ 27 Dec¹ (2018³).
- Bombus (Pyrobombus) sandersoni Franklin, 1913 (pratorum group)³⁷ Adams³, Allegheny¹, Bucks¹, Carbon¹, Centre^{1,3,6,7}, Chester¹, Cumberland¹, Dauphin¹, Delaware¹, Franklin¹, Huntingdon¹, Lackawanna², Lebanon⁶, Lehigh¹, McKean¹, Monroe¹, Northumberland¹, Perry¹, Philadelphia¹, Schuylkill², Sullivan¹, Tioga¹, Union⁸, Westmoreland¹; 29 Apr² 15–16 Aug⁷ (2017⁷).
- Bombus (Pyrobombus) ternarius Say, 1837 (lapponicus group)³⁷ Bradford^{1,4,6,8}, Carbon^{1,6}, Centre^{1,44}, Clinton¹, Columbia^{1,5}, Crawford¹, Huntingdon¹, Lackawanna^{1,2}, Lancaster^{3,44}, Luzerne^{1,2}, Lycoming¹, McKean¹, Monroe^{1,2}, Perry¹, Schuylkill⁶, Sullivan¹, Wayne²; 25 Apr¹ 16 Oct¹ (2015⁵).
- Bombus (Pyrobombus) vagans vagans Smith, 1854 (vagans group)³⁷ Adams^{1,3,8}, Allegheny¹, Beaver^{1,44}, Bedford¹, Berks², Blair², Bradford^{4,8}, Bucks^{1,8}, Butler¹, Cambria¹, Centre^{1,3,7,15,44}, Chester^{1,8}, Clearfield⁴, Clinton¹, Columbia^{1,2,5}, Crawford^{1,4,6}, Cumberland¹, Dauphin¹, Delaware^{1,2}, Erie^{1,9}, Fayette¹, Forest¹, Franklin¹, Fulton¹, Huntingdon^{1,2,8}, Juniata^{1,44}, Lackawanna^{2,4}, Lancaster^{1,3}, Lebanon¹, Lehigh¹, Luzerne¹, Lycoming^{1,8,44}, McKean^{1,4}, Monroe², Montgomery^{1,8}, Northumberland¹, Perry¹, Philadelphia¹, Pike^{1,2,4}, Schuylkill^{1,2,4}, Somerset⁶, Sullivan¹, Susquehanna⁸, Tioga^{1,6}, Union^{1,8}, Warren^{1,6}, Washington¹, Westmoreland¹, Wyoming¹, York^{1,4,8}; **31** Mar³ 3 Nov¹ (2018³).

Subgenus Subterraneobombus Vogt

Bombus (Subterraneobombus) borealis Kirby, 1837 – Adams³, Allegheny¹, Beaver¹, Tioga¹; 11 Aug¹ – 24 Sep³ (2015³).

Subgenus Thoracobombus Dalla Torre

Bombus (Thoracobombus) fervidus (Fabricius, 1798) (pensylvanicus group)³⁷ – Adams^{1,3,8}, Allegheny¹, Berks^{1,2}, Bradford⁸, Bucks^{1,8}, Centre^{1,7,44}, Chester^{1,8}, Clinton¹, Columbia^{1,2,5}, Crawford⁴, Cumberland¹, Dauphin^{1,6}, Delaware^{1,4,6}, Erie¹, Forest¹, Franklin¹, Greene¹, Huntingdon^{1,2}, Lackawanna², Lancaster^{1,3,5,8,15}, Lawrence¹, Lehigh¹,

Luzerne¹, Lycoming⁸, Mifflin¹, Montgomery^{1,2,8}, Northampton⁵, Northumberland¹, Philadelphia^{1,2,4}, Tioga¹, Washington¹, Westmoreland¹, York^{1,8}; **31 Mar³** – 4 Nov¹ (**2018**³).

Bombus (Thoracobombus) pensylvanicus (DeGeer, 1773) (pensylvanicus group)³⁷ – Adams³, Allegheny¹, Beaver¹, Berks², Centre^{1,44}, Chester¹, Clarion¹, Columbia^{1,2,5}, Crawford¹, Cumberland¹, Dauphin¹, Delaware^{1,4}, Erie¹, Fayette¹, Jefferson¹, Juniata¹, Lancaster¹, Lebanon¹, Mifflin¹, Monroe², Montgomery¹, Philadelphia^{1,2}, Tioga¹, Union¹, Washington¹, Westmoreland¹, York¹; 23 Apr¹ – 15 Oct¹ (2018³).

Emphorini

Genus Melitoma Lepeletier and Serville

Taxonomy: Mitchell (1962).

Melitoma taurea (Say, 1837) – Adams³, Lancaster^{3,8}; 12 Jun³– 2 Oct³ (2018³).

Genus Ptilothrix Smith

Taxonomy: Mitchell (1962).

Ptilothrix bombiformis (Cresson, 1878) – Adams^{3,8}, Delaware^{1,4}, Montgomery⁸, York⁸; 26 Apr³ – 2 Oct³ (2018³).

Eucerinae Eucerini

Genus Eucera Scopoli

Taxonomy: Dorchin et al. (2018).

Subgenus Cemolobus Robertson

Taxonomy: Mitchell (1962). Monotypic.

Eucera (*Cemolobus*) *ipomoeae* (Robertson, 1891) – Adams³; 5 Jul³ – 30 Jul³ (2017³).

Subgenus Peponapis Robertson

Revision: Hurd and Linsley (1964). **Key:** Ayala and Griswold (2012).

Eucera (Peponapis) pruinosa (Say, 1837)³⁷ – Adams^{3,8}, Allegheny¹, Armstrong⁶, Beaver⁴⁴, Berks⁶, Bradford^{6,8}, Bucks⁸, Centre^{1,5,6,7,15,44}, Chester⁸, Columbia⁵, Crawford⁴, Cumberland⁶, Dauphin^{1,6}, Delaware⁴, Erie^{1,9}, Franklin⁶, Fulton⁴⁴, Huntingdon^{3,8}, Jefferson⁶, Juniata⁴⁴, Lancaster^{3,5,6,8,15,44}, Lebanon⁶, Lycoming^{8,44}, Monroe⁶, Montgomery^{6,8,44}, Perry⁶, Philadelphia¹, Union⁸, Wayne¹, Westmoreland¹, York^{1,6,8}; 5 May¹ – 12 Oct³ (2018³).

Subgenus Synhalonia Patton

Revision: Timberlake (1969).

- Eucera (Synhalonia) atriventris (Smith, 1854)³⁷ Adams³, Allegheny¹, Centre¹, Cumberland¹, Dauphin¹, Delaware¹, Franklin¹, Huntingdon^{3,8}, Montgomery¹, Philadelphia¹, York¹; 12 Apr¹ 29 Jul³ (2017³).
- *Eucera (Synhalonia) dubitata (*Cresson, 1878)³⁷ Adams³, Lycoming⁸; 27 Apr³ 24 Sep³ (2017³).
- *Eucera (Synhalonia) hamata* (Bradley, 1942) Adams^{3,8}, **Delaware**⁴, **Huntingdon**⁸, **Lancaster**^{3,5,8}, **York**⁸; **31 Mar³ 17 Aug³ (2018**³).

Eucera (Synhalonia) rosae (Robertson, 1900) – Adams³; 17 Apr³ – 5 Jul³ (2017³).

Genus Melissodes Latreille

Taxonomy: LaBerge (1955, 1956a, b, 1961); Mitchell (1962).

Subgenus Apomelissodes LaBerge

Revision: LaBerge (1956b).

- *Melissodes (Apomelissodes) apicatus* Lovell & Cockerell, 1906 Montgomery⁷; 26 27 Jun⁷ (2017⁷).
- Melissodes (Apomelissodes) fimbriatus Cresson, 1878 Adams^{3,51}; 21 Jun³ 28 Jun–5 Jul⁵¹ (2012^{3,51}).

Subgenus Eumelissodes LaBerge

Revision: LaBerge (1961).

- *Melissodes* (*Eumelissodes*) *agilis* Cresson, 1878³⁷ Allegheny¹, Centre^{15,44}, Dauphin¹, Lancaster^{1,8}, Lebanon¹, Philadelphia¹; 14 Jul¹ 12 Aug¹ (**2015**⁸).
- *Melissodes (Eumelissodes) boltoniae* Robertson, 1905³⁷ Centre¹, Forest¹; 25 Jun¹ 27 Aug¹ (1956¹).

- *Melissodes* (*Eumelissodes*) *denticulatus* Smith, 1854³⁷ **Adams**³, Allegheny¹, Armstrong¹, Beaver¹, Centre^{15,44}, Cumberland¹, Dauphin¹, **Elk**⁶, Erie⁹, **Lancaster**³, Perry^{1,4}, Philadelphia¹, Washington¹, York¹; **26 May**³ 8 Oct¹ (**2018**³).
- Melissodes (Eumelissodes) dentiventris Smith, 1854³⁷ Adams³, Allegheny¹, Carbon⁶, Cumberland¹, Dauphin¹, Philadelphia¹, York¹; **3 Jul**³ 17 Oct¹ (2015³).
- Melissodes (Eumelissodes) druriellus (Kirby, 1802)³⁷ Adams³, Allegheny¹, Bradford⁸, Centre^{1,7,15,44}, Columbia², Crawford⁴, Dauphin^{1,6}, Delaware¹, Huntingdon⁶, Lackawanna¹, Lycoming⁸, Monroe^{1,2}, Montgomery¹, Philadelphia¹, Tioga¹, Union⁸, Westmoreland¹; 11 Jun⁶ – 29 Sep² (2017⁷).
- Melissodes (Eumelissodes) fumosus LaBerge, 1961 Centre⁴⁴; dates not reported⁴⁴ (2010 2012⁴⁴).
- Melissodes (Eumelissodes) illatus Lovell & Cockerell, 1906³⁷ Adams³, Centre¹⁵, Erie⁹; 11 Jun³ 17 Aug³ (2016⁹).
- Melissodes (Eumelissodes) niveus Robertson, 1895 Center⁴⁴, Delaware¹; 3 Sep¹ (2010 2012⁴⁴).
- Melissodes (Eumelissodes) subillatus LaBerge, 1961³⁷ Adams³, Huntingdon², Lancaster³; 14 Jun³ – 6 Sep³ (2014³).
- Melissodes (Eumelissodes) trinodis Robertson, 1901³⁷ Adams³, Allegheny¹, Bucks⁸, Centre⁷, Chester⁸, Cumberland¹, Dauphin^{1,6}, Delaware^{1,4}, Lancaster^{3,5}, Lycoming⁸, Montgomery⁸, Philadelphia¹, York⁸; 4 Jun³ – 13 Oct³ (2018³).

Subgenus Heliomelissodes LaBerge

Revision: LaBerge (1956b).

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Melissodes (Heliomelissodes) desponsus Smith, 1854³⁷ – Adams^{1,3}, Bradford^{4,8}, Centre^{1,2,15,44}, Columbia⁵, Cumberland¹, Dauphin⁶, Delaware⁴, Erie⁹, Forest¹, Franklin⁶, Huntingdon^{3,8}, Lancaster^{3,8}, Lebanon^{1,4}, Lycoming⁸, Philadelphia¹, Snyder⁴, Somerset⁶, Washington⁶, York^{6,8}; 23 Apr² – 1 Oct³ (2018³).

Subgenus Melissodes Latreille s. s.

Revision: LaBerge (1956a).

- Melissodes (Melissodes) bimaculatus bimaculatus (Lepeletier, 1825)³⁷ Adams^{1,3,8}, Allegheny¹, Bedford⁶, Bradford⁸, Bucks^{1,8}, Carbon⁶, Centre^{1,15,44}, Chester^{1,8}, Columbia^{2,5}, Cumberland¹, Dauphin^{1,6}, Delaware^{1,4}, Erie⁹, Franklin¹, Fulton⁴⁴, Huntingdon^{1,3,8}, Juniata^{1,3}, Lancaster^{1,3,4,5,6,8,15}, Lebanon¹, Lycoming^{8,44}, Mifflin¹, Montgomery^{1,8,44}, Montour¹, Perry^{1,4}, Philadelphia^{1,4}, Union⁸, Washington¹, York^{1,6,8}; 26 Apr³ 31 Oct¹ (2018³).
- *Melissodes* (*Melissodes*) *communis communis* Cresson, 1878 Allegheny¹; dates and year not reported¹.
- Melissodes (Melissodes) tepaneca Cresson, 1878 Adams³; 13 Aug³ (2015³).

Genus *Svastra* Holmberg Subgenus *Anthedonia* Michener

Revision: LaBerge (1955).

Svastra (Anthedonia) compta (Cresson, 1878) – Philadelphia¹; dates and year not reported¹.

Subgenus Epimelissodes Ashmead

Revision: LaBerge (1956a).

Svastra (Epimelissodes) obliqua (Say, 1837) caliginosa (Cresson, 1878) – Adams³, Delaware⁴, Lancaster³; 30 Jun³ – 9 Sep⁴ (2018³).

Nomadinae Ammobatoidini

Genus Holcopasites Ashmead

Taxonomy: Mitchell (1962); Hurd and Linsley (1972).

Holcopasites calliopsidis calliopsidis (Linsley, 1943) – Adams^{3,8}, Centre^{1,6,7}, Dauphin¹, Delaware², Indiana¹, Lackawanna¹, Lancaster^{3,15}, Lehigh⁶, Philadelphia¹, Westmoreland⁶, York^{1,6}; 24–25 May⁷ – 18 Aug³ (2017³).
Holcopasites illinoiensis (Robertson, 1891) – Bucks¹; 28 Jun¹ (1936¹).

Epeolini

Genus Epeolus Latreille

Taxonomy: Mitchell (1962); Brumley (1965); Onuferko (2017, 2018).

Epeolus americanus (Cresson, 1878)³⁷ – Dauphin^{1,37}; 6 Jun¹ - 27 Jun³⁷ (1923³⁷). *Epeolus autumnalis* Robertson, 1902 – Centre¹, Huntingdon¹, Philadelphia²; 27 Apr² – 20 Sep¹ (2003¹).

Epeolus bifasciatus Cresson, 1864^{37,39} – **Adams**³, Berks², Centre^{1,15,38,44}, Dauphin¹, Huntingdon¹, Lancaster^{3,15}, Lehigh¹, Luzerne², Philadelphia¹; **2 Jul**³ – 5 Sep¹ (2016³⁸).

Epeolus lectoides Robertson, 1901 – Adams⁶, Philadelphia¹; 14 Aug⁶ – 17 Sep¹ (2008⁶).

Epeolus pusillus Cresson, 1864 – Columbia^{1,2}, **Lycoming**⁸, **Union**⁸; 25 Sep² – **28 Sep**⁸ (**2014**⁸).

Epeolus scutellaris Say, 1824³⁷ – Bradford³⁹, Centre^{1,7}, Erie¹, Huntingdon¹, Monroe^{1,2}, Philadelphia²; 9 Aug² – 25 Sep¹/Aug–Oct³⁹ (**2017**⁷).

Genus Triepeolus Robertson

Revision: Rightmyer (2008).

Triepeolus atripes Mitchell, 1962 – Lancaster³⁷; 5 Sep³⁷ (1954³⁷).

- Triepeolus concavus (Cresson, 1878) Adams³, Lancaster³; 12 Jul³ 26 Jul³ (2012³).
- *Triepeolus donatus* (Smith, 1854)³⁷ Centre⁷, Forest¹, Westmoreland⁶; 25 May¹ 24–25 Jul⁷ (2017⁷).
- *Triepeolus helianthi* (Robertson, 1897) Beaver¹, Centre^{1,15}, Franklin¹; 9 Jul¹ 19 Aug¹ (2009¹⁵).
- *Triepeolus lunatus* (Say, 1824)³⁷ Adams^{1,3}, Allegheny¹, **Bucks**⁸, Cumberland¹, Dauphin¹, Delaware¹, Lancaster^{1,3,6}, Montgomery^{1,8}, **Perry**⁴, Somerset¹, York¹; **25 Jun**³ – 11 Sep¹ (**2018**³).

Triepeolus nevadensis (Cresson, 1878) – Adams³; 4 Aug³ (2016³).

- *Triepeolus pectoralis* (Robertson, 1897) Columbia², Delaware^{1,2}, York¹; 4 Sep^{1,2} 29 Sep² (1992²).
- *Triepeolus quadrifasciatus* (Say, 1823) *atlanticus* Mitchell, 1962 Huntingdon¹; 10 Sep¹ (1996¹).

Triepeolus remigatus (Fabricius, 1804)³⁷ – Adams³, Bucks⁸, Centre^{1,6,44}, Chester⁸, Columbia⁵, Dauphin¹, Delaware^{1,2,4}, Huntingdon¹, Juniata⁴⁴, Lancaster^{1,3,4,5,15}, Lycoming⁴⁴, Montgomery^{8,44}, Philadelphia¹, York⁸; 9 Jul⁸ – 7 Sep¹ (2014⁵).

- Triepeolus rhododontus Cockerell, 1921 Huntingdon¹; 26 Aug¹ (1996¹).
- Triepeolus rugosus Mitchell, 1962 Huntingdon¹; 26 Aug¹ (1996¹).

Triepeolus simplex Robertson, 1903 – Union⁸, York¹; 6 Aug¹ – 24 Aug⁸ (2015⁸).

Melectini

Genus *Melecta* Latreille Subgenus *Melecta* Latreille s. s.

Revisions: Linsley (1939); Hurd and Linsley (1951).

Melecta (Melecta) pacifica Cresson, 1878 – Adams³; 13 Apr³ (2017³).

Nomadini

Genus Nomada Scopoli

Taxonomy: Alexander and Schwarz (1994); Broemeling and Moalif (1988); Droege et al. (2010); Evans (1972); Mitchell (1962); Schwarz and Gusenleitner (2004). *Nomada* is in serious need of revision (Gibbs et al. 2017a). This list of species is likely to change considerably following the publication of updated taxonomy for the genus.

- Nomada affabilis Cresson, 1878 (edwardsii group) Adams³; 7 Jun³ 12 Jun³ (2013³).
- Nomada armatella Cockerell, 1903 (*ruficornis* group) **Cumberland**⁶, Elk¹; 9 Apr¹ **16 Apr⁶** (2008⁶).
- *Nomada articulata* Smith, 1854 (*erigeronis* group)³⁷ Adams³, Bucks⁸, Cumberland¹, Dauphin¹, Delaware¹, Erie^{1,9}, Huntingdon^{1,2,8}, Luzerne¹, Lycoming⁸, Montgomery¹, Philadelphia¹, Union¹; 25 Apr¹ 8 Jul¹ (2018³).
- Nomada australis Mitchell, 1962 (erigeronis group) Adams³; 24 May³ 3 Jun³ (2016³).
- *Nomada bella* Cresson, 1863 (*ruficornis* group: bidentate mandible) Centre^{1,2}, Cumberland¹, Elk¹, Huntingdon¹, Philadelphia^{1,2}; 27 Mar¹ 12 Jun¹ (2009²).
- *Nomada bethunei* Cockerell, 1903 (*ruficornis* group) Centre¹, Cumberland^{1,6}, **Hunt-ingdon³**, **Jefferson⁶**, Northumberland¹⁶, Perry^{1,16}, **Washington⁶**; **16** Apr⁶ 29 Aug¹ (**2008**⁶).
- *Nomada ceanothi* Cockerell, 1907 (*ruficornis* group) **Columbia**⁵, Cumberland¹, Delaware¹, **Huntingdon**³, Montgomery¹, York¹; 19 Apr¹ – 25 Jun¹ (**2013**⁵).
- *Nomada composita* Mitchell, 1962 (*ruficornis* group) Adams³, Centre¹, Huntingdon⁸, Lycoming⁸, Perry⁶, Susquehanna⁸, Union⁸, York⁸; 2 Apr¹ 30 May³ (2015⁸).
- Nomada cressonii Robertson, 1893 (ruficornis group)³⁷ Adams^{1,3}, Blair^{1,2}, Bradford^{6,8}, Bucks⁸, Centre^{1,7}, Crawford¹, Cumberland¹, Dauphin¹, Delaware¹, Elk¹, Erie^{1,9}, Huntingdon^{1,8}, Lancaster⁸, Lehigh¹, Lycoming⁸, Montgomery¹, Perry^{1,6}, Philadelphia¹, Somerset¹, Susquehanna⁸, Tioga¹, Union⁸, York^{1,8}; 4 Apr⁶ – 20 Aug¹ (2016^{3,7,9}).
- *Nomada cuneata* (Robertson, 1903) (*ruficornis* group: bidentate mandible)³⁷ Adams², Blair^{1,2}, Centre¹, Dauphin¹, Erie¹, Franklin¹, Huntingdon¹, Perry¹, Pike^{1,4}, Sullivan¹, York¹; 3 Apr¹ 26 Jun¹ (2006^{1,2}).
- Nomada denticulata Robertson, 1902 (*ruficornis* group)³⁷ **Bradford**⁸, **Bucks**⁸, **Centre**^{7,8}, **Columbia**⁵, Cumberland¹, Dauphin¹, Delaware¹, Elk¹, Erie⁹, Franklin¹, **Huntingdon**^{3,8}, Pike¹, York^{1,8}; **15 Apr**⁸ **15 Jun**⁸ (**2017**⁷).
- Nomada depressa Cresson, 1863 (ruficornis group) Adams³, Bradford⁸, Bucks⁸, Centre¹, Crawford⁶, Cumberland⁶, Dauphin^{1,6}, Huntingdon^{1,8}, Lancaster⁸, Luzerne¹,
 - Lycoming⁸, Perry⁶, Susquehanna⁸, Union⁸, Warren⁶; 4 Apr⁶ 19 Sep¹ (2016³).
- Nomada fervida Smith, 1854 (vegana group) Adams³, Erie¹; **3** Jun³ 30 Jul¹ (**2008**³). Nomada fragariae Mitchell, 1962 (ruficornis group) – Centre¹, Mercer⁶; 5 May¹ (**2009**⁶).
- *Nomada gracilis* Cresson, 1863 (*ruficornis* group) **Dauphin**⁶, Huntingdon¹, **Susquehanna**⁸, **Union**⁸; **11 Apr**⁶ 28 May¹ (**2014**⁸).
- Nomada illinoensis Robertson, 1900 (*ruficornis* group) Adams³, Dauphin¹; 26 Apr³ 1 Jul³ (2018³).
- Nomada imbricata Smith, 1854 (*ruficornis* group)³⁷ Adams³, Bradford⁸, Centre^{1,7,8}, Crawford¹, Cumberland¹, Dauphin¹, Delaware^{1,2}, Erie⁹, Huntingdon^{1,2,8}, Lancaster⁸, Mercer⁶, Montour⁶, Philadelphia^{1,2,4}, Susquehanna⁸, Union⁸, York^{1,8}; 14 Apr³ – 15 Jun⁸ (2018³).

- *Nomada integerrima* Dalla Torre, 1896 (*ruficornis* group)³⁷ **Somerset**⁶, **Washington**⁶; **28 May**⁶ **13 Jun**⁶ (**2009**⁶).
- Nomada lehighensis Cockerell, 1903 (*ruficornis* group)³⁷ Adams¹⁶, Carbon¹⁶, Dauphin¹⁶, Erie^{1,16}, **Huntingdon⁸**, Lehigh^{1,16}, **Lycoming⁸**, Northampton¹⁶, Schuylkill²; **1 Apr¹⁶** – 21 Jul¹ (**2015**⁸).
- *Nomada lepida* Cresson, 1863 (*ruficornis* group: bidentate mandible)³⁷ Adams³, Columbia⁵, Cumberland¹, Dauphin¹, Delaware¹, Erie¹, Huntingdon³, Philadelphia¹; 10 Apr³ – 30 Jun¹ (2016³).
- Nomada luteola Olivier, 1812 (ruficornis group) Adams³, Dauphin¹, Delaware¹, Huntingdon¹, Montgomery¹, Philadelphia^{1,2}, York⁸; 23 Apr³ 21 Jun¹ (2016³).
- *Nomada luteoloides* Robertson, 1895 (*ruficornis* group) Adams^{3,8}, Bradford⁸, Bucks⁸, Centre^{1,7,8}, Cumberland¹, Dauphin^{1,6}, Delaware¹, Erie¹, Franklin¹, Huntingdon^{1,3,8}, Lancaster⁸, Luzerne¹, Lycoming⁸, Perry⁶, Philadelphia¹, Schuylkill^{1,2}, Susquehanna⁸, Union⁸, York^{1,8}; 31 Mar³ – 11 Jun^{1,8} (2017⁷).
- Nomada maculata Cresson, 1863 (*ruficornis* group: bidentate mandible) Adams³, Bradford⁸, Bucks⁸, Centre^{1,7}, Chester¹, Columbia⁵, Dauphin¹, Delaware¹, Erie^{1,9}, Huntingdon^{1,2,8}, Lancaster⁸, Lycoming⁸, Montgomery¹, Perry¹, Philadelphia^{1,2}, Pike^{1,4}, Schuylkill^{1,2}, Susquehanna⁸, Tioga¹, Union⁸, York^{1,8}; 13 Apr¹ – 17 Jun¹ (2017⁷).
- *Nomada obliterata* Cresson, 1863 (*ruficornis* group) Cumberland¹, Dauphin¹, York¹; 30 Apr¹ 27 Jun¹ (1970¹).
- *Nomada ovata* (Robertson, 1903) (*ruficornis* group: bidentate mandible)³⁷ Adams³, Centre¹, Cumberland¹, Huntingdon¹; **16 Apr³** 11 Jul¹ (**2013**³).
- Nomada parva Robertson, 1900 (ruficornis group)³⁷ Chester⁶, Dauphin¹; 6 May¹ 13 Jul⁶ (2008⁶).
- Nomada perplexa Cresson, 1863 (*ruficornis* group: bidentate mandible)³⁷ Centre¹, Crawford¹, Dauphin¹, Erie¹, Huntingdon¹, **Lancaster**³, Lehigh¹, Monroe², Philadelphia²; 5 Mar¹ 14 Jul¹ (**2013**³).
- *Nomada placida* Cresson, 1863 (*roberjeotiana* group) Cumberland^{1,12}, Delaware^{1,2}; 28 Aug^{1,12} 25 Sep² (1947¹).
- Nomada pygmaea Cresson, 1863 (ruficornis group)³⁷ Adams³, Bradford⁸, Bucks^{2,8}, Centre⁷, Columbia⁵, Cumberland¹, Dauphin¹, Delaware¹, Erie⁹, Huntingdon^{2,8}, Lancaster⁸, Lehigh¹, Lycoming⁸, Mercer⁶, Montgomery¹, Philadelphia¹, Pike^{1,4}, Susquehanna⁸, Union⁸, York^{1,8}; 15 Apr⁸ – 29–30 Jun⁷ (2017⁷).
- *Nomada rubicunda* Olivier, 1812 (*erigeronis* group) Philadelphia¹; dates and year not reported¹.
- *Nomada sayi* Robertson, 1893 (*ruficornis* group)³⁷ Adams³, Chester⁶, Crawford¹, Dauphin^{1,6}, Franklin¹, Huntingdon¹, Montgomery¹, Philadelphia¹; 17 Apr⁶ 11 Jul¹ (2016³).
- *Nomada skinneri* Cockerell, 1908 (*ruficornis* group)³⁷ Carbon¹³, Lehigh¹³, Northampton¹³; 30 Jun¹³ (year not reported¹³).
- Nomada sulphurata Smith, 1854 (ruficornis group) Adams³, Dauphin¹, Montgomery¹; 28 Apr¹ – 26 May³ (2016³).

Nomada superba Cresson, 1863 (superba group) – Adams³; 5 May³ – 12 May³ (2016³).
Nomada tiftonensis Cockerell, 1903 (vegana group) – Philadelphia²; 5 May² (1905²).
Nomada ulsterensis Mitchell, 1962 (ruficornis group)³⁷ – Philadelphia⁵⁰; 18 Jun⁵⁰ (1905⁵⁰).
Nomada valida Smith, 1854 (ruficornis group) – Adams³, Clinton¹, Crawford¹; 3 Apr¹ – 28 May¹ (2015³).
Nomada vicina Cresson, 1863 (ruficornis group) – Centre^{1,7}, Erie¹, Huntingdon¹; 12 Aug¹ – 20 Sep¹ (2017⁷).
Nomada xanthura Cockerell, 1908 (ruficornis group) – Centre^{1,7}, Pike¹; 1 May¹ – 31 May–1 Jun⁷ (2017⁷).

Osirini

Genus Epeoloides Giraud

Taxonomy: Mitchell (1962).

Epeoloides pilosulus (Cresson, 1878) – Dauphin¹, Lehigh¹; 9 Jun¹ – 30 Jun¹ (1911¹).

Xylocopinae Ceratinini

Genus *Ceratina* Latreille Subgenus *Zadontomerus* Ashmead

Taxonomy: Mitchell (1962); Daly (1973); Rehan and Richards (2008); Rehan and Sheffield (2011).

- Ceratina (Zadontomerus) calcarata Robertson, 1900^{14,37} Adams^{1,3,6,8}, Allegheny^{1,6}, Armstrong⁶, Berks^{1,6}, Bradford^{1,4,6,8}, Bucks^{1,6,8}, Carbon⁶, Centre^{1,6,7,8,15,44}, Chester^{1,6}, Clarion⁶, Clearfield^{1,4}, Clinton¹, Columbia⁵, Crawford¹, Cumberland^{1,6}, Dauphin^{1,6}, Delaware^{1,4}, Erie^{1,6,9}, Forest¹, Franklin⁶, Greene⁶, Huntingdon^{2,3,8}, Indiana⁶, Jefferson⁶, Juniata^{1,6}, Lackawanna⁴, Lancaster^{3,5,6,8,15,44}, Lehigh^{1,6}, Lycoming⁸, Monroe¹, Montgomery^{4,6}, Northampton^{1,6}, Northumberland¹, Perry^{1,4,6}, Philadelphia^{1,4}, Schuylkill⁶, Somerset¹, Susquehanna⁸, Union⁸, Washington¹, Westmoreland¹, York^{1,6,8}; 23 Mar³ 6 Nov³ (2018³). Notes. Older records for *C. calcarata*, especially pre-2011 determinations, may be attributable to *C. mikmaqi* (see Rehan and Sheffield 2011).
- *Ceratina (Zadontomerus) dupla* Say, 1837^{14,37} Adams^{1,3,6,8}, Allegheny¹, Berks^{1,6}, Bradford^{1,6,8}, Bucks^{1,6,8}, Carbon¹, Centre^{1,6,7,8,15,44}, Chester^{1,6}, **Clearfield⁶**, **Clinton⁶**, **Columbia⁵**, Crawford^{1,6}, Cumberland^{1,6}, Dauphin^{1,6}, Delaware^{1,4}, Erie^{1,6,9}, Franklin^{1,6}, Huntingdon^{1,3,8}, **Jefferson⁶**, **Juniata^{3,6}**, Lackawanna^{1,4}, Lancaster^{3,5,6,15}, Lawrence¹,

Lehigh^{1,6}, Lycoming^{6,8}, Montgomery^{1,4,6,7,44}, Northumberland¹, Perry^{1,6}, Philadelphia^{1,6}, Pike¹, Schuylkill⁶, Tioga¹, Union⁸, Warren⁶, Washington⁶, York^{1,6,8}; 20 Feb¹ – 22 Dec¹ (2018³).

- Ceratina (Zadontomerus) floridana Mitchell, 1962 Delaware⁴; 21 May⁴ (2007⁴).
 Ceratina (Zadontomerus) mikmaqi Rehan & Sheffield, 2011⁴¹ Adams^{3,8}, Bradford⁸, Bucks⁸, Centre^{7,8}, Dauphin⁴⁸ (AMNH_BEE00172273), Erie⁹, Huntingdon⁸, Lancaster^{3,5,8}, Lycoming⁸, Montgomery⁷, Union⁸, York⁸; 29 Mar³ 6 Nov³ (2018³).
 Notes. Older records for female *C. calcarata* and male *C. dupla*, especially pre-2011 determinations, may be attributable to *C. mikmaqi* (see Rehan and Sheffield 2011).
- *Ceratina (Zadontomerus) strenua* Smith, 1879 Adams^{1,3,6,8}, Allegheny¹, Armstrong⁶, Berks^{2,6}, **Bradford^{6,8}**, Bucks^{1,2,8}, Centre^{6,7,8,15}, Chester^{1,6,8}, **Clarion⁶**, Crawford¹, Cumberland^{1,6}, Dauphin^{1,6}, Delaware^{1,4}, Erie^{6,9}, Franklin^{1,6}, Huntingdon^{1,2,3,8}, Juniata^{1,6}, Lancaster^{1,3,6,8,15}, **Lehigh⁶**, Lycoming⁸, Monroe⁴, Montgomery^{4,6,7,8}, Northampton⁶, Northumberland^{1,14}, Perry^{1,4,6}, Philadelphia^{1,4}, Pike^{1,4}, Union⁸, Washington⁶, Westmoreland¹, York^{1,6,8}; **31 Mar³ – 4 Dec⁶ (2018³)**.

Xylocopini

Genus *Xylocopa* Latreille Subgenus *Xylocopoides* Michener

Taxonomy: Hurd (1961); Mitchell (1962).

Xylocopa (Xylocopoides) virginica virginica (Linnaeus, 1771) – Adams^{1,3,8}, Allegheny^{1,2}, Blair¹, Bradford⁶, Bucks^{1,6,8}, Butler¹, Centre^{1,3,5,6,7,15,44}, Chester^{1,8}, Clearfield¹, Columbia^{1,2,5}, Crawford¹, Dauphin^{1,6}, Delaware¹, Erie^{1,9}, Fayette¹, Forest¹, Greene¹, Huntingdon^{1,3,8}, Indiana¹, Jefferson¹, Juniata¹, Lackawanna², Lancaster^{1,2,3,5,15}, Lebanon⁴, Lehigh¹, Luzerne¹, Lycoming⁸, Montgomery^{1,7,8}, Perry^{1,4}, Philadelphia^{1,2,4}, Schuylkill^{1,2}, Snyder⁴, Union^{1,8}, Washington¹, Westmoreland^{1,2}, York^{1,8}; 5 Mar¹ – 30 Oct³ (2018³).

Megachilidae Megachilinae Anthidiini

Genus Anthidiellum Cockerell Subgenus Loyolanthidium Urban

Taxonomy: Mitchell (1962); Urban (2001).

Anthidiellum (Loyolanthidium) notatum notatum (Latreille, 1809) – Centre¹, Huntingdon^{1,2}, Lancaster³, Mifflin¹, Monroe¹, Northampton⁶, Philadelphia¹; 12 Jul^{1,2} – 22 Aug³ (2012³). Revision: Gonzalez and Griswold (2013).

Subgenus Anthidium Fabricius s. s.

Anthidium (Anthidium) manicatum manicatum (Linnaeus, 1758)* (1990^{1,6}) – Adams^{3,8}, Bradford⁸, Centre^{1,2,6,15,44}, Cumberland^{1,6}, Dauphin^{1,6}, Delaware⁴, Erie^{6,9}, Huntingdon^{1,3}, Lancaster⁸, Lehigh^{3,6}, Lycoming⁸, Montgomery⁴⁴, Philadelphia¹, Schuylkill⁶, Sullivan¹, Union⁸, Washington⁶, York^{1,8}; 25 Mar⁶ – 19 Oct³ (2018³).

Subgenus Proanthidium Friese

Anthidium (Proanthidium) oblongatum oblongatum (Illiger, 1806)* (1994¹) – Adams^{3,6}, Bradford⁸, Bucks^{4,8}, Centre¹, Columbia¹, Crawford¹, Cumberland⁶, Dauphin^{1,6}, Delaware^{1,4}, Erie⁹, Lackawanna⁴, Lancaster^{1,8}, Lehigh^{1,6}, Lycoming⁸, Northampton⁶, Philadelphia^{1,4}, Union⁸, Westmoreland⁴, York⁸; 14 May³ – 17 Oct¹ (2018³).

Genus Paranthidium Cockerell and Cockerell

Taxonomy: Schwarz (1926).

Subgenus Paranthidium Cockerell and Cockerell s. s.

Paranthidium (Paranthidium) jugatorium jugatorium (Say, 1824) – Bedford¹, Centre¹; 28 Jul¹ – 29 Aug¹ (2006¹).

Genus Pseudoanthidium Friese

Taxonomy: Michener and Griswold (1994); Portman et al. (2019).

Subgenus Pseudoanthidium Friese s. s.

Pseudoanthidium (Pseudoanthidium) nanum (Mocsáry, 1881)* (2008⁶) – Allegheny⁴⁹ (BugGuide Image IDs: 1538244/1538247/1538248/1538249), Dauphin⁶, Lycoming⁸; 3 Jun⁶ – 28 Aug⁸ (2018⁴⁹).

Genus Stelis Panzer

Taxonomy: Parker and Bohart (1979); Mitchell (1962).

Subgenus Dolichostelis Parker and Bohart

Stelis (Dolichostelis) louisae Cockerell, 1911 – Bucks⁴⁹ (BugGuide Image IDs: 1417130/1417131/1417132/1416293), Lehigh⁴⁹ (BugGuide Image IDs: 747710/747711/747712); 28 Jul⁴⁹ – 1 Aug⁴⁹ (2017⁴⁹).

Subgenus Stelis Panzer s. s.

Stelis (Stelis) coarctatus Crawford, 1916³⁷ – Adams^{1,3}, Sullivan³⁷; 22 May¹ – 23 Jul³⁷ (2009³).
Stelis (Stelis) foederalis Smith, 1854 – Huntingdon¹; 17 May¹ – 27 May¹ (1999¹).
Stelis (Stelis) labiata (Provancher, 1888) – locations, dates, and year not reported³⁷.
Stelis (Stelis) lateralis Cresson, 1864³⁷ – Adams³, Allegheny¹, Columbia⁵, Erie⁹; 7 May³ – 5–7 Jul⁹ (2015^{3,9}).

Megachilini

Genus Coelioxys Latreille

Taxonomy: Mitchell (1962, 1980); Baker (1975); Rocha Filho and Packer (2016).

Subgenus Allocoelioxys Tkalců

Coelioxys (Allocoelioxys) coturnix Pérez, 1884* (2014⁸) – Lancaster⁸, York⁸; 1 Jun⁸ – 21 Jul⁸ (2015⁸).

Subgenus Boreocoelioxys Mitchell

Revision: Baker (1975).

- Coelioxys (Boreocoelioxys) banksi Crawford, 1914 Allegheny¹, Centre¹; 24 Aug¹ (1996¹). Coelioxys (Boreocoelioxys) moestus Cresson, 1864¹⁰ – Adams³, Allegheny¹, Blair^{1,2}, Centre⁷, Lawrence¹, Philadelphia¹; 24 May³ – 15 Sep³ (2017⁷).
- Coelioxys (Boreocoelioxys) octodentatus Say, 1824¹⁰ Adams³, Allegheny¹, Centre⁷, Dauphin¹, Forest¹, Lancaster³, Lehigh¹, Philadelphia^{1,4}; 26 May³ – 24 Aug^{1,4} (2016^{3,7}).
- *Coelioxys (Boreocoelioxys) porterae* Cockerell, 1900¹⁰ Allegheny¹, Centre¹, Lehigh¹; 25 Jun¹ – 23 Jul¹ (1954¹).
- *Coelioxys (Boreocoelioxys) rufitarsis* Smith, 1854^{10,37} Adams³, Allegheny¹, Beaver¹, Berks¹, Bradford⁸, Bucks¹, Centre⁷, Erie^{1,2}, Lehigh¹, Monroe², Philadelphia¹, York¹; **11 Jun³** 25 Sep¹ (2017⁷).
- Coelioxys (Boreocoelioxys) sayi Robertson, 1897^{10,37} Adams³, Allegheny¹, Berks¹, Bucks^{1,8}, Centre^{1,7}, Chester¹, Columbia¹, Crawford⁴, Cumberland¹, Dauphin¹, Delaware^{1,2}, Erie¹, Fayette¹, Franklin⁶, Huntingdon^{1,2}, Lancaster², Lawrence¹, Lehigh¹, Monroe¹, Montgomery¹, Northampton⁶, Philadelphia^{1,2,4}, Union⁸, York⁸; 29 May² 28 Sep⁸ (2017⁷).

Subgenus Cyrtocoelioxys Mitchell

Key: Baker (1975).

Coelioxys (*Cyrtocoelioxys*) *modestus* Smith, 1854³⁷ – Allegheny¹, **Centre**⁷, Lehigh¹; Jun¹ – **16–17 Aug**⁷ (**2017**⁷).

Subgenus Paracoelioxys Gribodo

Revision: Baker (1975 as subgenus Schizocoelioxys Mitchell).

Coelioxys (Paracoelioxys) funerarius Smith, 1854^{10,37} – Northampton⁶; 25 Jul⁶ (2010⁶).

Subgenus Synocoelioxys Mitchell

Revision: Baker (1975).

Coelioxys (Synocoelioxys) alternatus Say, 1837^{10,37} – Adams³, Huntingdon^{1,2}, Lehigh⁶; 7 May⁶ – 2 Sep³ (2009³). Coelioxys (Synocoelioxys) hunteri Crawford, 1914 – Washington¹; 13 Jul¹ (1910¹).

Subgenus Xerocoelioxys Latreille s. s.

Revision: Baker (1975); Rocha-Filho and Packer (2016).

Coelioxys (Xerocoelioxys) immaculatus Cockerell, 1912 – Allegheny¹, Philadelphia²; 8 Jul² (2005²).

Genus Megachile Latreille

Taxonomy: Mitchell (1934, 1935a; b, 1936a; b, 1937a; b; c, 1962); Parker (1978); Ivanochko (1979); Sheffield et al. (2011b).

Subgenus Callomegachile Michener

Megachile (Callomegachile) sculpturalis Smith, 1853* (1996¹) – Adams³, Bradford¹, Bucks⁸, Centre^{1,6,7,44}, Clinton¹, Dauphin^{1,3,6}, Erie¹, Huntingdon¹, Jefferson^{1,2,6}, Lycoming⁴⁴, Northampton⁶, Schuylkill⁶, Tioga¹; 28 Jun³ – 15 Aug³ (2018³).

Subgenus Chelostomoides Robertson

Revision: Mitchell (1937c).

- *Megachile (Chelostomoides) campanulae* (Robertson, 1903)³⁷ Adams³, Allegheny¹, Beaver¹, Bucks⁸, Centre^{1,7}, Dauphin¹, Erie⁹, Huntingdon^{1,2}, Jefferson⁶, Lancaster³, Monroe¹, Philadelphia^{1,4}; 15 May¹ – 24 Aug^{1,4} (2018³).
- Megachile (Chelostomoides) exilis Cresson, 1872 Adams³, Bucks⁸, Philadelphia^{1,4}; 29 Jun³ 23 Aug^{1,4} (2017³).

Subgenus Eutricharaea Thomson

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Taxonomy: Parker (1978); Mitchell (1980); Soltani et al. (2017).

- Megachile (Eutricharaea) apicalis Spinola, 1808* (1996¹) Bucks⁴, Carbon⁶, Dauphin^{1,6}, Lancaster⁸, Lehigh⁶, Lycoming⁸, Northampton⁶, Schuylkill⁶, Union⁸, York⁸; 7 May⁶ – 28 Sep⁸ (2015⁸).
- Megachile (Eutricharaea) pusilla Pérez, 1884* (1946¹)³⁷ Centre¹; 20 Jul¹ (1946¹).
- Megachile (Eutricharaea) rotundata (Fabricius, 1787)* (1946¹) Adams^{3,6,8}, Bradford^{1,6,8}, Bucks^{4,8}, Carbon⁶, Centre^{1,6,8,15,44}, Clinton^{1,6}, Dauphin^{1,6}, Delaware^{1,4}, Erie^{6,9}, Franklin⁶, Lancaster^{3,6,8}, Lehigh⁶, Lycoming⁸, Montgomery⁸, Northampton⁶, Philadelphia^{1,4}, Schuylkill⁶, Union⁸, Westmoreland⁶, York⁸; 7 May⁶ – 9 Oct³ (2016⁹).

Subgenus Leptorachis Mitchell

Taxonomy: Mitchell (1934).

Megachile (Leptorachis) petulans Cresson, 1878³⁷ – Berks⁶, Delaware¹, Warren¹; 30 Jul¹ – 12 Aug⁶ (2008⁶).

Subgenus Litomegachile Mitchell

Taxonomy: Mitchell (1935a); Bzdyk (2012).

- Megachile (Litomegachile) brevis Say, 1837³⁷ Adams^{1,3,8}, Allegheny¹, Bradford⁸, Bucks⁸, Centre^{1,15,44}, Columbia⁵, Crawford⁴, Cumberland¹, Dauphin^{1,6}, Delaware^{1,4}, Erie⁹, Franklin¹, Huntingdon⁶, Juniata¹, Lancaster^{5,15}, Lycoming⁸, Montgomery^{1,7,8}, Perry¹, Philadelphia^{1,4}, York⁸; 1 Jun⁸ – 15 Oct³ (2018³).
- Megachile (Litomegachile) mendica Cresson, 1878³⁷ Adams^{3,8}, Allegheny¹, Berks^{2,6},
 Bradford⁸, Bucks^{1,4,8}, Carbon⁶, Centre^{1,7,8,15,44}, Chester^{1,8}, Columbia², Crawford⁶,
 Cumberland¹, Dauphin^{1,2,6}, Delaware¹, Erie^{1,6,9}, Fulton⁴⁴, Huntingdon^{1,2,3,8}, Jefferson⁶, Juniata³, Lancaster^{1,2,3,15}, Lehigh¹, Luzerne¹, Lycoming⁸, Mifflin¹, Monroe¹,
 Montgomery^{1,2,7,8,44}, Northampton^{4,6}, Northumberland¹, Perry⁴, Philadelphia^{1,2,4},
 Schuylkill⁶, Sullivan¹, Union⁸, Westmoreland¹, York⁸; 6 Mar¹ 16 Oct³ (2018³).
- *Megachile (Litomegachile) texana* Cresson, 1878³⁷ Erie⁹, Lehigh¹, Philadelphia^{1,2,4}; 7 Jul¹ 25 Aug^{1,4} (**2016**⁹).

Subgenus Megachile Latreille s. s.

Revision: Mitchell (1935b as *Delomegachile*).

- *Megachile (Megachile) centuncularis* (Linnaeus, 1758)³⁷ Adams¹, Allegheny^{1,2}, **Brad-ford⁸**, **Bucks⁴**, Centre¹, Dauphin¹, Delaware¹, Erie^{1,9}, Franklin¹, Huntingdon², **Montgomery⁸**, Philadelphia^{1,4}, York^{1,6}; 15 May¹ 24 Sep¹ (**2016**⁹).
- *Megachile (Megachile) inermis* Provancher, 1888³⁷ Adams³, Centre^{1,7}, Fayette¹, Forest¹, Huntingdon¹; 24 Jun¹ 9 Sep¹ (2017⁷).
- *Megachile (Megachile) montivaga* Cresson, 1878³⁷ Adams^{3,8}, Bradford¹, Bucks⁴, Centre^{1,7}, Chester⁸, Crawford¹, Dauphin^{1,6}, Erie⁹, Lancaster³, Lycoming⁸, Montgomery⁷, Pike^{1,4}, Sullivan¹, Washington⁶; 15 May⁶ 28 Sep⁸ (2018³).
- Megachile (Megachile) relativa Cresson, 1878³⁷ Adams³, Allegheny¹, Blair^{1,2}, Bradford⁸, Centre^{1,7,15}, Clearfield¹, Dauphin^{1,2,6}, Erie⁹, Huntingdon^{1,2,3}, Lancaster^{1,4}, Lycoming⁸, Monroe¹, Perry¹, Somerset^{1,2}, Sullivan¹, Susquehanna⁸, Union⁸, Washington¹, Wyoming⁴; 1 Jun³ 3 Oct¹ (2017⁷).

Subgenus Megachiloides Mitchell

Revision: Mitchell (1936b).

Megachile (Megachilodes) integra Cresson, 1878 – Adams³, Bucks¹, Dauphin¹, Huntingdon¹, Northampton⁶, Perry¹, Philadelphia¹; 5 May¹ – 18 Sep¹ (2012³).

Subgenus Sayapis Titus

Revision: Mitchell (1937b).

- Megachile (Sayapis) frugalis frugalis Cresson, 1872³⁷ Adams³, Carbon⁶, Centre¹, Dauphin^{1,6}, Delaware⁴, Lehigh¹, Northampton⁶; 26 May¹ 6 Aug⁶ (2017³).
- Megachile (Sayapis) inimica Cresson, 1872 sayi Cresson, 1878³⁷ Adams³, Allegheny¹, Bucks^{4,8}, Centre^{1,7,8}, Cumberland¹, Dauphin^{1,6}, Erie¹, Huntingdon¹, Lancaster³; 10 Jun⁶ 28 Sep⁸ (2017^{3,7}).
- Megachile (Sayapis) pugnata pugnata Say, 1837³⁷ Adams³, Allegheny¹, Beaver¹, Centre^{1,7,15,44}, Dauphin¹, Huntingdon^{1,2,3}, Lancaster³, Union¹, Washington¹; **29 May³ 16–17 Aug⁷** (2018³).

Subgenus Xanthosarus Robertson

Revision: Mitchell (1936a).

Megachile (Xanthosarus) addenda Cresson, 1878³⁷ – Adams^{1,3}, Allegheny¹, Centre¹⁵, Dauphin^{1,6}, Erie⁹, Lehigh¹; **16 May³** – 15 Jul¹ (**2015**⁹).

- Megachile (Xanthosarus) frigida frigida Smith, 1853³⁷ Centre¹, Dauphin¹, Erie¹, Forest¹, Lebanon¹, Lycoming⁸, Monroe², Montgomery⁸; 30 May¹ - 20 Aug¹ (2015⁸).
- Megachile (Xanthosarus) gemula gemula Cresson, 1878³⁷ Adams³, Allegheny¹, Bucks⁸, Centre^{1,7}, Cumberland¹, Dauphin¹, Elk¹, Huntingdon³, Lehigh¹, Monroe^{1,2}, Philadelphia¹, Sullivan^{1,2}; 30 Apr¹ 6 Sep³ (2018³).
- *Megachile (Xanthosarus) ingenua* Cresson, 1878³⁷ locations, dates, and year not reported³⁷.
- *Megachile (Xanthosarus) latimanus* Say, 1823³⁷ Adams³, Allegheny¹, Bradford⁸, Bucks¹, Carbon⁶, Centre^{1,7}, Columbia², Cumberland^{1,2}, Dauphin^{1,2}, Delaware¹, Erie^{1,9}, Franklin¹, Huntingdon¹, Lackawanna⁶, Lancaster², Lehigh¹, Monroe¹, Philadelphia¹, Schuylkill¹, Sullivan^{1,2}, Washington¹, Westmoreland¹, Wyoming¹; 2–4 Jun⁹ – 1 Oct¹ (2017⁷).
- Megachile (Xanthosarus) melanophaea melanophaea Smith, 1853³⁷ Adams³, Allegheny¹, Dauphin¹, Sullivan¹, Westmoreland⁶; 4 Jun¹ – 14 Jul⁶ (2016³).
- Megachile (Xanthosarus) mucida Cresson, 1878 Crawford⁶, Forest¹; 19 Jul¹ 13 Aug⁶ (2008⁶).

Osmiini

Genus *Chelostoma* Latreille Subgenus *Gyrodromella* Michener

Taxonomy: Eickwort (1980); Buck et al. (2005); Müller (2015).

Chelostoma (Gyrodromella) rapunculi (Lepeletier, 1841)* (2015⁹) – Erie⁹; **2–4 Jun⁹ – 9–11 Jun⁹ (2016**⁹).

Subgenus Prochelostoma Robertson

Taxonomy: Eickwort (1980); Buck et al. (2005).

Chelostoma (Prochelostoma) philadelphi (Robertson, 1891)³⁷ – Adams³, Allegheny¹,
 Bucks⁸, Centre⁶, Dauphin¹, Delaware¹, Erie⁹, Fayette¹, Fulton¹, Lycoming¹, Montgomery¹, Northumberland¹, Perry¹, Philadelphia¹, Pike¹, Westmoreland¹; 18 Apr⁶ – 27 Jul¹ (2018³).

Genus *Heriades* Spinola Subgenus *Neotrypetes* Robertson

Taxonomy: Michener (1938); Mitchell (1962).

Heriades (Neotrypetes) carinata Cresson, 1864 – Adams³, Allegheny¹, Bucks⁸, Centre^{7,15}, Chester⁸, Cumberland¹, Erie¹, Lancaster³, Lehigh¹, Philadelphia¹; 2 Jun¹ – 14 Aug³ (2018³).
- Heriades (Neotrypetes) leavitti Crawford, 1913 Adams³, Centre⁷; 4 Jun³ 24–25 Jul⁷ (2017⁷).
- Heriades (Neotrypetes) variolosa (Cresson, 1872) Adams³, Centre¹⁵, Montgomery⁸; 11 Jul⁸ – 15 Sep³ (2011⁸).

Genus Hoplitis Klug

Taxonomy: Michener (1947); Mitchell (1962); Sedivy et al. (2013).

Subgenus Alcidamea Cresson

- Hoplitis (Alcidamea) albifrons albifrons (Kirby, 1837) (tuberculata group) Adams³, Somerset²; 24 Jun² – 10 Jul³ (2015³).
- Hoplitis (Alcidamea) pilosifrons (Cresson, 1864) (producta group) Adams³, Blair^{1,2}, Brad-ford⁶, Centre⁷, Dauphin⁶, Delaware², Huntingdon^{1,2}, Lancaster³, Monroe⁴, Mont-gomery⁷, Northumberland¹, Perry¹, Philadelphia^{1,2}, York⁸; 30 Apr³ 18 Oct³ (2018³).
- Hoplitis (Alcidamea) producta producta (Cresson, 1864) (producta group)³⁷ Adams³, Allegheny¹, Blair⁶, Bradford^{6,8}, Butler, Centre^{6,7,8,15}, Chester¹, Clinton⁶, Crawford¹, Cumberland¹, Dauphin^{1,6}, Delaware⁴, Erie⁶, Jefferson⁶, Lehigh¹, Monroe⁴, Montgomery⁷, Philadelphia², Union⁸, Washington⁶, York⁸; 4 May³ 16–17 Aug⁷ (2018³).
- Hoplitis (Alcidamea) spoliata (Provancher, 1888) (tuberculata group) Centre^{1,7}, Crawford⁴, Dauphin^{1,6}, Huntingdon^{1,2,8}, Lehigh¹, Lycoming⁸, Monroe², Perry¹; 27 May¹ 19–20 Aug⁴ (2017⁷).
- Hoplitis (Alcidamea) truncata truncata (Cresson, 1878) (truncata group) Adams³, Bradford⁶, Clarion¹, Cumberland¹, Franklin¹, Lehigh¹, Northumberland⁶, York⁸; 1 Jun¹ – 9 Aug¹ (2015⁸).

Subgenus Hoplitis Klug s. s.

Hoplitis (Hoplitis) anthocopoides (Schenck, 1853) (Annosmia-Hoplitis group)* (2012³) – Adams³; 31 May³ – 14 Jun³ (2012³).

Subgenus Robertsonella Titus

Hoplitis (Robertsonella) simplex (Cresson, 1864) – Bradford⁶, Bucks⁸, Dauphin⁶, Lancaster⁸, York⁸; 8 May⁶ – 16 Jun⁶ (2014⁸).

Genus Osmia Panzer

Taxonomy: Sandhouse (1939); Mitchell (1962); Rust (1974).

Subgenus Diceratosmia Robertson

Revision: Michener (1949).

Osmia (Diceratosmia) conjuncta Cresson, 1864 – Adams³, Huntingdon⁸; 27 Apr⁸ – 15 Jun⁸ (2015⁸).

Subgenus Helicosmia Thomson

Revision: Rust (1974 as Chalcosmia).

- *Osmia (Helicosmia) caerulescens* (Linnaeus, 1758)* (1905¹)³⁷ Adams³, Allegheny¹, Bradford¹, Butler¹, Centre¹, Cumberland¹, Dauphin¹, Franklin¹, Perry¹, Philadelphia¹, Pike¹, Washington^{1,2}; 10 Apr² 29 Aug¹ (**2017**³).
- Osmia (Helicosmia) chałybea Smith, 1853 Delaware¹, Philadelphia²; 16 May² 22 Jun¹ (1907¹).
- Osmia (Helicosmia) coloradensis Cresson, 1878 Bradford¹; 13 Jun¹ 2 Jul¹ (1939¹).
- *Osmia* (*Helicosmia*) georgica Cresson, 1878³⁷ Adams³, Allegheny¹, Bradford⁸, Bucks⁸, Centre⁷, Dauphin¹, Delaware¹, Erie⁹, Huntingdon⁸, Lancaster^{3,8}, Lycoming⁸, Montgomery⁴, Perry⁶, Susquehanna⁸, Union⁸, York^{1,8}; 15 Apr⁸ 21 Jul³ (2018³).
- Osmia (Helicosmia) texana Cresson, 1872 Adams³, Allegheny¹, Bradford⁸, Centre⁸, Cumberland⁶, Greene¹, Huntingdon¹, Lancaster⁸, Washington⁶; 25 May¹ 15 Sep⁸ (2018³).

Subgenus Melanosmia Schmiedeknecht

Taxonomy: Rightmyer et al. (2010).

- Osmia (Melanosmia) albiventris Cresson, 1864³⁷ Centre¹, Clarion⁶, Dauphin⁶, Huntingdon⁸, Lehigh¹, Montgomery¹, Philadelphia¹, Tioga¹, Union⁸, York⁸; 23 Apr¹ 3 Jul⁶ (2015⁸).
- Osmia (Melanosmia) atriventris Cresson, 1864³⁷ Adams³, Allegheny¹, Blair², Bradford^{1,8}, Bucks⁸, Centre^{7,8,15}, Dauphin¹, Delaware^{1,2}, Huntingdon⁸, Lancaster⁸, Lycoming⁸, Monroe¹, Montgomery⁷, Perry⁶, Philadelphia^{1,2}, Pike^{1,4}, Susquehanna⁸, Tioga¹, Union⁸, York⁸; 29 Mar³ 26–27 Jul⁷ (2018³).
- *Osmia (Melanosmia) bucephala* Cresson, 1864³⁷ Adams^{1,3,8}, Berks¹, **Bradford**⁸, **Bucks**⁸, Centre^{2,6,7,15}, Dauphin^{1,6}, Delaware¹, Erie⁹, Huntingdon^{1,3,6,8}, **Northumberland**⁶, Pike^{1,4}, Schuylkill^{1,2}, **Susquehanna**⁸, **Union**⁸, Washington¹, **York**⁸; 10 Apr^{1,3} – 4 Jul¹ (**2018**³).
- Osmia (Melanosmia) collinsiae Robertson, 1905³⁷ Adams³, Allegheny¹, Bucks⁸, Centre⁷, Cumberland⁶, Perry⁶, York⁸; 12 Apr⁶ 1 Jul¹ (2017⁷).
- *Osmia (Melanosmia) distincta* Cresson, 1864³⁷ Adams³, Cumberland⁶, Dauphin^{1,6}, Delaware¹, Huntingdon^{1,2}, Luzerne¹, Monroe⁴, Montgomery⁷, Perry⁶, Pike^{1,4}, York⁸; 9 Apr² 1–30 Jun⁴ (2017⁷).
- Osmia (Melanosmia) felti Cockerell, 1911³⁷ Adams³, Perry⁶; 12 Apr⁶ 20 May³ (2009³).

- Osmia (Melanosmia) inspergens Lovell & Cockerell, 1907³⁷ Centre⁷, Huntingdon⁸, Susquehanna⁸; 28 Apr⁸ – 24–25 May⁷ (2015⁸).
- Osmia (Melanosmia) proxima Cresson, 1864 Sullivan¹, York¹; 27 Apr¹ 15 Aug¹ (1941¹).
- Osmia (Melanosmia) pumila Cresson, 1864³⁷ Adams^{1,3}, Bedford⁶, Blair^{1,2}, Bradford^{1,6,8}, Bucks^{2,8}, Centre^{1,2,7,8,15}, Chester¹, Columbia⁵, Crawford¹, Cumberland^{1,6}, Dauphin^{1,6}, Delaware^{1,2,4}, Erie^{6,9}, Franklin^{1,6}, Greene⁶, Huntingdon^{1,8}, Jefferson⁶, Lackawanna⁶, Lancaster^{1,3,8}, Lehigh¹, Lycoming^{6,8}, Montgomery^{1,4}, Montour⁶, Perry⁶, Philadelphia^{1,2}, Pike^{1,4}, Somerset^{1,2}, Susquehanna⁸, Union⁸, Warren⁶, Washington^{1,6}, York⁸; 13 Mar⁶ 29 Jul⁶ (2018³).
- Osmia (Melanosmia) sandhouseae Mitchell, 1927 Adams³, Huntingdon⁸; 23 Apr³ – 28 Apr⁸ (2015^{3,8}).
- *Osmia (Melanosmia) simillima* Smith, 1853³⁷ Adams¹, Centre¹, Cumberland¹, Montgomery¹, Philadelphia¹, Tioga¹; 8 May¹ – 12 Jul¹ (1909¹).
- Osmia (Melanosmia) virga Sandhouse, 1939³⁷ Adams³, Bucks⁸, Lancaster⁸, Lycoming⁸, Union⁸, York⁸; 15 Apr⁸ – 15 Jun⁸ (2015⁸).

Subgenus Osmia Panzer s. s.

Revision: Rust (1974).

- Osmia (Osmia) cornifrons (Radoszkowski, 1887)* (2002³) Adams³, Bradford⁸, Bucks⁸, Centre^{2,5,6,7,8,15}, Cumberland⁶, Dauphin⁶, Erie⁹, Huntingdon⁸, Lancaster⁸, Lycoming^{6,8}, Montgomery⁷, Susquehanna⁸, Union⁸, York⁸; 29 Mar³ – 29 Jul⁶ (2018³).
- *Osmia* (*Osmia*) *lignaria lignaria* Say, 1837³⁷ Adams^{1,3}, Allegheny¹, Butler¹, Cambria¹, Centre¹, Cumberland¹, Dauphin^{1,4}, Delaware^{1,2}, Franklin¹, Fulton¹, Huntingdon^{1,3,8}, **Jefferson**⁶, **Juniata**⁶, **Lancaster**⁸, Lehigh¹, Montgomery^{1,2,7}, Perry¹, Philadelphia², Somerset¹, Washington¹, Westmoreland¹, **York**⁸; **31 Mar**³ 1 Sep¹ (**2017**^{3,7}).
- Osmia (Osmia) taurus Smith, 1873* (2008^{3,6}) Adams³, Bradford⁸, Centre^{6,7,8}, Clinton⁶, Cumberland⁶, Dauphin⁶, Erie⁹, Huntingdon⁸, Lancaster⁸, Lycoming⁸, Perry⁶, Susquehanna⁸, Union⁸, York⁸; 31 Mar³ – 29 Jul⁶ (2018³).

Lithurginae Lithurgini

Genus Lithurgus Berthold

Taxonomy: Snelling (1986).

Lithurgus chrysurus Fonscolombe, 1834* (2007¹) – Carbon⁶, Lehigh^{1,6}, Northampton⁶; 7 Jul¹ – 9 Aug⁶ (2009⁶).

Andrenidae Andreninae Andrenini

Genus Andrena Fabricius

Taxonomy: Mitchell (1960); LaBerge (1967, 1969, 1971, 1973, 1977, 1980, 1985, 1987, 1989); Ribble (1967, 1968, 1974); LaBerge and Bouseman (1970, 1977); LaBerge and Ribble (1972, 1975); Bouseman and LaBerge (1978).

Subgenus Andrena Fabricius s. s.

Revision: LaBerge (1980).

- Andrena (Andrena) carolina Viereck, 1909^{25,36} Centre^{1,6,7}, Elk¹, Luzerne¹, Lycoming⁸, Philadelphia^{1,2}, Pike^{1,4}; 9 Apr¹ **15–16 Aug**⁷ (**2017**⁷).
- Andrena (Andrena) clarkella (Kirby, 1802) Forest^{1,25}, Sullivan^{1,2}; 30 Mar² 6 May¹ (1983^{1,2}).
- Andrena (Andrena) cornelli Viereck, 1907 Adams³, Bucks⁸, Cumberland¹, Erie⁹, Perry²⁵, Philadelphia^{1,2,25}, Schuylkill²; 4 May⁸ 9–11 Jun⁹ (2016^{3,9}).
- Andrena (Andrena) frigida Smith, 1853³⁶ Union⁸, York⁸; 24 Apr⁸ 28 Apr⁸ (2015⁸).
- Andrena (Andrena) macoupinensis Robertson, 1900³⁶ Lancaster³, Philadelphia¹, Pike^{1,4}; 2 May¹ 30 May^{1,4} (2012³).
- Andrena (Andrena) mandibularis Robertson, 1892³⁶ Adams³, Allegheny^{1,25}, Bucks⁸, Centre^{1,7}, Crawford¹, Cumberland²⁵, Dauphin^{1,25}, Delaware², Franklin¹, Huntingdon³, Lycoming⁸, Montgomery^{1,25}, Philadelphia¹, Susquehanna⁸, Westmoreland^{1,25}; 5 Mar¹ – 13 Jun³ (2016^{3,7}).
- Andrena (Andrena) milwaukeensis Graenicher, 1903³⁶ Allegheny^{1,25}, Centre^{1,3,5,7}, Cumberland^{1,25}, Dauphin¹, Huntingdon⁸, Lycoming⁸, Monroe^{1,2}, Somerset^{1,25}, Susquehanna⁸, Westmoreland¹, Wyoming¹; 18 Apr¹ 22 Jun¹ (2018³).
- Andrena (Andrena) rufosignata Cockerell, 1902²⁵ Centre¹, Clinton¹, Forest^{1,25}, Huntingdon⁸, Lycoming⁸, Sullivan¹, Susquehanna⁸, Union⁸, Westmoreland¹, York⁸; 15 Apr⁸ – 16 Jul¹ (2015⁸).
- *Andrena (Andrena) thaspii* Graenicher, 1903 Adams³, Allegheny^{1,25}, Centre^{1,25}, Huntingdon³, Westmoreland²⁵; 1 May³ – 4 Jul¹ (2012³).
- Andrena (Andrena) tridens Robertson, 1902³⁶ Adams³, Bradford⁸, Centre^{1,7}, Erie^{6,9}, Franklin¹, Huntingdon⁸, Jefferson⁶, Lancaster⁸, Lebanon^{1,25}, Lycoming⁸, Perry¹, Philadelphia¹, Susquehanna⁸, Union⁸, Westmoreland¹, York⁸; 13 Mar³ – 24 Jul⁶ (2017³).

Subgenus Archiandrena LaBerge

Revision: LaBerge (1985).

- Andrena (Archiandrena) banksi Malloch, 1917 Bucks⁸, Susquehanna⁸; 28 Apr⁸ 22 May⁸ (2015⁸).
- *Andrena (Archiandrena) dimorpha* Mitchell, 1960 Philadelphia²⁶; dates and year not reported²⁶.

Subgenus Callandrena Cockerell s. l.

Revision: LaBerge (1967).

- Andrena (Callandrena s. l.) aliciae Robertson, 1891 (aliciae group) Allegheny¹, Dauphin¹, Fayette¹; 6 Aug¹ – 1 Sep¹ (1940¹).
- Andrena (Callandrena s. l.) asteris Robertson, 1891 (simplex group)³⁶ Allegheny¹, Beaver¹, **Bucks⁸**, Chester¹, Columbia², Dauphin¹, Delaware^{1,2}, Erie⁹, Lycoming¹, Philadelphia¹; 7 Sep¹ 29 Sep² (**2016**⁹).
- Andrena (Callandrena s. l.) asteroides Mitchell, 1960 (simplex group) Centre¹; 5 Mar¹ (1930¹).
- Andrena (Callandrena s. l.) gardineri Cockerell, 1906 (gardineri group) Adams³, Westmoreland¹; 18 May¹ 21 May³ (2013³).
- Andrena (Callandrena s. l.) helianthi Robertson, 1891 (helianthi group) Allegheny¹, Chester¹, Lackawanna⁶, Potter¹, Westmoreland¹; 21 Apr¹ 16 Sep¹ (2008⁶).
- Andrena (Callandrena s. l.) krigiana Robertson, 1901 (krigiana group) Dauphin¹, Montgomery^{1,7}, Perry¹, Philadelphia^{1,2}, **Susquehanna⁸**; 24 May¹ 3 Oct¹ (**2017**⁷).
- Andrena (Callandrena s. l.) placata Mitchell, 1960 (simplex group) Centre¹⁵, Erie⁹, Philadelphia¹; **11–13 Sep⁹** 19 Sep¹ (**2016**⁹).
- Andrena (Callandrena s. l.) rudbeckiae Robertson, 1891 (melliventris group) Huntingdon^{1,2}; 12 Jul² – 13 Jul¹ (2005^{1,2}).
- Andrena (Callandrena s. l.) simplex Smith, 1853 (simplex group)³⁶ Allegheny¹, Brad-ford⁸, Bucks⁶, Chester¹, Cumberland¹, Dauphin⁶, Delaware^{1,2}, Lycoming^{6,8}, Phila-delphia¹, Wyoming¹, York⁸; 8 Jun⁶ 23 Sep^{2,8} (2015⁸).

Subgenus Cnemidandrena Hedicke

Revision: Donovan (1977).

- *Andrena (Cnemidandrena) chromotricha* Cockerell, 1899³⁶ Allegheny¹, Cambria³⁶; 25 Aug³⁶ (1925³⁶).
- Andrena (Cnemidandrena) hirticincta Provancher, 1888³⁶ Allegheny¹, Beaver¹, **Centre**⁷, Chester¹, Cumberland¹, Delaware¹, Forest¹, Mercer¹, Monroe², Philadelphia¹, Tioga¹; 20 Jun¹ 2 Oct¹ (**2017**⁷).
- Andrena (Cnemidandrena) nubecula Smith, 1853 Adams³, Allegheny^{1,2}, Centre^{1,7,15}, Clarion¹, Cumberland¹, Delaware¹, Forest¹, Luzerne¹, Monroe^{1,2}, Montgomery¹, Union⁸, Wyoming¹; 21 Jul¹ 28 Sep⁸ (2018³).

Subgenus Conandrena Viereck

Revision: LaBerge (1986).

Andrena (Conandrena) bradleyi Viereck, 1907²⁶ – Bucks¹, Centre^{6,7}, Clinton^{1,26}, Crawford², Dauphin^{1,26}, Delaware²⁶, Huntingdon⁶, Lycoming⁸, Philadelphia²; 16 Apr¹ – 31 May–1 Jun⁷ (2017⁷).

Subgenus Derandrena Ribble

Revision: Ribble (1968).

Andrena (Derandrena) uvulariae Mitchell, 1960 – Westmoreland¹; 18 May¹ (1982¹).
 Andrena (Derandrena) ziziaeformis Cockerell, 1908³⁶ – Bradford⁸, Centre⁷, Dauphin¹, Delaware¹, Huntingdon⁸, Lycoming⁸, Monroe^{1,2}, Philadelphia¹, Pike^{1,4}, Union⁸, York¹; 30 Apr¹ – 15 Jun⁸ (2017⁷).

Subgenus Euandrena Hedicke

Revisions: LaBerge and Ribble (1975); LaBerge (1977).

- Andrena (Euandrena) algida Smith, 1853³⁶ Centre¹, Forest¹, **Montour**⁶; 8 May¹ 23 Jun¹ (**2008**⁶).
- Andrena (Euandrena) geranii Robertson, 1891³⁶ Allegheny^{1,24}, Bucks^{2,8}, Centre¹, Delaware¹, Fayette¹, Huntingdon³, Montgomery¹, Philadelphia², Union^{1,24}, Westmoreland^{1,24}; 22 Apr¹ – 30 Jun¹ (2006⁸).
- Andrena (Euandrena) nigrihirta (Ashmead, 1890)³⁶ Bucks¹, Centre¹, Huntingdon⁸, Monroe¹, Susquehanna⁸; 28 Apr⁸ – 16 Jul¹ (2015⁸).

Andrena (Euandrena) phaceliae Mitchell, 1960³⁶ – Centre¹; 22 May¹ (1947¹).

Subgenus Gonandrena Viereck

Revision: LaBerge and Ribble (1972).

- Andrena (Gonandrena) fragilis Smith, 1853 Adams³, Cumberland¹, Dauphin¹, Huntingdon², Lackawanna⁴, Lancaster^{1,30}, Lehigh¹, Montgomery¹, Philadelphia¹, Westmoreland¹, York¹; 28 May¹ – 15 Jul⁴ (2013⁴).
- *Andrena (Gonandrena) integra* Smith, 1853 Allegheny^{1,30}, **Bucks**⁸, Delaware², Huntingdon¹, Philadelphia², Westmoreland^{1,30}; 7 Apr² – 20 Jun¹ (**2007**⁸).
- *Andrena (Gonandrena) platyparia* Robertson, 1895³⁶ **Adams³**, Allegheny³⁰, Bradford³⁰, Centre¹, Columbia^{1,5}, Crawford¹, Dauphin¹, Lancaster³⁰, Montgomery¹; **19 May³** – 12 Jul¹ (**2017**³).

Subgenus Holandrena Pérez

Revision: LaBerge (1985).

Andrena (Holandrena) cressonii cressonii Robertson, 1891³⁶ – Adams^{1,3,8}, Allegheny^{1,26}, Blair², Bradford⁸, Bucks⁸, Centre^{1,3,7}, Chester^{1,2}, Clinton⁶, Columbia⁵, Cumberland^{1,26}, Dauphin^{1,6,26}, Delaware^{1,2,4,26}, Elk¹, Erie⁹, Franklin¹, Huntingdon^{2,8}, Lancaster^{3,8}, Lehigh¹, Lycoming⁸, Monroe⁴, Montgomery^{1,2,7,26}, Montour⁶, Northumberland²⁶, Perry^{1,26}, Philadelphia^{1,2,4,26}, Union⁸, Warren², Washington⁶, Westmoreland^{1,26}, York^{1,8,26}; 2 Apr³ – 1 Oct³ (2018³).

Subgenus Iomelissa Robertson

Revision: LaBerge (1985). Monotypic.

Andrena (Iomelissa) violae Robertson, 1891³⁶ – Adams³, Allegheny¹, Clinton¹, Crawford¹, Cumberland^{1.6}, Dauphin^{1.6}, Delaware^{1.26}, Huntingdon⁸, Jefferson⁶, Lancaster⁸, Lycoming⁸, Monroe⁴, Northumberland²⁶, Philadelphia¹, Susquehanna⁸, Union⁸, Westmoreland¹, York^{1.8}; 31 Mar³ – 1–30 Jun⁴ (2018³).

Subgenus Larandrena LaBerge

Revision: Ribble (1967).

Andrena (Larandrena) miserabilis Cresson, 1872³⁶ – Adams^{1,3}, Allegheny¹, Bucks^{1,8}, Centre^{1,5,7,8}, Chester¹, Cumberland¹, Dauphin¹, Delaware^{1,2}, Erie⁹, Forest¹, Huntingdon⁸, Lancaster^{3,8}, Lycoming⁸, Monroe¹, Montgomery^{1,2}, Philadelphia^{1,2}, Pike^{1,2,4}, Potter¹, Tioga¹, Union^{1,8}, Westmoreland¹, York^{1,8}; 14 Feb¹ – 9 Jul³ (2018³).

Subgenus Leucandrena Hedicke

Revision: LaBerge (1987).

- Andrena (Leucandrena) barbilabris (Kirby, 1802)³⁶ Bucks², Butler²⁷, Centre¹, Cumberland¹, Dauphin^{1,27}, Delaware^{1,27}, Fayette¹, Lawrence^{1,27}, Montgomery^{1,27}, North-umberland²⁷, Philadelphia^{1,27}, Washington⁶; 30 Mar¹ 28 May⁶ (2008⁶).
- Andrena (Leucandrena) erythronii Robertson, 1891³⁶ Allegheny^{1,27}, Bucks⁸, Centre¹, Crawford¹, Huntingdon⁸, Jefferson⁶, Lycoming⁸, Northumberland^{1,27}, Philadelphia², Union^{1,27}, Westmoreland¹; 4 Apr¹ – 6 Jun¹ (2015⁸).

Subgenus Melandrena Pérez

Revision: Bouseman and LaBerge (1979).

- Andrena (Melandrena) barbara Bouseman and LaBerge, 1979 Adams^{1,3}, Bucks⁸, Centre¹, Lancaster⁸, Westmoreland¹, York⁸; 20 Mar³ 17 May³ (2018³).
- Andrena (Melandrena) carlini Cockerell, 1901³⁶ Adams^{1,3,8}, Allegheny^{1,11}, Beaver^{1,11}, Berks¹, Bradford^{8,11}, Bucks⁸, Centre^{1,2,3,5,6,7,8,11,36}, Chester¹, Clinton¹, Crawford¹, Cumberland¹, Dauphin^{1,6}, Delaware^{1,2,11}, Erie⁹, Franklin¹, Huntingdon^{3,8}, Jefferson⁶, Lancaster⁸, Lehigh¹, Luzerne^{1,2,11}, Lycoming⁸, Montgomery^{1,4,7}, Northumberland¹, Perry^{1,6}, Philadelphia^{1,2,4,11}, Pike^{1,4,11}, Sullivan¹, Susquehanna⁸, Union^{1,8}, Wayne¹, Westmoreland^{1,11}, York^{1,8}; 20 Mar³ 1 Aug¹ (2018³).
- *Andrena (Melandrena) commoda* Smith, 1879³⁶ **Adams**³, Allegheny^{1,11}, Berks¹, Butler¹, Carbon¹¹, Centre^{1,11}, Cumberland¹, Dauphin^{1,11}, Delaware², Erie¹, **Lancaster**⁵, Lehigh¹¹, Monroe¹, Montgomery^{1,7}, Northumberland¹, Philadelphia^{1,11}, Pike^{1,2,11}, Tioga^{1,11}, York¹¹; **3 Apr**³ – 25 Jul¹ (**2018**³).
- Andrena (Melandrena) confederata Viereck, 1917 Adams³, Bucks⁸, Crawford¹, Delaware^{1,2,11}; 8 May⁸ – 6 Jun¹ (2018³).
- *Andrena (Melandrena) dunningi* Cockerell, 1898 Adams³, Allegheny^{1,11}, Bradford⁸, Centre^{1,8}, Chester^{1,11}, Cumberland¹, Dauphin¹, Huntingdon⁸, Lancaster^{5,8}, Lycoming⁸, Philadelphia^{1,2}, Susquehanna⁸, Union⁸, York⁸; 20 Mar³ 21 Jun³ (2018³).
- *Andrena (Melandrena) hilaris* Smith, 1853 Adams³, Centre³, Chester^{1,11}, Dauphin¹¹, Delaware^{1,2,11}, Philadelphia^{1,11}; 21 Apr¹ 10 Aug¹ (2018³).
- Andrena (Melandrena) illini Bouseman and La Berge, 1979 Erie⁹, Westmoreland¹; 18–20 May⁹ – 2 Jun¹ (2016⁹).
- *Andrena (Melandrena) nivalis* Smith, 1853³⁶ Adams³, Blair², Bradford^{1,11}, Carbon¹¹, Centre^{1,7}, Clinton^{1,6}, Crawford¹, Cumberland^{1,11}, Dauphin^{1,2}, Elk¹, Huntingdon³, Lehigh^{1,11}, Luzerne¹, McKean², Montgomery^{1,2,11}, Northampton⁶, Perry^{1,6}, Pike^{1,2,11}, Sullivan¹, Westmoreland^{1,11}; **16** Apr⁶ 26 Jul¹ (**2017**⁷).
- Andrena (Melandrena) pruni Robertson, 1891³⁶ Adams³, Allegheny^{1,11}, Bedford², Blair², Bucks^{2,8}, Centre¹, Cumberland¹, Dauphin¹, Delaware^{1,2}, Huntingdon², Montgomery^{1,4,7}, Philadelphia¹, York¹; 23 Mar³ 20 Jun³ (2018³).
- Andrena (Melandrena) regularis Malloch, 1917³⁶ Centre¹, Clinton^{1,2,11}; 25 Apr² 12 May¹ (1966^{1,2}).
- Andrena (Melandrena) sayi Robertson, 1891 Lycoming⁸, Montgomery⁷, Philadelphia¹; 28 Apr⁸ – 26–27 Jun⁷ (2017⁷).
- Andrena (Melandrena) vicina Smith, 1853³⁶ Adams³, Allegheny¹¹, Bradford¹¹,
 Bucks⁸, Butler¹, Centre^{1,7,11}, Columbia⁵, Cumberland⁶, Dauphin^{1,6,11}, Delaware^{1,2},
 Elk⁶, Erie⁹, Forest¹, Huntingdon^{1,2,8}, Jefferson⁶, Lancaster⁸, Lehigh¹, Luzerne¹, Lycoming⁸, Monroe¹, Montgomery^{1,11}, Northumberland¹, Philadelphia^{1,4,11}, Pike^{1,4},
 Westmoreland¹; 5 Apr³ 15–16 Aug⁷ (2018³).

Subgenus Micrandrena Ashmead

Revision: Ribble (1968).

Andrena (Micrandrena) lamelliterga Ribble, 1968 (piperi group) – Beaver¹; 5 Jun¹ (1931¹).

- Andrena (Micrandrena) melanochroa Cockerell, 1898 (piperi group) Adams³, Allegheny¹, York¹; 8 May¹ – 3 Jun³ (2009³).
- Andrena (Micrandrena) nigrae Robertson, 1905 (illinoiensis group) Adams³, Allegheny¹, Northumberland¹, Philadelphia¹, Washington⁶, York¹; 24 Apr¹ – 31 May³ (2018³).
- Andrena (Micrandrena) personata Robertson, 1897 (piperi group) **Bradford**⁸, **Bucks**⁸, **Centre**⁷, Delaware², Franklin¹, Philadelphia^{1,4}, York¹; 6 Apr¹ 7 Jun^{1,8} (**2016**⁷).
- Andrena (Micrandrena) salictaria Robertson, 1905 (*illinoiensis* group)³⁶ Allegheny¹, Franklin¹, Huntingdon¹, Westmoreland¹; 9 Apr¹ 4 May¹ (1966¹).
- Andrena (Micrandrena) ziziae Robertson, 1891 (piperi group) Allegheny¹, Bucks⁸,
 Dauphin⁶, Tioga¹, Washington⁶; 9 Apr⁶ 28 May⁶ (2008⁶). Notes. All specimens identified as *A. ziziae* should be reexamined as some may be attributable to *A. vernalis*, which has recently been resurrected from synonymy (see Portman et al., in press).

Subgenus Parandrena Robertson

Revision: LaBerge and Ribble (1972).

Andrena (Parandrena) nida Mitchell, 1960 – Butler³⁰, Lawrence^{1,30}; 27 Apr¹ (1940¹).

Subgenus Plastandrena Hedicke

Revision: LaBerge (1969).

Andrena (Plastandrena) crataegi Robertson, 1893 (crataegi group)^{21,36} – Adams³, Allegheny¹, Armstrong¹, Bedford², Butler¹, Centre^{1,3,7}, Crawford¹, Cumberland^{1,2}, Dauphin^{1,2}, Delaware², Erie^{1,9}, Forest¹, Fulton¹, Huntingdon^{1,3}, Indiana¹, Lehigh¹, Luzerne¹, Monroe¹, Montgomery^{1,7}, Northumberland¹, Pike^{1,2}, Potter¹, Snyder¹, Somerset¹, Susquehanna⁸, Tioga¹, Westmoreland¹; 22 Apr³ – 8 Aug¹ (2017^{3,7}).

Subgenus Ptilandrena Robertson

Revision: LaBerge (1987).

- *Andrena* (*Ptilandrena*) *distans* Provancher, 1888³⁶ Adams³, Allegheny^{1,27}, Centre¹, Delaware^{1,2}, Jefferson⁶, Philadelphia², Union^{1,27}; 17 Apr¹ 21 Jul¹ (2017³).
- Andrena (Ptilandrena) erigeniae Robertson, 1891 Adams^{3,8}, Allegheny^{1,27}, Bradford⁸, Bucks⁸, Butler^{1,27}, Centre^{2,8}, Crawford¹, Cumberland⁶, Dauphin^{1,27}, Delaware^{1,2,4,27}, Franklin^{1,27}, Huntingdon⁸, Lycoming⁸, Perry⁶, Philadelphia¹, Pike^{1,4}, Susquehanna⁸, Union⁸, Westmoreland^{1,27}, York^{1,8,27}; 15 Apr⁸ 9 Jun² (2015⁸).

Subgenus Rhacandrena LaBerge

Revision: LaBerge (1977).

- *Andrena (Rhacandrena) brevipalpis* Cockerell, 1930 Adams³, Allegheny^{1,24}, Berks²⁴, Butler¹, Centre⁷, Chester⁶, Cumberland^{1,2,24}, Dauphin^{1,2,24}, Fayette⁶, Northampton²⁴, Northumberland²⁴, Pike^{1,24}, Somerset^{1,24}, Westmoreland^{1,24}; 14 May¹ – 10 Oct⁶ (2016^{3,7}).
- Andrena (Rhacandrena) robertsonii Dalla Torre, 1896³⁶ Adams³, Bradford^{4,8}, Bucks⁸, Cumberland^{1,24}, Dauphin¹, Delaware², Franklin¹, Huntingdon⁸, Lancaster⁸, Lycoming⁶, Montgomery⁷, Philadelphia^{1,24}, Pike^{1,2}, Potter^{1,24}, Westmoreland¹, York¹; 26 Apr³ 3 Aug⁴ (2017⁷).

Subgenus Scaphandrena Lanham

Revision: Ribble (1974).

Andrena (Scaphandrena) arabis Robertson, 1897 (scurra group)³⁶ – Adams^{3,8}, Allegheny¹, Bradford⁸, Bucks⁸, Carbon¹, Centre⁸, Dauphin¹, Delaware¹, Huntingdon^{3,8}, Lancaster⁸, Luzerne^{1,2}, Lycoming⁸, Montgomery^{1,2}, Philadelphia^{1,2}, Union⁸, Washington¹, Westmoreland¹; 29 Mar¹ – 21 Jun¹ (2017³).

Subgenus Scrapteropsis Viereck

Revision: LaBerge (1971).

- Andrena (Scrapteropsis) alleghaniensis Viereck, 1907 (alleghaniensis group) Bucks⁸, Dauphin^{1,22}, Delaware², Erie⁹, Monroe²², Philadelphia^{1,22}; 10 May² 9–11 Jun⁹ (2016⁹).
- Andrena (Scrapteropsis) daeckei Viereck, 1907 (daeckei group) Centre¹, Luzerne²², Mifflin¹; dates not reported^{1,22} (2007¹).
- Andrena (Scrapteropsis) fenningeri Viereck, 1922 (*imitatrix* group) Adams³, Philadelphia^{1,2}, Venango⁶; 20 Apr³ – 9 May¹ (2015³).
- Andrena (Scrapteropsis) ilicis Mitchell, 1960 (imitatrix group) Philadelphia^{1,22}, Westmoreland¹; 16 May¹ – 8 Jun¹ (1950¹).
- Andrena (Scrapteropsis) imitatrix Cresson, 1872 (imitatrix group)^{22,36} Adams^{3,8}, Allegheny¹, Armstrong¹, Beaver¹, Bedford¹, Blair², Bradford⁸, Bucks^{2,8}, Butler¹, Centre^{1,5,7}, Crawford^{1,6}, Cumberland¹, Dauphin^{1,6}, Delaware^{1,2}, Franklin¹, Huntingdon^{1,8}, Lancaster^{3,5,8}, Luzerne¹, Lycoming⁸, Montgomery¹, Philadelphia¹, Pike^{1,2}, Susquehanna⁸, Union⁸, Westmoreland¹, York^{1,8}; 3 Mar³ 30 Jun¹ (2018³).
- Andrena (Scrapteropsis) morrisonella Viereck, 1917 (imitatrix group) Allegheny^{1,22},
 Lancaster⁸, Lycoming⁸, Philadelphia¹, Susquehanna⁸, York^{1,8}; 24 Apr⁸ Jul¹ (2014⁸).

Subgenus Simandrena Pérez

Revision: LaBerge (1989).

Andrena (Simandrena) nasonii Robertson, 1895^{28,36} – Adams^{3,8}, Allegheny^{1,28}, Armstrong⁶, Bedford², Blair², Bradford^{1,6,8}, Bucks⁸, Butler¹, Centre^{1,2,5,7,8}, Chester^{1,2,28}, Clinton¹, Columbia⁵, Crawford¹, Cumberland^{1,6,28}, Dauphin^{1,6,28}, Delaware^{1,2,4,28}, Erie⁹, Franklin¹, Huntingdon^{2,3,8}, Jefferson⁶, Lancaster^{3,8}, Lycoming^{6,8}, Mercer⁶, Monroe^{1,4}, Montgomery^{1,2,7,28}, Perry⁶, Philadelphia^{1,2,28}, Pike^{1,4}, Potter²⁸, Susquehanna⁸, Union⁸, Warren⁶, Washington^{6,28}, Westmoreland¹, York^{8,28}; 5 Mar³ – 1 Aug⁶ (2018³).

Subgenus Taeniandrena Hedicke

Revision: LaBerge (1989).

Andrena (Taeniandrena) wilkella (Kirby, 1802)* (1912¹)³⁶ – Adams³, Allegheny^{1,28}, Bedford⁶, Berks^{2,28}, Bradford⁸, Bucks^{1,8,28}, Butler¹, Centre^{1,7,44}, Chester⁸, Clarion²⁸, Clinton¹, Columbia⁵, Dauphin¹, Delaware², Erie^{1,28}, Franklin^{1,28}, Huntingdon^{1,2,8}, Jefferson⁶, Lackawanna⁴, Lancaster^{3,5,8}, Mifflin¹, Montgomery⁸, Northampton^{6,28}, Perry¹, Philadelphia^{1,28}, Schuylkill^{1,2}, Union⁸, Westmoreland⁶, York^{1,8,28}; 21 Apr¹ – 24–25 Jul⁷ (2018³).

Subgenus Thysandrena Lanham

Revision: LaBerge (1977).

- Andrena (Thysandrena) bisalicis Viereck, 1908³⁶ Adams³, Allegheny^{1,24}, Armstrong⁶, Carbon²⁴, Centre¹, Clinton^{1,24}, Crawford², Cumberland^{1,24}, Dauphin^{1,24}, Delaware^{1,24}, Erie⁹, Forest^{1,24}, Lehigh^{1,24}, Montgomery^{1,24}, Northampton²⁴, Washington¹, Westmoreland^{1,24}; **21 Mar³ – 10 Jun⁶ (2018³)**.
- Andrena (Thysandrena) w-scripta Viereck, 1904 Allegheny¹, Armstrong^{1,24}, Bedford⁶, Carbon²⁴, Cumberland¹, Dauphin^{1,24}, Huntingdon¹, Lawrence²⁴, Lehigh^{1,24}, Luzerne¹, Northampton²⁴, Philadelphia^{1,2}, Potter, Somerset^{1,24}, York⁸; 15 Apr⁸ – 28 Aug⁶ (2015⁸).

Subgenus Trachandrena Robertson

Revision: LaBerge (1973).

- Andrena (Trachandrena) ceanothi Viereck, 1917 Adams^{1,3}, Allegheny^{1,23}, Bedford^{2,23}, Carbon²³, Centre^{1,7}, Cumberland^{1,23}, Dauphin^{1,2}, Franklin¹, Lehigh^{1,23}, Northampton²³; **23 May³ – 28 Jun–1 Jul**⁷ (**2017**⁷).
- *Andrena (Trachandrena) forbesii* Robertson, 1891^{23,36} Adams^{3,8}, Allegheny¹, Armstrong¹, Bucks⁸, Centre^{1,5,7,8}, Chester¹, Crawford¹, Cumberland¹, Dauphin^{1,6}, Dela-

Andrena (Simandrena) wheeleri Graenicher, 1904^{28,36} – Adams³, Centre¹; 16 Apr³ – 10 May¹ (2008³).

ware^{1,2}, Franklin¹, **Huntingdon⁸**, **Lancaster^{3,8}**, **Lycoming⁸**, Mifflin¹, Montgomery¹, Philadelphia¹, Pike^{1,2}, Union^{1,8}, Westmoreland¹, **York⁸**; **20 Mar³** – 14 Jul¹ (**2018**³).

- Andrena (Trachandrena) heraclei Robertson, 1897 Adams³, Lancaster⁸, Philadelphia^{1,23}, York⁸; 29 Mar³ – 21 Jun³ (2018³).
- Andrena (Trachandrena) hippotes Robertson, 1897²³ Adams³, Allegheny¹, Armstrong¹, Bedford², Centre^{2,3}, Chester¹, Cumberland¹, Dauphin^{1,2}, Delaware^{1,2}, Franklin¹, Huntingdon⁸, Lancaster⁸, Lycoming⁸, Monroe¹, Northumberland¹, Philadelphia¹, Union⁸, Westmoreland¹, York⁸; 5 Mar³ 21 Sep¹ (2018³).
- Andrena (Trachandrena) mariae Robertson, 1891 Beaver¹, Northumberland¹, Philadelphia¹; 10 May¹ – 8 Jun¹ (1951¹).
- *Andrena (Trachandrena) miranda* Smith, 1879 Bradford²³, Crawford¹, Cumberland^{1,23}, Dauphin¹, Franklin¹, Montgomery¹, Philadelphia¹, York¹; 28 Apr¹ – 14 Jul¹ (2007¹).
- *Andrena (Trachandrena) nuda* Robertson, 1891³⁶ **Adams³**, Allegheny^{1,23}, Bucks^{1,2,8}, Chester^{1,23}, Crawford¹, Dauphin¹, Delaware^{1,2,23}, **Lancaster⁵**, Philadelphia^{1,2,23}, Westmoreland¹, York^{1,8}; **17 Apr⁸** 25 Jun¹ (**2017**³).
- Andrena (Trachandrena) rehni Viereck, 1907 Allegheny^{1,23}, Carbon²³, Dauphin^{1,23}, Delaware^{1,23}, Lehigh^{1,2,23}, Northampton²³, Westmoreland^{1,23}; 22 Jun¹ 29 Jul¹ (1910¹).
- Andrena (Trachandrena) rugosa Robertson, 1891³⁶ Adams³, Allegheny^{1,23}, Blair^{1,2},
 Bradford⁸, Bucks⁸, Butler²³, Centre^{1,2,3,5,7}, Crawford¹, Cumberland^{1,23}, Dauphin^{1,23},
 Delaware¹, Erie⁹, Forest^{1,23}, Franklin⁶, Lawrence^{1,23}, Lycoming⁸, Montgomery^{1,23},
 Philadelphia^{1,23}, Pike^{1,2,4}, Potter^{1,23}, Somerset²³, Susquehanna⁸, Westmoreland^{1,23},
 York¹; 20 Mar³ 22 Jun¹ (2017³).
- *Andrena (Trachandrena) sigmundi* Cockerell, 1902 Beaver²³, Clinton^{1,2,23}, Delaware¹; 25 Apr² 27 Apr¹ (1966^{1,2}).
- Andrena (Trachandrena) spiraeana Robertson, 1895³⁶ Adams³, Allegheny^{1,23}, Bedford^{2,23}, Berks², Bucks⁸, Carbon²³, Centre^{1,7,23}, Columbia¹, Cumberland^{1,23}, Dauphin^{1,23}, Delaware^{1,2,23}, Forest¹, Huntingdon¹, Lancaster¹, Lehigh^{1,23}, Montgomery²³, Northampton²³, Philadelphia^{1,23}, Union⁸, Washington⁶, Westmoreland^{1,23}, York^{1,8}; **30** Apr⁸ 13 Jul¹ (2017⁷).
- Andrena (Trachandrena) virginiana Mitchell, 1960 Bradford²³, Centre^{1,5,7}, Cumberland^{1,23}, Lackawanna⁴, Lancaster⁵, Lehigh¹; 25 Apr⁵ – 16–17 Aug⁷ (2017⁷).

Subgenus Tylandrena LaBerge

Revision: LaBerge and Bouseman (1970).

- Andrena (Tylandrena) erythrogaster (Ashmead, 1890)²⁹ Adams³, Allegheny¹, Cumberland¹, Dauphin¹, Northumberland¹, Philadelphia¹, Potter¹, Sullivan¹; 1 May³ 7 Jun¹ (2014³).
- Andrena (Tylandrena) perplexa Smith, 1853³⁶ Adams^{3,8}, Allegheny¹, Bradford⁸, Bucks^{6,8}, Centre^{1,6}, Cumberland¹, Delaware^{1,2,4,29}, Erie⁹, Fayette^{1,29}, Huntingdon⁸,

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Indiana¹, **Jefferson**⁶, Lackawanna¹, Lancaster^{1,2,5}, **Lycoming**⁸, Monroe¹, Montgomery²⁹, Perry^{1,29}, Philadelphia^{1,4,29}, **Susquehanna**⁸, Westmoreland^{1,29}, York^{1,8,29}; 5 Mar¹ – 7 **Jul**⁶ (**2018**³).

Andrena (Tylandrena) wilmattae Cockerell, 1906 – Allegheny^{1,29}, Union^{1,29}; 19 May¹ – 2 Jul¹ (1910¹).

Subgenus Xiphandrena LaBerge

Revision: LaBerge (1971). Monotypic.

Andrena (Xiphandrena) mendica Mitchell, 1960 – Allegheny¹; 15 Jun¹ (1937¹).

Panurginae Calliopsini

Genus Calliopsis Smith

Taxonomy: Mitchell (1960); Shinn (1967).

Subgenus Calliopsis Smith s. s.

Calliopsis (Calliopsis) andreniformis Smith, 1853^{36,43} – Adams^{1,3,6,8}, Bedford⁶, Berks⁶, Blair⁶, Bradford^{1,8}, Bucks^{1,8}, Cambria⁶, Centre^{1,6,7,8,15}, Chester^{6,8}, Clarion⁶, Clearfield⁶, Crawford^{1,4,6}, Cumberland, Dauphin^{1,6}, Delaware^{1,4}, Erie^{1,9}, Franklin^{1,6}, Fulton⁴⁴, Huntingdon^{2,8}, Jefferson^{2,6}, Lackawanna, Lancaster^{3,6,8,15}, Lehigh^{1,6}, Lycoming⁸, Monroe⁶, Montgomery⁸, Perry⁶, Pike^{1,4}, Somerset⁶, Union⁸, Warren⁶, Westmoreland^{1,6}, York^{1,6,8}; 12 May⁶ – 13 Oct³ (2018³).

Perditini

Genus Perdita Smith

Taxonomy: Mitchell (1960); Timberlake (1954, 1958, 1960, 1968).

Subgenus Perdita Smith s. s.

Taxonomy: Timberlake (1958, 1960, 1968).

Perdita (Perdita) halictoides (halictoides group) Smith, 1853 – Union⁸; 15 Jun⁸ (2014⁸).

Perdita (Perdita) octomaculata (Say, 1824) (octomaculata group) – Philadelphia¹; 15 Sep¹ (1901¹).

Protandrenini

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Genus Protandrena Cockerell

Taxonomy: Mitchell (1960); Timberlake (1967, 1973, 1976); see also Scott et al. (2011).

Subgenus Heterosarus Robertson

Protandrena (Heterosarus) parvus (Robertson, 1892) – Cumberland⁴⁷; dates and year not reported⁴⁷.
 Protandrena (Heterosarus) pauper (Cresson, 1878)⁴⁷ – Lehigh¹; 29 Jun¹ – 12 Jul¹ (1901¹).

Subgenus Metapsaenythia Timberlake

Protandrena (Metapsaenythia) abdominalis (Cresson, 1878)³⁶ – locations, dates, and year not reported¹.

Subgenus Pterosarus Timberlake

Protandrena (Pterosarus) aestivalis (Provancher, 1882) – Pike⁴⁸; 22 Aug⁴⁸ (1895⁴⁸) (AMNH_BEE00237743).

Protandrena (Pterosarus) andrenoides (Smith, 1853) – Adams³, Centre¹⁵; 18 Sep³ (2010³). Protandrena (Pterosarus) compositarum (Robertson, 1893) – Adams³, Chester¹; 16 Jun³ – 18 Oct³ (2015³).

Halictidae Halictinae Augochlorini

Genus Augochlora Smith Subgenus Augochlora Smith s. s.

Augochlora (Augochlora) pura pura (Say, 1837)³⁶ – Adams^{1,3,6}, Allegheny¹, Armstrong¹, Beaver^{1,44}, Bedford⁶, Berks^{1,2,6}, Blair⁶, Bradford^{1,6,8}, Bucks^{6,8}, Butler¹, Carbon⁶, Centre^{1,6,7,8,15,44}, Chester^{1,6,8}, Clarion⁶, Clearfield^{1,4,6}, Clinton^{1,6}, Columbia^{2,5}, Crawford^{1,6}, Cumberland^{1,6}, Dauphin^{1,6}, Delaware^{1,4}, Elk¹, Erie^{1,6,9}, Fayette¹, Forest¹, Franklin⁶, Fulton⁴⁴, Huntingdon^{1,2,3,8}, Indiana^{1,6}, Jefferson^{1,6}, Juniata^{1,3,6,44}, Lackawanna^{1,4,6}, Lancaster^{1,3,5,6,8,15,44}, Lawrence¹, Lebanon^{1,4,6}, Lehigh^{1,6}, Luzerne², Lycoming⁸, McKean^{1,4}, Monroe⁶, Montgomery^{1,6,7,8,44}, Northampton⁶, Perry^{1,6}, Philadelphia^{1,2}, Pike^{1,4}, Schuylkill^{1,2}, Somerset^{1,6}, Sullivan¹, Susquehanna⁸, Tioga¹, Union⁸, Venango⁶, Washington¹, Westmoreland^{1,6}, York^{1,4,6,8}; 13 Jan¹ – 14 Nov¹ (2018³).

Genus Augochlorella Sandhouse

Taxonomy: Coelho (2004); Mitchell (1960); Ordway (1966).

- Augochlorella aurata (Smith, 1853) (aurata group)³⁶ Adams^{1,3,8}, Allegheny¹, Armstrong⁶, Beaver⁴⁴, Bedford⁶, Berks^{1,2,6}, Blair⁶, Bradford^{1,6,8}, Bucks^{1,8}, Butler¹, Cambria^{1,4,6}, Cameron⁶, Carbon¹, Centre^{1,3,6,7,8,15,44}, Chester^{1,6,8}, Clarion⁶, Clearfield⁶, Clinton¹, Columbia^{1,2,5}, Crawford^{1,4,6}, Cumberland^{1,6}, Dauphin^{1,6}, Delaware^{1,4}, Erie^{1,6,9}, Fayette¹, Franklin^{1,6}, Huntingdon^{1,3,6,8}, Indiana⁶, Jefferson⁶, Juniata⁶, Lackawanna⁴, Lancaster^{1,3,5,8,15,44}, Lebanon⁴, Lehigh^{1,6}, Luzerne^{1,2}, Lycoming⁸, Monroe^{1,4}, Montgomery^{1,4,7,8}, Montour⁶, Northampton⁶, Northumberland¹, Perry^{1,6}, Philadelphia^{1,40}, Pike^{1,4}, Schuylkill⁴, Somerset^{1,6}, Sullivan¹, Susquehanna⁸, Tioga¹, Union^{1,8}, Venango¹, Warren⁶, Washington¹, Westmoreland¹, York^{1,6,8}; Feb¹ 5 Nov² (2018³).
- Augochlorella persimilis (Viereck, 1910) (aurata group) Adams³, Allegheny¹, Bucks¹,
 Clinton⁶, Delaware^{1,40}, Huntingdon⁸, Jefferson⁶, Lehigh⁶; 29 May⁶ 15 Sep³ (2016³).

Genus Augochloropsis Cockerell

Taxonomy: Mitchell (1960).

Subgenus Paraugochloropsis Schrottky

- Augochloropsis (Paraugochloropsis) metallica sensu lato (Fabricius, 1793) Adams³, Armstrong⁶, Beaver¹, Bradford⁶, Bucks⁸, Centre^{1,7,15}, Chester^{1,8}, Clinton^{1,6}, Columbia⁵, Dauphin^{1,6}, Delaware^{1,4}, Elk¹, Franklin⁶, Huntingdon^{1,2,3,8}, Lackawanna², Lebanon¹, Lehigh¹, Luzerne¹, Lycoming⁶, Monroe¹, Montgomery⁸, Northampton⁶, Perry¹, Philadelphia¹, Pike¹, Union⁸, York^{1,6}; 17 Apr³ 21 Oct³ (2017³). Notes. We can not rule out the possibility that the nominotypical subspecies of *A. metallica* does not occur in Pennsylvania. Thus, we present records for specimens not identified to the subspecies level here.
- Augochloropsis (Paraugochloropsis) metallica (Fabricius, 1793) fulgida (Smith, 1853) Centre⁷, Erie⁹; 18–20 May⁹ – 16–17 Aug⁷ (2017⁷).
- Augochloropsis (Paraugochloropsis) sumptuosa (Smith, 1853) Chester¹, Clinton⁶, Dauphin¹, Elk⁶, Juniata⁶; 16 Apr¹ – 2 Jul⁶ (2008⁶).

Halictini s. l.

Genus Agapostemon Guerin-Meneville

Taxonomy: Mitchell (1960); Roberts (1972).

Subgenus Agapostemon Guerin-Meneville s. s.

- Agapostemon (Agapostemon) sericeus (Förster, 1771) (sericeus group)⁴² Adams³, Allegheny¹, Armstrong^{1,6}, Beaver¹, Bradford⁸, Bucks^{1,8}, Centre^{1,15,44}, Columbia¹, Cumberland¹, Dauphin^{1,6}, Delaware¹, Elk¹, Erie^{1,6}, Fayette¹, Huntingdon^{1,2,3}, Lancaster^{3,8}, Lehigh¹, Lycoming⁸, Monroe¹, Montgomery^{1,8,44}, Northumberland¹, Perry¹, Philadelphia^{1,4}, Somerset¹, Union^{1,8}, Warren⁶, Washington¹, York¹; 1 Apr¹ – 30 Oct¹ (2015⁸).
- Agapostemon (Agapostemon) splendens (Lepeletier, 1841) (splendens group)⁴² Adams³, Allegheny¹, Centre¹, Crawford¹, Delaware¹, Erie¹, Fulton⁴⁴, Philadelphia¹; **5** Jul³ 29 Aug³ (2012³).
- Agapostemon (Agapostemon) texanus Cresson, 1872 (splendens group)⁴² Adams^{1,3,8}, Allegheny¹, Armstrong^{1,6}, Bedford⁶, Bucks⁸, Centre¹, Chester⁶, Cumberland¹, Dauphin⁶, Delaware^{1,4}, Erie^{1,6}, Franklin⁶, Huntingdon⁸, Lancaster^{3,8}, Lehigh¹, Lycoming⁸, Montgomery⁸, Northampton⁶, Northumberland¹, Philadelphia^{1,4}, Pike^{1,4}, Schuylkill⁶, Union⁸, Westmoreland¹, York^{6,8}; 5 Apr³ 26 Oct³ (2018³).
- Agapostemon (Agapostemon) virescens (Fabricius, 1775) (splendens group)^{42,36} Adams^{1,3,8}, Allegheny¹, Armstrong⁶, Beaver¹, Bedford⁶, Berks^{1,2}, Bradford⁸, Bucks^{1,8}, Butler¹, Cambria⁶, Centre^{1,6,8,15,44}, Chester^{6,8}, Clarion⁶, Clearfield^{1,6}, Clinton^{1,6}, Columbia^{1,2,5}, Crawford^{1,4}, Cumberland¹, Dauphin^{1,2,6}, Delaware^{1,4}, Elk⁶, Erie^{1,6,9}, Fulton⁴⁴, Greene¹, Huntingdon^{1,2,8}, Jefferson⁶, Juniata⁶, Lackawanna^{4,6}, Lancaster^{1,3,4,5,6,8,15}, Lehigh^{1,6}, Luzerne¹, Lycoming⁸, McKean⁶, Mifflin¹, Montgomery^{1,7,8}, Montour⁶, Northampton¹, Perry^{1,6}, Philadelphia¹, Pike^{1,4}, Somerset⁶, Sullivan¹, Tioga¹, Union⁸, Warren⁶, Washington^{1,6}, Westmoreland^{1,4,6}, York^{1,6,8}; 22 Mar¹ 26 Oct³ (2018³).

Genus Halictus Latreille

Revision: Mitchell (1960); Sandhouse (1941).

Subgenus Nealictus Pesenko

Halictus (Nealictus) parallelus Say, 1837 – Adams³, Allegheny¹, Armstrong⁶, Bedford⁶,
Bradford⁶, Bucks⁸, Clarion⁶, Crawford⁶, Dauphin⁶, Erie⁶, Juniata⁶, Lancaster³,
Philadelphia¹, Somerset⁶, Warren⁶, Wayne¹, Westmoreland⁶; 30 Apr⁸ – 20 Aug⁶ (2013³).

Subgenus Odontalictus Robertson

Halictus (Odontalictus) ligatus Say, 1837³⁶ – Adams^{1,3,6,8}, Allegheny^{1,6}, Beaver^{1,44}, Bedford⁶, Berks^{2,6}, Blair⁶, Bradford^{1,4,6,8}, Bucks^{1,6,8}, Butler¹, Carbon^{1,6}, Centre^{1,3,5,6,7,8,15,44}, Chester^{6,8}, Clarion⁶, Clearfield^{1,4}, Clinton^{1,6}, Columbia^{2,5}, Crawford^{1,6}, Cumberland^{1,6}, Dauphin^{1,6}, Delaware^{1,4}, Elk⁶, Erie^{6,9}, Forest¹, Franklin⁶, Fulton⁴⁴, Hunt-

ingdon^{1,2,8}, Jefferson^{2,6}, Juniata^{1,6,44}, Lackawanna^{4,6}, Lancaster^{1,2,3,4,5,6,8,15}, Lebanon⁴, Lehigh^{1,6}, Luzerne^{1,2}, Lycoming^{1,8}, McKean⁶, Monroe^{1,2,6}, Montgomery^{1,7,8}, Northampton⁶, Northumberland¹, Perry^{1,4,6}, Philadelphia^{1,4}, Pike^{1,4}, Schuylkill^{4,6}, Snyder⁴, Somerset⁶, Sullivan⁴, Tioga¹, Union⁸, Warren⁶, Washington⁶, York^{4,6,8}; 11 Apr³ – 25 Oct³ (2018³).

Subgenus Protohalictus Pesenko

Halictus (Protohalictus) rubicundus (Christ, 1791)³⁶ – Adams^{1,3,8}, Allegheny¹, Armstrong⁶, Beaver⁴⁴, Bedford⁶, Berks^{2,6}, Bradford⁸, Bucks^{1,8}, Butler¹, Cambria⁶, Centre^{1,5,7,15,44}, Chester^{6,8}, Clarion⁶, Clinton¹, Columbia⁵, Cumberland^{1,6}, Dauphin^{1,4,6}, Delaware^{1,4}, Erie⁹, Forest¹, Franklin¹, Fulton⁴⁴, Huntingdon^{3,8}, Jefferson⁶, Juniata⁶, Lancaster^{3,5,8,15}, Lehigh¹, Luzerne¹, Lycoming⁸, Monroe^{1,2}, Montgomery^{1,7,8}, Northampton⁶, Northumberland¹, Perry^{1,6}, Philadelphia¹, Somerset⁶, Susquehanna¹, Tioga^{1,4}, Union⁸, Warren⁶, Westmoreland¹, York⁸; 13 Apr¹ – 16 Oct³ (2018³).

Subgenus Seladonia Robertson

Halictus (Seladonia) confusus confusus Smith, 1853³⁶ – Adams^{1,3,6,8}, Allegheny¹, Beaver⁴⁴,
Bedford⁶, Berks⁶, Bradford^{1,6,8}, Bucks^{1,4,6,8}, Cambria^{1,4}, Carbon¹, Centre^{1,5,6,7,8,15,44},
Chester⁸, Clinton¹, Columbia⁵, Crawford^{1,4}, Cumberland¹, Dauphin^{1,6}, Delaware^{1,4}, Erie^{1,6,9}, Huntingdon^{2,3,8}, Jefferson^{2,6}, Juniata^{6,44}, Lackawanna⁴, Lancaster^{1,2,3,8,15}, Lehigh^{1,6}, Lycoming⁸, McKean⁶, Monroe¹, Montgomery^{1,8}, Northumberland¹, Perry¹, Philadelphia^{1,4}, Pike^{1,4}, Somerset⁶, Sullivan¹, Susquehanna¹, Tioga¹, Union⁸, Wayne¹, Westmoreland^{1,4,6,8}; 2 Apr⁶ – 5 Nov¹ (2017^{3,7}).

Subgenus Vestitohalictus Blüthgen

Halictus (Vestitohalictus) tectus Radoszkowski, 1876* (2005^{1,4}) – Philadelphia^{1,4}, **Somerset**⁶; **1 Aug**⁶ – 24 Aug^{1,4} (**2008**⁶).

Genus Lasioglossum Curtis

Taxonomy: Gibbs (2010, 2011, 2012); Gibbs et al. (2013); Knerer and Atwood (1964); McGinley (McGinley 1986, 2003); Mitchell (1960).

Subgenus *Dialictus* Robertson

Taxonomy: Gibbs (2010, 2011, 2012); Mitchell (1960).

Lasioglossum (Dialictus) abanci (Crawford, 1932) (viridatum group) – Adams³, Bradford^{1,8}, Carbon¹, Centre^{7,8}, Franklin¹, Huntingdon⁸, Lancaster⁸, Lehigh¹, Lycoming⁸, Perry¹, Union⁸; 23 Apr⁸ – 24 Aug⁸ (2017³).

- Lasioglossum (Dialictus) admirandum (Sandhouse, 1924) (viridatum group)³⁶ Adams^{1,3,8}, Beaver⁴⁴, Bradford^{1,8}, Bucks⁸, Centre^{1,15,44}, Chester^{1,8}, Clearfield¹, Clinton¹, Crawford¹, Cumberland¹, Dauphin¹, Delaware¹, Erie⁹, Franklin¹, Fulton⁴⁴, Huntingdon³, Juniata¹, Lancaster^{1,3,8,44}, Lehigh¹, Luzerne¹, Mifflin¹, Montgomery⁸, Perry¹, Philadelphia¹, Pike¹, Sullivan¹, Westmoreland¹, York^{1,8}; 2 Apr³ 21 Oct³ (2017³).
- Lasioglossum (Dialictus) albipenne (Robertson, 1890)³⁶ Adams³, Bucks⁸, Centre⁷, Clinton¹, Columbia⁵, Crawford⁴, Delaware¹, Lancaster⁸, Lehigh¹, Luzerne¹, Montgomery¹; 5 May¹ – 19–20 Aug⁴ (2017⁷).
- Lasioglossum (Dialictus) anomalum (Robertson, 1892) Adams³, Bucks⁸, Lycoming⁸, Pike¹; 28 Apr⁸ 15 Sep³ (2016³).
- Lasioglossum (Dialictus) apocyni (Mitchell, 1960) (viridatum group) Centre⁷, Montgomery⁷, Westmoreland⁴; 31 May–1 Jun⁷ – 16–17 Aug⁷ (2017⁷).
- *Lasioglossum (Dialictus) atwoodi* Gibbs 2010 (*viridatum* group) locations, dates, and year not reported¹⁸.
- Lasioglossum (Dialictus) bruneri (Crawford, 1902)³⁶ Adams³, Bucks⁸, Centre⁸, Columbia⁵, Dauphin¹, Delaware⁴, Erie⁹, Huntingdon⁸, Lycoming⁸, Philadelphia^{1,4}, York⁸; 24 Apr⁸ – 21 Sep³ (2017³).
- *Lasioglossum (Dialictus) callidum* (Sandhouse, 1924) Adams³, Centre⁵, Chester⁸, Delaware⁴, Lancaster^{3,5}, Montgomery⁸; 13 Apr³ 26 Oct³ (2018³). Notes. Older records for *L. versatum*, especially pre-2010 determinations, may be attributable to *L. callidum* (see Gibbs 2010).
- Lasioglossum (Dialictus) cattellae (Ellis, 1913) Adams³, Bucks⁸; 17 Apr⁸ 1 Aug⁸ (2008⁸).
- Lasioglossum (Dialictus) cephalotes (Dalla Torre, 1896) (cephalotes group) locations, dates, and year not reported³⁶.
- Lasioglossum (Dialictus) coeruleum (Robertson, 1893)³⁶ Adams³, Bradford¹, Bucks⁸, Butler¹, Centre^{1,15,44}, Clinton¹, Dauphin¹, Delaware^{1,4}, Erie⁹, Fulton⁴⁴, Huntingdon⁸, Jefferson⁶, Lancaster³, Lehigh¹, Lycoming⁸, Monroe¹, Montgomery^{1,7}, Perry¹, Philadelphia¹, Susquehanna⁸, Union⁸, York⁸; 17 Apr¹ – 4 Sep¹ (2017⁷).
- Lasioglossum (Dialictus) coreopsis (Robertson, 1902) Adams³, Bradford⁸, Bucks⁸, Pike^{1,4}; 30 May^{1,4} 18 Sep⁸ (2015³).
- Lasioglossum (Dialictus) cressonii (Robertson, 1890)^{18,36} Adams³, Allegheny¹, Bradford^{1,8}, Bucks⁸, Centre^{1,7,8}, Chester⁸, Clinton¹, Crawford¹, Cumberland¹, Dauphin¹, Delaware^{1,4}, Erie⁹, Fulton¹, Huntingdon^{1,2,8}, Indiana¹, Lackawanna¹, Lancaster⁸, Lebanon⁴, Lehigh¹, Lycoming⁸, Monroe¹, Montgomery⁸, Perry¹, Philadelphia¹, Pike¹, Susquehanna⁸, Union⁸, Washington¹, York⁸; 15 Apr⁸ 23 Oct³ (2017^{3,7}).
- Lasioglossum (Dialictus) dreisbachi (Mitchell, 1960) Centre⁵³; 28 Sep⁵³ (2018⁵³).
 Lasioglossum (Dialictus) ellisiae (Sandhouse, 1924) (tegulare group)¹⁸ Bucks⁸, Carbon¹⁷, Lehigh¹⁷, Erie⁹, Monroe¹⁷, Montgomery⁸, Northampton¹⁷, Somerset¹⁷, Union⁸; 9–11 Jun⁹ 19 Aug⁸ (2016⁹). Notes. Older records for L. tegulare,

especially pre-2009 determinations, may be attributable to *L. ellisiae* (see Gibbs 2009).

- Lasioglossum (Dialictus) ephialtum Gibbs, 2010 (viridatum group)¹⁸ Adams³, Bradford⁸, Bucks⁸, Centre^{5,7,8}, Erie⁹, Huntingdon⁸, Lancaster⁸, Lycoming⁸, Montgomery^{4,7,8}, Philadelphia¹⁷, Union⁸, York⁸; 15 Apr⁸ – 9 Oct³ (2017^{3,7}).
- Lasioglossum (Dialictus) georgeickworti Gibbs, 2011 (viridatum group) Lancaster⁸, Lycoming⁸, Montgomery⁸, York⁸; 11 Jun⁸ – 24 Jul⁸ (2015⁸).
- Lasioglossum (Dialictus) gotham Gibbs, 2011 Adams³, Bucks^{8,18}, Centre⁸, Columbia⁵, Erie⁹, Huntingdon^{2,8,18}, Lancaster^{3,5}, Lycoming⁸, Union⁸, York⁸; 21 Mar³ – 26 Sep³ (2017³).
- Lasioglossum (Dialictus) heterognathus (Mitchell, 1960)^{18,36} Centre^{1,7,8,36}, Cumberland¹, Huntingdon⁸, Lehigh¹, Luzerne¹, Lycoming⁸, Union⁸; 28 Apr^{1,8} – 28 Sep⁸ (2017⁷).
- Lasioglossum (Dialictus) hitchensi Gibbs, 2012¹⁸ Adams^{3,8}, Bradford⁸, Bucks⁸, Centre^{5,7,8}, Chester⁸, Columbia⁵, Delaware⁴, Erie⁹, Huntingdon⁸, Lancaster^{3,5,8}, Lehigh¹, Lycoming⁸, Montgomery^{4,8}, Perry¹, Tioga⁴, Union⁸, York⁸; 2 Apr³ 26 Oct³ (2018³).
- Lasioglossum (Dialictus) illinoense (Robertson, 1892)^{18,36} Adams³, Bucks⁸, Centre⁸, Chester⁸, Crawford¹, Cumberland¹, Dauphin^{1,17}, Delaware^{1,4}, Erie⁹, Franklin¹, Huntingdon⁸, Lancaster⁵, Lehigh¹, Lycoming⁸, Montgomery^{2,7,8}, Union⁸, York⁸; 23 Apr⁸ 19 Oct³ (2017^{3,7}).
- Lasioglossum (Dialictus) imitatum (Smith, 1853)^{18,36} Adams^{1,3,8}, Berks², Blair^{1,2}, Bradford^{1,4,8}, Bucks⁸, Centre^{1,5,7,8,15,44}, Chester⁸, Clinton¹, Columbia^{2,5}, Crawford¹, Cumberland¹, Dauphin^{1,17}, Delaware^{1,4}, Erie⁹, Franklin¹, Huntingdon^{1,2,8}, Lack-awanna⁴, Lancaster^{1,3,8}, Lebanon¹, Lehigh¹, Luzerne², Lycoming⁸, Mifflin¹, Monroe^{1,2}, Montgomery^{1,8}, Northampton¹, Perry^{1,4}, Philadelphia^{1,4}, Pike¹, Sullivan¹, Union^{1,8}, York^{1,4,8}; 18 Apr³ 21 Oct³ (2017³).
- Lasioglossum (Dialictus) izawsum Gibbs, 2011 (platyparium group) Westmoreland¹⁸; 29 May¹⁸ (1945¹⁸).
- Lasioglossum (Dialictus) katherineae Gibbs, 2011 (viridatum group) Adams³; 10 Apr³ 11 Sep³ (2014³).
- Lasioglossum (Dialictus) laevissimum (Smith, 1853)¹⁸ Adams³, Bradford^{1,8}, Bucks⁸, Centre^{1,5,7,8}, Clinton¹, Columbia⁵, Crawford¹, Dauphin¹, Delaware¹, Huntingdon⁸, Lancaster³, Sullivan¹, Susquehanna⁸, Union⁸; 25 Apr⁵ – 9 Oct³ (2018³).
- Lasioglossum (Dialictus) leucocomus (Lovell, 1908) (pilosum group) Adams³, Bradford⁸, Bucks⁸, Centre⁷, Lancaster⁸, Montgomery⁸; 1 Jun⁸ – 19 Oct³ (2018³).
 Notes. Older records for *L. pilosum*, especially pre-2010 determinations, may be attributable to *L. leucocomus* (see Gibbs 2010, 2011).
- Lasioglossum (Dialictus) lineatulum (Crawford, 1906)^{18,36} Adams³, Bradford^{1,8}, Centre^{1,5,7,8,44}, Clinton¹, Columbia⁵, Crawford¹, Dauphin¹, Erie⁹, Lancaster⁸, Lehigh¹, Lycoming⁸, Montgomery¹, Northumberland¹, Perry⁴, Philadelphia¹, Pike¹, Sullivan¹, Union⁸; 17 Apr¹ 24 Aug⁸ (2017⁷).

- Lasioglossum (Dialictus) lionotus (Sandhouse, 1923) (cephalotes group) Bradford⁸, Centre¹⁵, Dauphin¹, Lebanon¹, Lehigh^{1,4}, Schuylkill¹; 28 Apr¹ – 15 Sep⁸ (2015⁸).
- Lasioglossum (Dialictus) marinum (Crawford, 1904) Delaware¹; 18 Jul¹ (1901¹).
- Lasioglossum (Dialictus) michiganense (Mitchell, 1960) (platyparium group) Erie⁹, York⁸; 15 Apr⁸ 18–20 May⁹ (2016⁹).
- Lasioglossum (Dialictus) nigroviride (Graenicher, 1911)¹⁸ **Bucks**⁸, Centre^{1,7}, Forest¹, Jefferson², Lackawanna¹, Luzerne², **Lycoming**⁸, Monroe¹, Pike¹; **28** Apr⁸ 5 Sep² (**2017**⁷).
- Lasioglossum (Dialictus) oblongum (Lovell, 1905) (viridatum group)³⁶ Bradford¹, Bucks⁸, Centre¹, Delaware¹, Erie⁶, Forest¹, Huntingdon⁸, Lackawanna¹, Lancaster⁸, Lehigh¹, Lycoming⁸, Monroe¹, Sullivan¹, Susquehanna⁸, Union⁸, Westmoreland¹; 21 Apr⁸ – 23 Sep⁸ (2015⁸).
- Lasioglossum (Dialictus) obscurum (Robertson, 1892) (viridatum group)^{18,36} Adams^{1,3},
 Bucks⁸, Centre^{1,8}, Chester⁸, Columbia⁵, Cumberland¹, Dauphin¹, Delaware^{1,4},
 Erie⁹, Montgomery⁸, Northumberland¹, Perry¹, Westmoreland¹, York⁸; 16 Apr¹ 28 Sep⁸ (2017³).
- Lasioglossum (Dialictus) oceanicum (Cockerell, 1916)^{18,36} Adams^{3,8}, Berks², Bradford¹, Bucks⁸, Centre^{1,3}, Chester⁸, Clinton¹, Crawford¹, Cumberland¹, Dauphin¹, Delaware¹, Erie⁹, Huntingdon^{1,8}, Lancaster^{1,3}, Lehigh¹, Lycoming⁸, Monroe^{2,4}, Montgomery^{1,8}, Philadelphia¹, York⁸; 10 May¹ – 28 Sep⁸ (2016^{5,9}).
- Lasioglossum (Dialictus) paradmirandum (Knerer & Atwood, 1966) (viridatum group)¹⁸
 Adams³, Berks², Bradford⁸, Bucks^{8,17}, Carbon¹, Centre^{5,7}, Huntingdon⁸, Lackawanna⁴, Lancaster^{5,8}, Lehigh¹, Lycoming⁸, Montgomery^{8,17}, Union⁸, York⁸; 3
 Apr³ 18 Sep⁸ (2016^{5,7}).
- Lasioglossum (Dialictus) perpunctatum (Ellis, 1913)³⁶ Adams³, Beaver⁴⁴, Bradford³, Centre^{1,7,8,44}, Erie⁹, Fulton⁴⁴, Huntingdon⁸, Juniata⁴⁴, Lancaster^{8,44}, Monroe², Union⁸; 18–20 May⁹ – 24 Aug⁸ (2017⁷).
- Lasioglossum (Dialictus) pilosum (Smith, 1853) (pilosum group)^{18,36} Adams^{1,3,8}, Beaver⁴⁴, Berks^{1,2}, Bradford⁸, Bucks^{1,4,8}, Centre^{1,5,6,15,44}, Chester^{1,8}, Clinton^{1,6}, Columbia^{2,5}, Cumberland¹, Dauphin¹, Delaware^{1,4}, Erie⁹, Franklin^{1,6}, Fulton⁴⁴, Huntingdon⁸, Lackawanna⁴, Lancaster^{3,5,6,8,15,44}, Lehigh¹, Luzerne¹, Lycoming⁸, Monroe¹, Montgomery^{1,2,8}, Northumberland¹, Perry¹, Philadelphia^{1,4}, Pike¹, Sullivan¹, Union⁸, York⁸; 23 Mar³ 26 Oct³ (2018³). Notes. Older records for *L. pilosum*, especially pre-2010 determinations, may be attributable to *L. leucocomus* (see Gibbs 2010, 2011).
- Lasioglossum (Dialictus) planatum (Lovell, 1905) (viridatum group) Adams³, Bradford⁸, Bucks⁸, Crawford⁴, Montgomery⁸; 6 May⁸ – 21 Oct³ (2014⁸).
- Lasioglossum (Dialictus) platyparium (Robertson, 1895) (platyparium group)¹⁸ Adams³, Bradford⁸, Delaware⁴, Huntingdon⁸, Lancaster^{3,8}, Lycoming⁸, Montgomery⁸, York⁸; 14 Apr³ – 23 Oct³ (2017³).
- Lasioglossum (Dialictus) pruinosum (Robertson, 1892) (pilosum group) Beaver⁴⁴, Centre⁴⁴; dates not reported⁴⁴ (2010 20¹²⁴⁴).
- Lasioglossum (Dialictus) rozeni Gibbs, 2011 (platyparium group) Adams³, Bucks⁸, Chester⁸, Montgomery⁸; 5 Apr³ 26 Jul⁸ (2017³).

- Lasioglossum (Dialictus) simplex (Robertson, 1901)³⁶ (platyparium group) Centre¹; Aug¹ (1945¹).
- Lasioglossum (Dialictus) smilacinae (Robertson, 1897)¹⁸ Adams³, Erie⁹, Lehigh⁴, Lycoming⁸, Montgomery⁸, Union⁸, York⁸; 15 Apr⁸ – 6 Jul⁸ (2017³).
- Lasioglossum (Dialictus) subviridatum (Cockerell, 1938) (viridatum group) Adams³, Bradford⁸, Bucks⁸, Centre^{7,8}, Delaware⁴, Erie⁹, Huntingdon⁸, Lancaster⁸, Lycoming⁸, Montgomery⁸, Susquehanna⁸, Union⁸, York⁸; 15 Apr⁸ – 18 Oct³ (2017⁷).
- Lasioglossum (Dialictus) taylorae Gibbs, 2010 (viridatum group) Bucks⁸, Delaware⁴, York⁸; 15 Apr⁸ 13–26 Jul⁴ (2015⁸).
- Lasioglossum (Dialictus) tegulare (Robertson, 1890) (tegulare group)³⁶ Adams^{3,8}, Berks², Bradford^{1,8}, Bucks⁸, Centre^{7,8,15,44}, Chester⁸, Columbia⁵, Crawford⁴, Cumberland¹, Dauphin¹, Delaware^{1,4}, Erie^{6,9}, Franklin¹, Fulton⁴⁴, Huntingdon⁸, Juniata^{1,44}, Lancaster^{3,8,44}, Lehigh¹, Luzerne¹, Lycoming^{8,44}, Montgomery^{1,8}, Perry¹, Philadelphia^{1,4}, Schuylkill⁴, Somerset¹, Susquehanna⁸, Union⁸, York⁸; 5 Apr³ 24 Oct³ (2018³). Notes. Older records for *L. tegulare*, especially pre-2009 determinations, may be attributable to *L. ellisiae* (see Gibbs 2009).
- Lasioglossum (Dialictus) timothyi Gibbs, 2010 Centre⁷, Lycoming⁸, Union⁸; 27 Apr⁸ – 29–30 Jun⁷ (2017⁷).
- Lasioglossum (Dialictus) trigeminum Gibbs, 2011 Adams^{3,8}, Bucks⁸, Centre⁷, Chester⁸, Delaware⁴, Erie⁹, Huntingdon⁸, Lancaster^{3,8}, Lycoming⁸, Montgomery⁸, York⁸; 29 Mar³ – 19 Oct³ (2017^{3,7}).
- Lasioglossum (Dialictus) versans (Lovell, 1905)¹⁸ (ruidosense group) Adams³, Bradford^{1,8}, Centre^{1,7,8,44}, Columbia⁵, Dauphin¹, Erie⁹, Huntingdon⁸, Lackawanna⁴, Lancaster⁸, Lycoming⁸, Pike¹, Sullivan¹, Susquehanna⁸, Union⁸, York⁸; 23 Apr⁸ – 24 Oct³ (2016^{3,7,9}).
- Lasioglossum (Dialictus) versatum (Robertson, 1902)^{18,36} Adams^{1,3,8}, Beaver⁴⁴, Bradford^{1,8}, Bucks⁸, Centre^{1,5,7,8,44}, Chester⁸, Clearfield^{1,4}, Clinton¹, Columbia⁵, Crawford^{1,4}, Dauphin¹, Delaware^{1,4}, Erie⁹, Franklin¹, Huntingdon^{2,3,8}, Juniata³, Lackawanna^{1,4}, Lancaster^{1,3,8}, Lehigh¹, Lycoming⁸, Monroe⁴, Montgomery^{1,7,8}, Northumberland¹, Perry¹, Philadelphia^{1,4}, Pike^{1,4}, Schuylkill⁴, Sullivan¹, Susquehanna⁸, Tioga⁴, Union⁸, Westmoreland¹, York^{1,8}; 29 Mar¹ 6 Nov³ (2017^{3,7}). Notes. Older records for *L. versatum*, especially pre-2010 determinations, may be attributable to *L. callidum* (see Gibbs 2010).
- Lasioglossum (Dialictus) viridatum (Lovell, 1905) (viridatum group) Adams³, Centre⁴⁴, Erie⁶, Fulton⁴⁴, Lancaster^{1,8,44}, Lycoming⁸, Union⁸, York⁸; 15 Apr⁸ – 23 Jul⁶ (2015⁸).
- Lasioglossum (Dialictus) weemsi (Mitchell, 1960)¹⁸ Adams³, Bradford⁸, Bucks⁸, Centre⁸, Chester⁸, Columbia⁵, Delaware⁴, Erie⁹, Huntingdon⁸, Lancaster^{3,8}, Lycoming⁸, Monroe⁴, Montgomery⁸, Philadelphia¹⁷, Union⁸, York⁸; 21 Apr³ 15 Oct³ (2017³).
- Lasioglossum (Dialictus) zephyrus (Smith, 1853)^{18,36} Adams^{3,8}, Beaver⁴⁴, Blair², Brad-ford^{1,8}, Bucks⁸, Centre^{1,8}, Chester⁸, Columbia^{2,5}, Cumberland¹, Dauphin¹, Delaware¹, Erie^{1,9}, Fulton⁴⁴, Huntingdon⁸, Lancaster^{3,5,8,44}, Lehigh¹, Lycoming⁸, Montgomery^{1,8}, Northumberland¹, Philadelphia^{1,4}, Union^{1,8}, York⁸; 10 Apr³ 23 Oct³ (2017³).

Subgenus Evylaeus Robertson

Taxonomy: Gibbs et al. (2013).

Lasioglossum (Evylaeus) cinctipes (Provancher, 1888)³⁶ – Allegheny²⁰, Centre^{1,5,7}, Chester⁸, Cumberland¹, Dauphin¹, Erie⁹, Lehigh²⁰, Susquehanna^{1,20}, Tioga²⁰, Union⁸, Westmoreland²⁰; 28 Apr⁸ – 14 Oct¹ (2017⁷).

Subgenus Hemihalictus Cockerell

Revision: Gibbs et al. (2013).

- Lasioglossum (Hemihalictus) birkmanni (Crawford, 1906) Adams³, Allegheny²⁰, Dauphin¹, Erie²⁰, Lackawanna⁴, Lancaster⁸, Union⁸; 23 Apr³ – 21 Jul⁸ (2017³). Notes. Older records for *L. macoupinense*, especially pre-2013 determinations, are attributable to *L. birkmanni* (see Gibbs et al. 2013).
- Lasioglossum (Hemihalictus) foxii (Robertson, 1895) Adams³, Allegheny²⁰, Bucks⁸, Centre⁷, Clinton²⁰, Dauphin¹, Erie²⁰, Fayette²⁰, Lehigh¹, Lycoming⁸, Philadelphia⁴, Pike²⁰, Potter²⁰, Schuylkill², Union⁸, Westmoreland²⁰, York⁸; 2 Apr³ – 2 Jul⁸ (2017^{3,7}).
- Lasioglossum (Hemihalictus) inconditum (Cockerell, 1916) Susquehanna⁸; 6 May⁸ (2014⁸).
- Lasioglossum (Hemihalictus) macoupinense (Robertson, 1895) Adams³, Allegheny²⁰, Bucks^{1,8}, Erie²⁰, Susquehanna⁸; 30 Apr⁸ – 26 Jul³ (2014⁸). Notes. Older records for *L. macoupinense*, especially pre-2013 determinations, are attributable to *L. birk-manni* (see Gibbs et al. 2013).
- Lasioglossum (Hemihalictus) nelumbonis (Robertson, 1890) Pike^{1,4}; 29 May^{1,4} (2005¹).
- Lasioglossum (Hemihalictus) pectinatum (Robertson, 1890) Adams³, Bucks^{8,20}, Lancaster²⁰; 10 Jul⁸ – 20 Oct³ (2016³).
- Lasioglossum (Hemihalictus) pectorale (Smith, 1853) Adams^{1,3}, Allegheny²⁰, Bucks^{1,2,8}, Centre⁴⁴, Columbia², Cumberland¹, Erie⁹, Franklin¹, Huntingdon^{1,2,8}, Lehigh¹, Lycoming⁸, Philadelphia²⁰, Westmoreland²⁰; 16 Apr³ – 25 Aug³ (2017³).

Subgenus Lasioglossum Curtis s. s.

Revision: McGinley (1986).

- Lasioglossum (Lasioglossum) acuminatum McGinley, 1986 (forbesii group) Adams³, Carbon³², Centre^{1,7,8,15}, Clinton¹, Huntingdon^{1,32}, Lehigh^{1,32}, Lycoming⁸, Monroe^{1,32}, Northampton³², Pike^{1,2,32}, Somerset¹, Union⁸; 26 Apr³ – 7 Oct¹ (2017⁷).
- Lasioglossum (Lasioglossum) athabascense (Sandhouse, 1933)³⁶ Adams¹, Allegheny^{1,32}, Bradford¹, Carbon³², Centre¹, Clearfield^{1,4}, Clinton¹, Crawford¹, Cumberland^{1,32}, Dauphin^{1,32}, Lehigh^{1,32}, Sullivan¹, Wyoming³²; 11 May¹ – 29 Aug¹ (2007^{1,4}).

- Lasioglossum (Lasioglossum) coriaceum (Smith, 1853)³⁶ Adams³, Allegheny^{1,32}, Beaver^{1,32,44}, Bradford^{1,8}, Bucks⁸, Butler^{1,32}, Centre^{1,3,7,8,32}, Clinton¹, Crawford^{1,32}, Cumberland^{1,32}, Dauphin^{1,32}, Delaware^{1,4,32}, Elk¹, Erie^{1,6,9,32}, Fayette^{1,32}, Forest¹, Huntingdon^{1,8}, Jefferson¹, Lancaster¹, Lehigh^{1,32}, Lycoming⁸, Monroe¹, Montgomery^{7,8}, Northumberland^{1,32}, Perry¹, Pike^{1,4,32}, Sullivan¹, Susquehanna⁸, Tioga¹, Union^{1,32}, Washington¹, Westmoreland^{1,32}, York^{1,8,32}; 16 Apr¹ 23 Oct³ (2017^{3,7}).
- Lasioglossum (Lasioglossum) forbesii (Robertson, 1890) (forbesii group)³⁶ Adams³, Cumberland¹, Fayette^{1,32}, Westmoreland^{1,32}; 16 Apr³ 22 Jul¹ (2015³).
- Lasioglossum (Lasioglossum) fuscipenne (Smith, 1853) Adams³, Bradford¹, Bucks⁸, Centre¹, Crawford¹, Cumberland¹, Dauphin^{1,32}, Delaware³², Huntingdon³, Montgomery⁷, York^{1,8,32}; 30 Apr⁸ – 23 Oct³ (2017⁷).

Subgenus Leuchalictus Warncke

Revision: McGinley (1986).

- Lasioglossum (Leuchalictus) leucozonium (Schrenk, 1781)* (2007¹) Adams^{1,3}, Beaver⁴⁴, Bradford^{1,4,8}, **Bucks⁸**, Centre^{7,15,44}, Crawford^{1,4}, Erie⁹, Lackawanna⁴, Lancaster⁴⁴, Lycoming⁸, Union⁸; **31 May–1 Jun⁷ 19 Sep³ (2017**⁷).
- Lasioglossum (Leuchalictus) zonulum (Smith, 1848)* (2002³) Adams³, Bradford^{1,8}, Centre⁷, Crawford¹, Erie^{6,9}, Huntingdon³, Lackawanna⁴, Lycoming⁸, Monroe⁶, Susquehanna⁸; 8 May⁸ 11–13 Sep⁹ (2017⁷).

Subgenus Sphecodogastra Ashmead

Revision: Gibbs et al. (2013).

- *Lasioglossum (Sphecodogastra) comagenense* (Knerer & Atwood, 1964) (*fulvicorne* group) locations, dates, and year not reported⁴⁶.
- Lasioglossum (Sphecodogastra) oenotherae (Stevens, 1920) (lusorium group) Cumberland³³, Erie⁹, Lycoming⁸; 9–11 Jun⁹ – 24 Aug⁸ (2016⁹).
- Lasioglossum (Sphecodogastra) quebecense (Crawford, 1907) (fulvicorne group)³⁶ Adams³, Bradford⁸, Bucks⁸, Centre^{1,7}, Chester⁶, Clinton²⁰, Dauphin¹, Delaware⁴, Erie⁹, Fayette¹, Huntingdon⁸, Lancaster⁸, Monroe^{2,20}, Montgomery⁷, Pike²⁰, Susquehanna⁸, Union⁸, Westmoreland^{1,20}, York⁸; 5 Apr³ – 13 Oct³ (2018³).
- Lasioglossum (Sphecodogastra) truncatum (Robertson, 1901) (calceatum group)³⁶ Adams³, Allegheny²⁰, Beaver²⁰, Bradford^{1,8}, Bucks⁸, Centre^{1,5,6,7}, Chester⁸, Columbia⁵, Crawford¹, Huntingdon⁸, Lehigh²⁰, Lycoming⁸, Montgomery^{8,20}, Somerset²⁰, Tioga²⁰, Westmoreland²⁰; 16 Apr³ – 19 Aug⁵ (2017^{3,7}).

Genus Sphecodes Latreille

Taxonomy: Mitchell (1960). *Sphecodes* is in particular need of revision (Gibbs et al. 2017a).

- Sphecodes antennariae Robertson, 1891 (mandibularis group) Adams³; 9 Oct³ (2008³).
- Sphecodes aroniae Mitchell, 1960 (ranunculi group)³¹ **Bucks⁸**, Philadelphia²; **9 May⁸** 26 May² (**2007**⁸).
- Sphecodes atlantis Mitchell, 1956 (mandibularis group) Adams³, Bradford⁸, Bucks⁸, Centre⁸, Erie^{1,2}, Huntingdon⁸, Lancaster³, Lycoming⁸, Union⁸, York⁸; 11 Jun⁸ 4 Sep³ (2015⁸).
- Sphecodes autumnalis Mitchell, 1956 (mandibularis group) Susquehanna⁸; 28 Aug⁸ (2015⁸).
- Sphecodes banksii Lovell, 1909 (mandibularis group) Adams³; 9 Oct³ (2008³).
- Sphecodes clematidis Robertson, 1897 (dichrous group) Centre⁸, Susquehanna⁸; 24 Jul⁸ 28 Aug⁸ (2015⁸).
- Sphecodes confertus Say, 1837 (confertus group) Crawford²; 4 Jul² (1960²).
- Sphecodes coronus Mitchell, 1956 (mandibularis group) Adams³, Blair², Centre⁷, Lancaster³, Monroe², Philadelphia¹; 16 May³ 8 Oct³ (2017⁷).
- Sphecodes cressonii (Robertson, 1903) (mandibularis group)³⁶ Dauphin¹, Lancaster⁸, Susquehanna⁸, Union⁸; 6 May⁸ 23 Sep⁸ (2014⁸).
- Sphecodes dichrous Smith, 1853 (dichrous group)³⁶ Centre^{1,8}, Chester⁸, Cumberland¹, Dauphin¹, Erie¹, Lancaster^{1,3}, Monroe², Warren⁶; 28 Apr⁸ 30 Jul³ (2015⁸).
- Sphecodes galerus Lovell & Cockerell, 1907 (mandibularis group) Centre⁷, Lancaster³; 16 Jul³ – 16–17 Aug⁷ (2017⁷).
- Sphecodes heraclei heraclei Robertson, 1897 (dichrous group) Bucks⁸, Centre^{1,7}, Delaware¹, Montgomery⁸; 29–30 Jun⁷ – 19 Aug¹ (2017⁷).
- Sphecodes illinoensis (Robertson, 1903) (mandibularis group) Tioga⁶; 27 Jun⁶ (2008⁶).
- Sphecodes levis Lovell & Cockerell, 1907 (mandibularis group) Erie¹; 4 Jun¹ (1966¹).
- Sphecodes mandibularis Cresson, 1872 (mandibularis group) Blair², Bucks⁸, Erie⁶, Lancaster⁸; 3 May⁸ 21 Jul⁸ (2015⁸).
- Sphecodes minor Robertson, 1898 (dichrous group) Bradford⁸, Dauphin¹, Delaware², Lancaster³, York^{1,8}; 15 Apr⁸ – 31 Jul³ (2015⁸).
- Sphecodes pimpinellae Robertson, 1900 (mandibularis group) Dauphin¹, Erie¹; 4 Jul¹ (year not reported¹).
- Sphecodes prosphorus Lovell & Cockerell, 1907 (*dichrous* group) Centre^{1,15,44}, Lancaster³; 10 Jul³ – 14 Aug³ (2013³).
- Sphecodes ranunculi Robertson, 1897 (ranunculi group)³⁶ Bedford², Bradford⁸, Centre⁸, Dauphin, Delaware², Erie, Huntingdon^{1,8}, Montgomery, Philadelphia², Union⁸; 28 Apr⁸ 14 Jul (2015⁸).
- Sphecodes smilacinae Robertson, 1897 (mandibularis group) Adams³; 24 May³ (2011³).
- Sphecodes solonis Graenicher, 1911 (dichrous group) Adams³; 28 Jul³ (2015³).
- Sphecodes townesi Mitchell, 1956 (mandibularis group) Lycoming⁸; 15 Jun⁸ (2014⁸).

Nomiinae Dieunomiini Genus *Dieunomia* Cockerell

Revision: Blair (1935).

Subgenus Dieunomia Cockerell s. s.

Dieunomia (Dieunomia) heteropoda heteropoda (Say, 1824) – Philadelphia¹; 10 Sep¹ (1971¹).

Nominiini

Genus Nomia Latreille

Taxonomy: Mitchell (1960); Ribble (1965)

Subgenus Acunomia Cockerell

Nomia (Acunomia) nortoni Cresson, 1868 – Allegheny¹; dates and year not reported¹.

Colletidae Colletinae Colletini

Genus Colletes Latreille

Taxonomy: Mitchell (1960); Stephen (1954).

- *Colletes aestivalis* Patton, 1879 (*aestivalis* group) Dauphin¹, Monroe¹, Montgomery⁴⁵; 4 Jun¹ 4 Jul¹ (1918¹).
- *Colletes americanus* Cresson, 1868 (*americanus* group) Bedford¹, Delaware¹, Philadelphia², York¹; 20 Sep¹ – 8 Oct² (1909¹).
- *Colletes compactus compactus* Cresson, 1868 (*compactus* group)³⁶ Adams³, Allegheny¹, Bedford¹, Centre¹, Clearfield⁴, Clinton¹, Columbia^{1,2}, Delaware², Huntingdon¹, Philadelphia², Tioga¹; 20 Aug¹ 8 Oct² (2014³).
- Colletes eulophi Robertson, 1891 (simulans group)³⁶ Bedford¹, Centre¹; 20 Jul¹ 20 Sep¹ (1954¹).
- Colletes inaequalis Say, 1837 (inaequalis group)³⁶ Adams³, Allegheny¹, Bradford⁸, Bucks⁸, Centre¹, Cumberland¹, Dauphin^{1,6}, Erie¹, Huntingdon^{1,3,8}, Lancaster⁵, Lehigh¹, Lycoming⁸, Montgomery^{1,2}, Perry¹, Philadelphia^{1,2,4}, Washington¹, York^{1,8}; 17 Mar⁶ 31 Aug² (2018³).

- *Colletes latitarsis* Robertson, 1891 (*latitarsis* group)³⁶ Adams³, Allegheny¹, Centre¹, Dauphin¹, Lancaster^{3,8}, Montgomery⁸, Perry¹, Venango¹, Washington¹; 13 Jun³ 23 Sep⁸ (2014⁸).
- *Colletes nudus* Robertson, 1898 (*nudus* group)³⁶ Adams³, Dauphin¹, Erie¹, Franklin¹; 20 May¹ 23 Jul³ (2015³).
- *Colletes productus* Robertson, 1891 (*productus* group) Dauphin¹, Philadelphia^{1,2}; 27 Apr¹ 9 Jul² (1909²).
- *Colletes simulans* Cresson, 1868 *armatus* Patton, 1879 (*simulans* group) Centre^{1,7}, Clinton¹, Huntingdon¹, Jefferson^{1,2}, Monroe^{1,2}; 23 Jul¹ 16 Sep¹ (**2017**⁷).
- Colletes thoracicus Smith, 1853 (thoracicus group) Dauphin⁶, Delaware⁴, Huntingdon^{1,2}, Montgomery⁷; 14 May⁶ – 10 Jun¹ (2017⁷).
- *Colletes validus* Cresson, 1868 (*inaequalis* group)^{36,45} Centre^{1,7}, Huntingdon¹, Philadelphia²; 29 Apr² – **24–25 May**⁷ (**2016**⁷).
- *Colletes willistoni* Robertson, 1891 (*willistoni* group) locations, dates, and year not reported³⁶.

Hylaeinae Hylaeini

Genus Hylaeus Fabricius

Taxonomy: Mitchell (1960); Snelling (1966, 1968, 1970).

Subgenus Hylaeus Fabricius s. s.

Revision: Snelling (1970).

- Hylaeus (Hylaeus) annulatus (Linnaeus, 1758) Bradford⁸, Centre^{7,15}, Clarion⁶, Columbia⁵, Dauphin¹, Erie⁹, Jefferson², Lackawanna¹, Monroe², Sullivan¹, Tioga¹, Venango⁶, Warren⁶, Wyoming⁴; 6 Jun⁶ – 22 Aug⁵ (2017⁷).
- *Hylaeus (Hylaeus) leptocephalus* (Morawitz, 1871)* (2005^{1,4}) Centre¹⁵, Erie⁹, Lancaster³, Northumberland¹, Philadelphia^{1,4}, Susquehanna⁸, York⁸; 7 Jun⁸ 25 Aug^{1,4} (2015⁸).
- Hylaeus (Hylaeus) mesillae (Cockerell, 1896) cressoni (Cockerell, 1907) Adams^{1,3,8}, Blair², **Bradford^{4,8}**, **Bucks⁸**, Centre^{7,8,15}, Dauphin^{1,4}, Delaware^{1,4}, Erie⁹, Franklin¹, Huntingdon², **Lackawanna⁴**, **Lancaster³**, **Lebanon⁴**, Lehigh¹, **Lycoming⁸**, Monroe^{1,2}, Montgomery^{2,8}, **Tioga⁴**, **Union⁸**, **York⁴**; **30** Apr³ – **21** Oct³ (2018³).

Hylaeus (Hylaeus) saniculae (Robertson, 1896) – Lehigh¹; 29 Jun¹ – 19 Jul¹ (1903¹).

Subgenus Metziella Michener

Revision: Snelling (1968).

Hylaeus (Metziella) sparsus (Cresson, 1869)³⁶ – Adams³, Bucks⁸; 9 May⁸ – 10 Jul³ (2015³).

Subgenus Paraprosopis Popov

Revision: Snelling (1970).

Hylaeus (Paraprosopis) floridanus (Robertson, 1893) – Lycoming⁸; 19 Jun⁸ (2015⁸).

Hylaeus (Paraprosopis) pictipes Nylander, 1852* (2015^{9,19}) – Crawford¹⁹, Erie⁹; 15 – 17 Jul¹⁹ – **2–4 Aug⁹** (2016^{9,19}).

Subgenus Prosopis Fabricius

- Hylaeus (Prosopis) affinis (Smith, 1853)³⁶ Adams^{1,3}, Allegheny¹, Berks⁶, Bradford^{6,8}, Centre^{1,6,7,15,44}, Chester^{1,6}, Clinton⁶, Crawford¹, Dauphin^{1,6}, Delaware^{1,4}, Erie⁶, Franklin¹, Fulton¹, Huntingdon^{1,2,3}, Jefferson⁶, Juniata⁶, Lackawanna⁴, Lancaster^{1,3}, Lebanon⁴, Lehigh^{1,6}, Lycoming⁸, Monroe^{1,2}, Montgomery¹, Northumberland¹, Philadelphia¹, Schuylkill⁴, Somerset⁶, Sullivan¹, Susquehanna¹, Tioga¹, Venango¹, Westmoreland¹, Wyoming⁴, York^{1,8}; 4 May³ 25 Oct³ (2018³).
- Hylaeus (Prosopis) illinoisensis (Robertson, 1896) Adams³, Bucks⁸; 19 May³ 23 May⁸ (2016³).
- Hylaeus (Prosopis) modestus modestus Say, 1837³⁶ Adams^{1,3}, Allegheny¹, Bedford⁶, Bradford^{1,6,8}, Bucks^{1,6}, Butler¹, Centre^{1,7,15,44}, Chester^{1,6}, Clarion⁶, Clinton⁶, Crawford¹, Cumberland¹, Dauphin^{1,6}, Delaware^{1,4}, Elk¹, Erie^{1,6,9}, Franklin¹, Huntingdon^{1,2,3}, Jefferson², Lackawanna⁴, Lancaster^{3,8,44}, Lehigh¹, Luzerne^{1,2}, Monroe¹, Montgomery¹, Perry^{1,4}, Philadelphia¹, Pike^{1,4}, Sullivan¹, Tioga^{1,4,6}, Union⁸, Westmoreland¹, York⁴; 5 Apr³ 6 Nov³ (2017^{3,7}).
- Hylaeus (Prosopis) schwarzii (Cockerell, 1896) Delaware⁴; dates not reported⁴ (2008⁴).

Subgenus Spatulariella Popov

Taxonomy: Sheffield et al. (2011a).

Hylaeus (Spatulariella) hyalinatus Smith, 1842* (2009⁴) – Adams³, Bradford⁸, Centre⁸, Dauphin⁴, Erie⁹, Lancaster⁸, Lebanon⁴, Lehigh⁴⁸ (AMNH_BEE00270811), Lycoming⁸, Montgomery⁸, Union⁸, York⁸; 18–20 May⁹ – 28 Sep⁸ (2016⁹).

Species excluded from the list of bees in Pennsylvania

Several valid bee species have been previously recorded from Pennsylvania, but their occurrence in the state is based on doubtful or erroneous identifications or otherwise cannot be confirmed. These species are listed below with brief comments.

Apidae

Nomada bisignata Say, 1824 (ruficornis group) – Donovall and vanEngelsdorp (2010) recorded this species as a new state record but indicated that no location or date data were available. The identity of this species is unclear since the original description could apply to numerous species and the type is likely not extant. Say (1824) did not specify its range below the country level. It is unclear how the identity of this species was determined by Donovall and vanEngelsdorp. It is possible that the specimen(s) reported in Donovall and vanEngelsdorp (2010) were/are located at the Department of Entomology, Academy of Natural Sciences (ANSP).

Andrenidae

- Andrena (Scaphandrena) nigerrima Casad, 1896 Westmoreland¹; 18 May¹ (1982¹). This species is not known to occur in the eastern United States (LaBerge and Bouseman 1977). The location of the specimen(s) reported under this name in Donovall and vanEngelsdorp (2010) cannot be confirmed.
- Andrena (Scrapteropsis) kalmiae Atwood, 1934 (daeckei group) Centre¹; dates not reported¹ (2007¹). Pennsylvania is outside of the known range of the species; the closest records are in Massachusetts and Connecticut (LaBerge 1971). It is possible that the specimen(s) reported in Donovall and vanEngelsdorp (2010) were/are located at PSUB. However, to our knowledge, they were not included in the Biddinger Laboratory Database under this name or as an updated entry.

Halictidae

- Augochlorella gratiosa (Smith, 1853)³⁶ Berks⁶; 8 Jun⁶ (2009⁶). Though this species was reported from Pennsylvania by Mitchell (1960), it has not been reported from north of North Carolina since the genus was revised by Coelho (2004). The specimen in the López-Uribe Laboratory was likely identified using keys in Mitchell (1960) and was not reexamined as part of this study. Until further evidence is available, we regard this species report as dubious.
- Halictus (Odontalictus) poeyi Lepeletier, 1841 Delaware^{1,4}; 24 May^{1,4} (2007^{1,4}). Though this species is known from the eastern United States, it is only verified as far north as Maryland (Packer et al. 2016). It is also cryptic and generally considered indistinguishable from *H. ligatus* without genetic analysis (Carman and Packer 1996; Danforth et al. 1998). We are unable to confirm details about the identification methods used for this specimen.
- *Lasioglossum (Dialictus) halophitus* (Graenicher, 1927) Centre¹; 3 Jul¹ (2007¹). This species is a coastal salt march specialist and its occurrence north of Maryland has yet to be verified (Gibbs 2011). The location of the specimen(s) reported in Donovall and vanEngelsdorp (2010) cannot be confirmed.

Lasioglossum (Dialictus) subversans (Mitchell, 1960) – Centre¹; 25 May¹ – 13 Jul¹ (2007¹). This species has a generally boreal distribution, and is only confirmed to extend south into the United States in Maine and Michigan (Gibbs 2010, 2011; Gibbs et al. 2017a). It is possible that the specimen(s) reported in Donovall and vanEngelsdorp (2010) were/are located at PSUB. However, to our knowledge, they were not included in the Biddinger Laboratory Database under this name or as an updated entry.
Lasioglossum (Dialictus) testaceum (Robertson, 1897) – Pike¹; 3 Aug¹ (1936¹). This species seems to occur primarily in the Great Plains, being more uncommon east of the Mississippi (Gibbs 2011). It is possible that the specimen(s) reported in Donovall and vanEngelsdorp (2010) were/are located at the Illinois Natural History Survey Biological Collections (INHS).

Colletidae

Colletes brimleyi Mitchell, 1951 (*nudus* group) – Lawrence¹; 17 Jun¹ (1961¹). This is a southeastern species that reaches its northern extent in the New Jersey Pine Barrens (Mitchell 1960). A record from Lawrence County is implausible. We were not able to locate the specimen in the PADA collection to confirm its identity.

Species expected to occur in Pennsylvania

The following species are anticipated to occur in Pennsylvania based on their known ranges. While they occur in neighboring regions, they have not yet been reported in the state.

Melittidae

Melitta americana (Smith, 1853) – This species is a *Vaccinium* L. specialist that ranges throughout the east and been confirmed from several surrounding states, including New Jersey (Mitchell 1960; Fowler 2016; Dibble et al. 2017).

Apidae

Triepeolus cressonii (Robertson, 1897) – This species is widespread across the eastern United States and has been reported from several surrounding states, including New Jersey (Mitchell 1962).

Andrenidae

Andrena (Parandrena) andrenoides (Cresson, 1878) – This Salix L. specialist is notably absent from the state based on its distribution across the eastern United States, which includes Ohio (Mitchell 1960; LaBerge and Ribble 1972).

- Andrena (Cnemidandrena) canadensis Dalla Torre, 1896 This Solidago L. specialist is notably absent from the state. It has been reported from several neighboring states, including Ohio, New Jersey, and New York, and is widely distributed in the eastern United States (Mitchell 1960; Fowler 2016; Dibble et al. 2017).
- Andrena (Micrandrena) vernalis Mitchell, 1960 This species has been treated as a synonym of Andrena (Micrandrena) ziziae Robertson, 1891 (piperi group) since Ribble (1968). In a recent study, Portman et al. (in press) have shown that A. vernalis is a valid species. Mitchell (1960) and Portman et al. (in press) record this species from several northeastern states, including neighboring New York and Ohio. Pennsylvanian specimens identified as A. ziziae should be reexamined to confirm their identity and future studies should consider the possibility that both species occur in the state.
- *Calliopsis (Verbenapis) nebraskensis* Crawford, 1902 This *Verbena* L. specialist has been recorded from the northeastern United States, including northern New Jersey (Shinn 1967; Fowler 2016). It is possible that it also occurs in Pennsylvania.
- *Perdita novaeangliae* Viereck, 1907 This rare species has reported from the northeastern United States, including Maryland and New Jersey, and is expected to occur in Pennsylvania (Mitchell 1960; North American Native Bee Collaborative 2017).
- *Perdita swenki* Crawford, 1915 This species has reported from the northeastern United States, including New York, and may occur in Pennsylvania (Mitchell 1960).

Halictidae

- Sphecodes davisii (mandibularis group) Robertson, 1897 This species is widespread across the eastern United States (Mitchell 1960; Dibble et al. 2017).
- Sphecodes fattigi (mandibularis group) Mitchell, 1956 This species occurs across the eastern United States (Mitchell 1960; Gibbs et al. 2017a).

Colletidae

Hylaeus (Spatulariiella) punctatus (Brullé, 1832)* – This exotic species has spread to a number of urban centers in Canada and the United States since its first detection in California in 1981 (Sheffield et al. 2011a; USGS Native Bee Laboratory 2019). It has been reported from the District of Columbia and New York (Ascher et al. 2006; Matteson et al. 2008). It seems likely that it may soon be found in Pennsylvania.

Data accessibility

Supplementary materials 1–17 are available for download as .csv files. Complete specimen records from databases may be available from the cited literature, future publications, or the contributors (upon request to the appropriate individuals) listed in Table 1.

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Bee species of Pennsylvania: taxonomy, collection dates, persistence, and distribution data

Authors: Shelby Kerrin Kilpatrick, Jason Gibbs, Martin M. Mikulas, Sven-Erik Spichiger, Nancy Ostiguy, David J. Biddinger, Margarita M. López-Uribe

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Bartomeus et al. (2013) specimen records

Authors: Shelby Kerrin Kilpatrick, Jason Gibbs, Martin M. Mikulas, Sven-Erik Spichiger, Nancy Ostiguy, David J. Biddinger, Margarita M. López-Uribe Data type: specimen records

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Supplementary material 3

Biddinger Database specimen records

Authors: Shelby Kerrin Kilpatrick, Jason Gibbs, Martin M. Mikulas, Sven-Erik Spichiger, Nancy Ostiguy, David J. Biddinger, Margarita M. López-Uribe

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Supplementary material 4

Droege Database specimen records

Authors: Shelby Kerrin Kilpatrick, Jason Gibbs, Martin M. Mikulas, Sven-Erik Spichiger, Nancy Ostiguy, David J. Biddinger, Margarita M. López-Uribe

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Integrated Crop Pollination (ICP) Project: Fleischer Laboratory Database specimen records

Authors: Shelby Kerrin Kilpatrick, Jason Gibbs, Martin M. Mikulas, Sven-Erik Spichiger, Nancy Ostiguy, David J. Biddinger, Margarita M. López-Uribe Data type: specimen records

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Supplementary material 6

López-Uribe Laboratory Database specimen records

Authors: Shelby Kerrin Kilpatrick, Jason Gibbs, Martin M. Mikulas, Sven-Erik Spichiger, Nancy Ostiguy, David J. Biddinger, Margarita M. López-Uribe Data type: specimen records

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Supplementary material 7

Winfree Laboratory Database specimen records

Authors: Shelby Kerrin Kilpatrick, Jason Gibbs, Martin M. Mikulas, Sven-Erik Spichiger, Nancy Ostiguy, David J. Biddinger, Margarita M. López-Uribe Data type: specimen records

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Mahan et al. (in prep) specimen records

Authors: Shelby Kerrin Kilpatrick, Jason Gibbs, Martin M. Mikulas, Sven-Erik Spichiger, Nancy Ostiguy, David J. Biddinger, Margarita M. López-Uribe Data type: specimen records

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Link: https://doi.org/10.3897/jhr.77.49622.suppl8

Supplementary material 9

Choate et al. (2018) specimen records

Authors: Shelby Kerrin Kilpatrick, Jason Gibbs, Martin M. Mikulas, Sven-Erik Spichiger, Nancy Ostiguy, David J. Biddinger, Margarita M. López-Uribe

Data type: specimen records

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Link: https://doi.org/10.3897/jhr.77.49622.suppl9

Supplementary material 10

Pennsylvania bee species literature review records

Authors: Shelby Kerrin Kilpatrick, Jason Gibbs, Martin M. Mikulas, Sven-Erik Spichiger, Nancy Ostiguy, David J. Biddinger, Margarita M. López-Uribe

Data type: specimen records

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Additional Pennsylvania bee specimen records

Authors: Shelby Kerrin Kilpatrick, Jason Gibbs, Martin M. Mikulas, Sven-Erik Spichiger, Nancy Ostiguy, David J. Biddinger, Margarita M. López-Uribe Data type: specimen records

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Link: https://doi.org/10.3897/jhr.77.49622.suppl11

Supplementary material 12

Pennsylvanian Andrenidae specimen records from BugGuide

Authors: Shelby Kerrin Kilpatrick, Jason Gibbs, Martin M. Mikulas, Sven-Erik Spichiger, Nancy Ostiguy, David J. Biddinger, Margarita M. López-Uribe

Data type: specimen records

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Supplementary material 13

Pennsylvanian Apidae specimen records from BugGuide

Authors: Shelby Kerrin Kilpatrick, Jason Gibbs, Martin M. Mikulas, Sven-Erik Spichiger, Nancy Ostiguy, David J. Biddinger, Margarita M. López-Uribe

Data type: specimen records

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Pennsylvanian Colletidae specimen records from BugGuide

Authors: Shelby Kerrin Kilpatrick, Jason Gibbs, Martin M. Mikulas, Sven-Erik Spichiger, Nancy Ostiguy, David J. Biddinger, Margarita M. López-Uribe Data type: specimen records

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Supplementary material 15

Pennsylvanian Halictidae specimen records from BugGuide

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Supplementary material 16

Pennsylvanian Megachilidae specimen records from BugGuide

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Pennsylvanian bee specimen records from iNaturalist

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RESEARCH ARTICLE



A new species of Andrena (Trachandrena) from the Southwestern United States (Hymenoptera, Andrenidae)

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Abstract

A new species of *Andrena* Fabricius, 1775, subgenus *Trachandrena* Robertson, 1902 is described and illustrated, *A. hadfieldi* **sp. nov.**, from Arizona, United States. The new species, presently known only from the female holotype, was collected in a Malaise trap in 1994, and remained unstudied until recently. In addition, *Trachandrena* is compared to similar subgenera in North America to assist in recognizing new members.

Keywords

Bee, new species, Trachandrena, North America, Arizona

Introduction

Andrena Fabricius, 1775 is one of the largest genera of bees, with 1,556 species (Ascher and Pickering 2020). Dubitzky et al. (2010) estimated that there are likely ca 2,000 species, suggesting there are many undescribed species, especially in Mesoamerica and in the dry regions of Central Asia. Though the genus is mainly Holarctic, it extends into Mesoamerica, parts of Africa and tropical Asia (Michener 2007).

The subgenus *Trachandrena* Robertson, 1902 is represented by 30 species globally (Gusenleitner and Schwarz 2002; Michener 2007), 24 of which occur in the

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Nearctic region (LaBerge 1973). Robertson (1902) originally described Trachandrena as a genus and included many species still placed in the subgenus today, but also included A. claytoniae Robertson, 1891 (= A. imitatrix Cresson, 1872) and A. crataegi Robertson, 1893. Viereck (1917) initially, and incorrectly applied the name Scrapter Lepeletier and Serville, 1828 (a genus of Colletidae) as a subgenus of Andrena for certain species, including among others A. imitatrix and A. morrisonella Viereck, 1917, but later (Viereck 1922) proposed Scrapteropsis because he felt it differed significantly from the Old World species incorrectly assigned to Scrapter (LaBerge 1971). Thus, Viereck (1924) recognized at least two subgenera of Andrena within Robertson's (1902) initial concept of Trachandrena. Cockerell (1929) provided further discussion on Robertson's (1902) Trachandrena, though in general supported Viereck's (1924) opinion of subgeneric rank status, and also felt Robertson's (1902) concept of Trachandrena likely involved multiple subgenera. For instance, Cockerell (1929) realized that the mainly eastern treatments of Robertson (1902) and Viereck (1924) were not fully representative of the western North American bee fauna and noted similarities of some of these to certain Old World species, sharing some characteristics with Trachandrena, but very distinct, particularly species with males that have a yellow clypeus. These taxa are now placed in the subgenus Plastandrena Hedicke, 1933, and most species in North America (excluding the mainly eastern A. crataegi) have males with a yellow clypeal maculation.

Lanham (1949) subsequently placed *Scrapteropsis* into synonymy with *Trachandrena*, and proposed subgenus *Mimandrena* Lanham, 1949 (with type species *A. imitatrix*) for *Trachandrena*-like species which have a propodeal corbicula with plumose hairs internally, presumably not realizing (as per LaBerge 1971) that Viereck's *Scrapteropsis* shared this feature (as indicated above, he included *A. imitatrix* in his subgenus). Lanham (1949), Mitchell T (1960) and LaBerge (1964) placed those species with simple internal hairs into the subgenus *Trachandrena*. Warncke (1968) later placed *Trachandrena* and *Mimandrena* into synonymy with the Old World subgenus *Biareolina* Dours, 1873, which is now considered monotypic (Michener 2007). LaBerge (1971) later reinstated *Scrapteropsis* as a valid North American subgenus, placing *Mimandrena* into synonymy. Species which Warncke (1968) placed in *Bareolina* are now included in *Scrapteropsis* (Nearctic only) or *Trachandrena* (Holarctic) (Michener 2007).

Robertson's (1902) concept of *Trachandrena* suggested close affinities of *Plastandrena*, *Scrapteropsis* and *Trachandrena* which was supported in a recent morphology-based phylogeny (Dubitzky et al. 2010). In that work, *Trachandrena* was recovered as a taxon belonging to a larger clade (i.e., the *Trachandrena* clade) containing *Scrapteropsis*, *Plastandrena*, *Agandrena* Warncke, 1968 and *Biareolina* (Dubitzky et al. 2010), the latter two subgenera absent from the Nearctic (Michener 2007). However, in an earlier phylogenetic analysis using mitochondrial and nuclear DNA sequences, *Scrapteropsis* was not recovered as a monophyletic group, instead being interspersed within *Trachandrena*, with *Plastandrena* not as closely related (Larkin et al. 2006). The somewhat contrasting results from both studies (Larkin et al. 2006; Dubitzky et al. 2010) suggest that more analysis with more taxa included is required to resolve the relationship of *Trachandrena* to other subgenera. Since LaBerge's (1973) revision of the subgenus *Trachandrena* in the Nearctic region no additional North American species have been recognized. Here a new species of *Trachandrena* is described from Arizona, United States. A diagnosis and full description of the female is provided. In addition, a partial key, modified from that of LaBerge (1973) is provided to allow females of the new species to be recognized from other species.

Materials and methods

For consistency with species treatments published elsewhere, the description generally follows the format used by LaBerge (1973). Other terminology and measurement methods follow that of Michener (2007); body length was measured as the sum of the length from the antennal base to the posterior propodeal surface and the length of the metasoma in lateral view. The following abbreviations are used: F = flagellomere, numbered from base to apex; pd = puncture diameter; T = metasomal tergum, and S =metasomal sternum, both numbered from the base to apex.

Photomicrography was undertaken with a Canon EOS 5D Mark II digital camera with an MP-E 65 mm 1:2.8 1–5× macro lens. Measurements were made with an ocular micrometer on a Nikon SMZ1000 stereomicroscope.

Taxonomy

Family Andrenidae Fabricius, 1775 Subfamily Andreninae Fabricius, 1775

Genus Andrena Fabricius, 1775

Andrena Fabricius, 1775: 376. Type species: *Apis helvola* Linnaeus, 1758, by designation of Viereck, 1912: 613.

Anthrena Illiger, 1801: 127, unjustified emendation of *Andrena* Fabricius, 1775. *Anthocharessa* Gistel, 1850: 82, unjustified replacement for *Andrena* Fabricius, 1775.

Type species. Apis helvola Linnaeus, 1758, autobasic.

Subgenus Trachandrena Robertson, 1902

Trachandrena Robertson, 1902: 187, 189.

Type species. Andrena rugosa Robertson, 1891, by original designation.

Diagnosis. *Trachandrena*, particularly the females, are relatively easy to recognize among most other subgenera of *Andrena* in the Nearctic region based on the combina-



Figure 1. Dorsal enclosure of propodeum (i.e., propodeal triangle) of a female *Andrena rugosa* Robertson, the type species of *Trachandrena* Robertson.

tion of the coarsely rugose metapostnotum (i.e., propodeal triangle) (Fig. 1) and the generally coarse body sculpturing (being less strongly sculptured in most other subgenera), the structure of the metasomal terga, especially T2, which have broad apical marginal zones that usually extend ¹/₂ the median length of the tergum (Fig. 2B) or more (Fig. 2A, C, D) (other subgenera in the Nearctic have narrower marginal zones), and the characteristic structure of the facial fovea, which is typically much narrower in the lower half (Fig. 3) (more parallel-sided for entire length in other Nearctic subgenera). As indicated above, in the Nearctic region Trachandrena is most similar to Plastandrena and Scrapteropsis. In addition to both of these subgenera having terga with much narrower marginal zones (Fig. 4), both sexes of Plastandrena usually have weakly to strongly curved inner hind tibial spurs (Fig. 5A) whereas these are straight in Trachandrena (Fig. 5B), and the facial fovea of females of both subgenera are typically broad throughout. Males of Scrapteropsis are difficult to distinguish from Trachandrena (Viereck 1924), though each has unique genital capsules (LaBerge 1971, 1973), the marginal zone of T2 is longer in Trachandrena, the antenna usually being slightly longer. Male Trachandrena also have S6 usually flat, not with a reflexed apical margin or with apicolateral teeth as in some Plastandrena (i.e., A. crataegi; LaBerge 1969; Michener 2007). In addition, most *Plastandrena* in North America, excluding A. crataegi, have the clypeus yellow or otherwise maculated (LaBerge 1969), not black as in Trachandrena.



Figure 2. Dorsal surface of metasoma of female *Trachandrena*. **A** *Andrena rugosa*, the type species of the subgenus, with relatively wide apical impressed area of T2; **B** *A*. *hippotes* Robertson, with a relatively narrow apical impressed area of T2 (but still wider than basal area); **C** *A*. *cleodora* (Viereck); **D** *A*. *hadfieldi*, nov. sp. Both of the latter species have broad apical impressed areas of T2 which are impunctate.



Figure 3. Facial fovea of *Andrena rugosa*. The lower half of the facial fovea in *Trachandrena* is usually much narrower than the upper portion, though this species is the most extreme example.

Andrena (Trachandrena) hadfieldi sp. nov.

http://zoobank.org/4D279B93-23E4-4263-940B-7D192BD43078

Material examined. *Holotype* female, USA, Arizona, Santa Cruz Co., Patagonia Sonorita Creek Reserve, 31.53N, 110.77W, 14.iv.1994, M[alaise] T[rap], B. Brown & E. Wilk / Royal Saskatchewan Museum Entomology RSKM_ENT_E-219414. The single specimen is housed at the Royal Saskatchewan Museum (RSKM) in Regina, Saskatchewan, Canada. The dataset for *Andrena hadfieldi* is archived with Canadansys (http://community.canadensys.net/) under resource title "A new Trachandrena from the Southwestern USA" and can be accessed using the following: https://doi.org/10.5886/em2mri.

Diagnosis. The female of *Andrena hadfieldi* is unique among *Trachandrena* in the Nearctic region in having very wide (i.e., at least 2/3 of the median tergal length) marginal zones of T2-T4 which are shiny and impunctate (Fig. 2D), a feature shared only with *A. cleodora* (Viereck) (Fig. 2C). *Andrena hadfieldi* is smaller than *A. cleodora* (9 mm, versus 10–13 mm body length in *A. cleodora*), and differs from *A. cleodora* in hav-



Figure 4. Dorsal surface of metasoma of female **A** *Plastandrena* Hedicke, *Andrena crataegi* Robertson, and **B** *Scrapteropsis* Viereck, *A. kalmiae* Atwood. Both subgenera differ from *Trachandrena* Robertson in having the apical impressed area of T2 narrower than the basal area.

ing the terga black (Fig. 2D) instead of black with strong metallic bluish reflections (Fig. 2C), and in having entirely pale pubescence, including the scopa (Figs 6, 7); the hair on the metasoma (Fig. 2C) and scopa of A. cleodora are black, and the pubescence of the dorsum of thorax is yellowish to red (subspecies *cleodora*; widespread in western North America) or entirely black (subspecies melanodora Cockerell; known from southern California). The structure of the pubescence on the dorsum of the thorax also differs between these two species, being long, very thin, and weakly plumose in A. hadfieldi (Fig. 6), but shorter and densely plumose, almost scale-like, in A. cleodora (Fig. 8). The process of the labrum in A. hadfieldi is more than 3× as wide basally as long medially (Fig. 9A); in *A. cleodora* the labral process is larger, subtriangular, with the base 2.5× as wide as the medial length (Fig. 9B). The body surface sculpture of A. hadfieldi is much finer than for A. cleodora; as examples, the face of A. hadfieldi is generally more finely and sparsely punctate, with shiny interspaces > two pd on the lower paraocular area (Fig. 10A), while in *A. cleodora* the lower paraocular area is more coarsely and closely punctate (interspaces < pd) (Fig. 10B); the surface of the propodeal corbicula is smooth with a few short rugae in A. hadfieldi (Fig. 11A), while coarsely rugose in A. cleodora (Fig. 11B).

The male of A. hadfieldi is unknown.

Description. Holotype, female (Figs 6, 7, 9A, 10A, 11A, 12). Body length 9 mm; head length 1.9 mm; head width 2.5 mm; intertegular width 2.1 mm; fore wing length 6.9 mm.



Figure 5. Inner hind tibial spur of A Plastandrena, Andrena crataegi, and B Trachandrena, A. hippotes.



Figure 6. Holotype female of Andrena (Trachandrena) hadfieldi. Lateral view.



Figure 7. Holotype female of Andrena (Trachandrena) hadfieldi. Dorsal view.

Colour. Black except as follows: F3-F10 dark reddish-brown below; tegula moderately translucent, brown, becoming reddish brown in posterior half; wing membranes slightly infumate, veins yellowish-brown; legs dark brown, apical tarsal segments reddish brown.

Structure. Labrum with process trapezoidal, more than three times as wide at base as long medially, apical edge entire (Fig. 9A). Clypeus with coarse, close round to irregular shaped punctures, becoming finer apically, interspaces shiny and linear, less than 0.5 pd, without obvious median impunctate line but with a small shiny subapical boss extending for less than 1/5th median length of clypeus (Fig. 10A). Supraclypeal area with distinct round punctures separated by 0.5 pd, surface rather shiny (Fig. 10A). Mandible short, extending beyond middle of labrum by about ¹/₄ its length in repose. Malar space extremely short (Fig. 10A). Lower paraocular area shiny with small punctures separated by > two pd (Fig. 10A). Face above antennal socket with rugulae extending to ocelli, without obvious punctures. Facial fovea long, extending from middle level of lateral ocellus to basal edge of clypeus; lower portion narrow, from below level of antennal socket about 1/3 as wide as upper portion, outer edge slightly incurved from inner margin of compound eye just above level of antennal socket, this area



Figure 8. Dorsal thoracic surface of Andrena (Trachandrena) cleodora, showing the short, thick pubescence.

smooth, shiny and impunctate (Fig. 10A). Compound eye just over three times as long as broad in frontal view, inner margin converging slightly toward mandibles. Genal area in profile about as broad as compound eye, surface shiny with minute punctures separated by 2 pd, posterior half dull with reticulate shagreening, without apparent punctures except near base of mandible. Vertexal area above lateral ocellus subequal to one ocellar diameter, dulled by crowded punctures and dense reticulate shagreening. Antennal scape length equal to combined length of F1-F3; F1 about 1.5 times as long as broad at apex, and 1.5 times longer than F2; F2-F5 quadrate, F6-F9 about 1.2 times longer than broad, F10 more elongate, about 1.5 times longer than broad.

Pronotum somewhat shiny, with distinct punctures dorsally, separated by about two pd, laterally mostly impunctate with surface somewhat dull. Mesoscutum with large, round deep punctures, between parapsidal lines and posteromedially separated mostly by ½ to one pd, anteriorly and laterally separated by less than ½ pd, becoming somewhat rugosopunctate along anterior edge (Fig. 7), surface dull, reticularly shagreened. Scutellum similarly punctured though punctures slightly sparser anteriorly, and surface mostly shiny. Metanotum dull and tessellate laterally, becoming somewhat shiny and punctate medially. Metapostnotum with rather shallow but distinct rugae, these somewhat irregular (Fig. 12); dorsolateral and posterior surfaces of propodeum moderately coarsely rugosopunctate, tessellate, dull; propodeal corbicular surface moderately shiny, tessellate, with a few short rugae (Fig. 11A). Mesepisternum coarsely rugose and somewhat shiny. Metepisternum surface smooth, with a slight shine. Fore femur with base round in outline. Posterior hind tibial spur straight. Tarsal claws with a small subbasal tooth.

T1 shiny and largely impunctate, with basal area (= disc) punctures obscure, shallow, sparse, separated by \geq 5pd; marginal zone impunctate and shiny, occupying about



Figure 9. Labral process of A Andrena (Trachandrena) hadfieldi, and B A. (Trachandrena) cleodora.

 $3/5^{th}$ of median length of tergum, a few sparse minute punctures visible at extreme lateral edge, surface smooth (Fig. 2D). T2 with marginal zone clearly longer than basal area (about $3/4^{th}$ medial with); basal area shiny with punctures separated by one pd, a



Figure 10. Face of A holotype female of Andrena (Trachandrena) hadfieldi, and B A. (Trachandrena) cleodora.



Figure 11. Propodeal corbicula of **A** *Andrena* (*Trachandrena*) *hadfieldi* showing long plumose hairs on the dorsal and posterior surface, no hairs on the anterior margin, and long simple internal hairs, and the rather smooth surface, and **B** *A*. (*Trachandrena*) *cleodora*, with the surface coarsely rugose.



Figure 12. Holotype female of Andrena (Trachandrena) hadfieldi. Dorsal view, propodeal enclosure.

narrow dull impunctate area adjacent to gradulus; marginal zone smooth, shiny and impunctate (Fig. 2D). T3-T4 similar to T2 but marginal zone of T4 shorter, about 3/5th of median length of tergum (Fig. 2D). T5 with basal area broader than marginal zone, basal area tessellate, with distinct punctures separated by 2–3 pd, becoming closer adjacent to marginal zone (Fig. 2D); marginal zone dull, largely obscured by prepygidial fringe (Fig. 2D). Pygidial plate U-shaped with rounded apex about ½ as wide as base, with sharply pointed, internal, raised triangular area on median surface. S2-S5 with surface somewhat shiny, punctures uniformly dense, separated by 1 pd; S2 with a medial U-shaped depression.

Vestiture. Generally white to pale yellowish (Figs 6, 7), somewhat reddish on mandible and apical margin of labrum. Propodeal corbicula with long plumose hairs on dorsal and posterior edges, lacking anterior hairs, with long simple hairs internally (Fig. 11A). Trochanteral flocculus complete. Tibial scopal hairs long and simple. Prepygidial fimbria and T6 with reddish brown hairs (Fig. 2D). Terga lacking apical fasciae except reduced to small lateral patches of sparse hairs on T2 and T3 (Fig. 2D); a few long pale subappressed hairs arising laterally from the premarginal line and overlaying marginal zone (Fig. 2D). T1 with sparse pale hairs laterally and on declivitous anterior surface (Fig. 2D). S2 to S5 with sparse, pale, elongate plumose hairs apically, these becoming longer laterally (i.e., ½ length of succeeding segment).

Male unknown.

Distribution. United States, southern Arizona.

Etymology. It is a privilege to name this new species after Canadian astronaut Col. Chris Hadfield for his many achievements as a pilot, astronaut, author, lecturer, and science educator.

Partial key to species of Trachandrena (modified from LaBerge 1973)

4(2)	T2 with basal area (i.e., visible base of tergum to gradulus) less than half as long medially as apical area and often less than one-third as long (Fig. 2A, C, D) 5
_	T2 with basal area (i.e., visible base of tergum to gradulus) more extensive, at
	least half as long medially as apical area and often longer (Fig. 2B)14
5(4)	Mesoscutum with posteromedian area impunctate, or punctures separated by
	two or three or more pd; face above antennal socket rugose; metasoma often
	red Andrena striatifrons Cockerell
_	Mesoscutum with posteromedian area punctate, punctures usually separated
	by one or two pd, if by more than two pd, then face above antennal socket
	punctate or rugosopunctate, not strongly rugose; metasoma black or mostly
	so
6(5)	Metasomal hairs entirely black or dark brown (Fig. 2C); leg hairs, including
	tibial scopa, brown to black or largely so7
_	Metasomal hairs largely pale in color (Fig. 2D); at least scopal hairs and often
	leg hairs entirely pale in color (Fig. 6)
7(6)	T2-T4 with apical areas impunctate, often with metallic blue reflections
	(Fig. 2C); face above antennal socket with coarse longitudinal rugae, espe-
	cially in upper half Andrena cleodora (Viereck)
_	T2-T4 with apical areas with fine but distinct punctures, without strong me-
	tallic blue reflections; face above antennal socket with rugae weak or absent,
	usually with deep punctures with interspaces shiny, or weakly shagreened
7a(6)	T2-T4 with apical areas impunctate (Fig. 2D) Andrena hadfieldi sp. nov.
_	T2-T4 with apical areas distinctly punctate (Fig. 2A)8 (in LaBerge 1973)

Discussion

Nothing is known about the biology of this species as it is known only from the holotype female which was collected in a Malaise trap. However, like other *Trachandrena* in the Nearctic region, this is a vernal species that probably visits spring flowering trees and shrubs (LaBerge 1973). It is hoped that by publishing a full description of the new species and a partial key to the *Trachandrena* in North America that includes this species, that additional specimens, including the male, will be discovered in other entomology collections or through survey work. The American Southwest is one of the most diverse regions for bees globally (Michener 1979, 2007), so it is likely that many other bee species await recognition.

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Foraging distances in six species of solitary bees with body lengths of 6 to 15 mm, inferred from individual tagging, suggest 150 m-rule-of-thumb for flower strip distances

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Citation: Hofmann MM, Fleischmann A, Renner SS (2020) Foraging distances in six species of solitary bees with body lengths of 6 to 15 mm, inferred from individual tagging, suggest 150 m-rule-of-thumb for flower strip distances. Journal of Hymenoptera Research 77: 105–117. https://doi.org/10.3897/jhr.77.51182

Abstract

Bees require suitably close foraging and nesting sites to minimize travel time and energy expenditure for brood provisioning. Knowing foraging distances in persistent ('healthy') populations is therefore crucial for assessing harmful levels of habitat fragmentation. For small bees, such distances are poorly known because of the difficulty of individual tagging and problems with mark-recapture approaches. Using apiarist's number tags and colour codes, we marked 2689 males and females of four oligolectic and two polylectic species of Osmiini bees (Megachilidae, genera *Chelostoma, Heriades, Hoplitis, Osmia*) with body lengths of 6 to 15 mm. The work was carried out in 21 ha-large urban garden that harbours at least 106 species of wild bees. Based on 450 re-sightings, mean female flight distances ranged from 73 to 121 m and male distances from 59 to 100 m. These foraging distances suggest that as a rule of thumb, flower strips and nesting sites for supporting small solitary bees should be no further than 150 m apart.

Keywords

Anthophila, body size, foraging distances, individual tagging, Megachilidae, solitary bees, urban garden

Introduction

Wild bees are pollinators of high conservation concern. One reason for this derives from the relatively small spatial and temporal scale of their life cycles, habitat ranges, and nesting behaviour (Westrich 1996; Gathmann and Tscharntke 2002; Greenleaf et al. 2007; Franzén et al. 2009; Zurbuchen et al. 2010a; Wood et al. 2016), which makes them vulnerable to landscape fragmentation. Bees are central-place foragers, with females shuttling between foraging sites and nests to provide brood cells with pollen, nectar or oil, and the distance between these resources largely determines bees' reproductive success (Zurbuchen et al. 2010b). The further nest and food sources are apart, the higher bees' energetic and reproductive costs (Williams and Tepedino 2003; Zurbuchen et al. 2010b). Thus, in the European solitary species Hoplitis adunca and Chelostoma rapunculi (Megachilidae), the number of brood cells provisioned per time decreased by a third to almost half (31% or 46%) when foraging flight distances were experimentally increased by 200 or 500 m (Zurbuchen et al. 2010b). In the solitary Megachile rotundata, 74% fewer offspring were produced when flight distances increased by 150 m (Peterson and Roitberg 2006). Increased flight requirements reduce adult lifespan (Schmid-Hempel and Wolf 1988), and absences from the nest increase brood cell parasitism, as parasites enter the nest while the nest owner is away (Seidelmann 2006). Proximity of nesting and foraging sites is therefore crucial for the reproductive success of bees, and we need more data on foraging distances to predict the effects of habitat enhancements for conservation purposes (Nicholson et al. 2019).

Bee foraging distances have been investigated with a range of methods, including microsatellite DNA markers to determine to which colony a bumblebee worker belongs (Chapman et al. 2003; Knight et al. 2005), pollen analysis to check the content of pollen loads or brood cells for plants occurring at known distances (Williams and Tepedino 2003; Beil et al. 2008), and radio tracking for species large enough for carrying a transmitter (Carreck et al. 1999). The two most widely used methods are translocation experiments (e.g., Gathmann and Tscharntke 2002) and mark-recapture studies (e.g., Osborne et al. 2008; Wolf and Moritz 2008; Franzén et al. 2009; Zurbuchen et al. 2010a). In translocation experiments, bees are removed from their nest and released at increasing distances until no more returnees are recorded at the nesting sites. This is biologically highly different from a natural foraging flight in which a bee travels from, and returns to, its nest. Mark-recapture studies instead involve marking, releasing, and recapturing bees, but not transporting them (in darkened boxes) away from their nests.

All these approaches aim to find maximal flight distances, which are key to inferring body size/distance relationships. A linear regression model that included body length and maximum flight distance in 17 European solitary bees showed that distance roughly triples as body length doubles (Gathmann and Tscharntke 2002), with the smallest species studied being *Chelostoma florisomne* (7 to 11 mm), the largest the European carpenter bee *Xylocopa violacea* (20 to 30 mm). A non-linear regression analysis of the maximum distances of 62 species worldwide that regressed intertegular distance as a proxy for body size on distance found that larger bees had disproportionately larger foraging distances than smaller bees (Greenleaf et al. 2007). Maximum flight distances can be treated as a species-level trait, i.e., the result of the averaged physiological and mechanical capacities of a species. In the present study, we *instead* focus on mean flight distances (which is not a species-level trait, but instead context-dependent), using a mark-release-re-sighting approach on large numbers of individuals of several species. Such data are needed to help conservation measures, such as the planting of flower strips or other resource stepping stones. Of 436 Central European species for which we compiled body sizes, 92% are between 4.5 and 13.5 mm long (Hofmann et al. 2019). We therefore selected six small species to quantify *average* flight distances in a flower-rich and nesting-site-rich botanic garden that harbours at least 106 species of wild bees (Hofmann et al. 2018). This provides independent data to compare to the flight distances of 150–600 m for 5.5 to 12 mm-long bees obtained in the above analysis in which bees were marked individually with 'tip-ex' or acrylic colour, transported to various release points, and the distance from the release site to the nest then measured (Gathmann and Tscharntke 2002).

Material and methods

Study sites and species

The study took place in the Munich Botanic Garden during the 2017 and 2018 bee foraging seasons (March to August). The garden opened in May 1914, covers about 21 ha and borders on the 210-ha-large Nymphenburg Palace Park at 48°09'45"N, 11°30'06"E at 500 m above sea level. It is currently home to 106 bee species whose abundances were scored in 1997–1999 and again in 2016/2017 by repeated monitoring walks (Hofmann et al. 2018). Several cavity nest boxes for solitary bees are located in the garden, with the larger ones harbouring well-established populations. The botanical garden provides a flower-rich habitat with both flower beds and near-natural meadows blooming throughout the year.

We investigated six above-ground nesting species of Osmiini (Megachilidae) with different flight times (Table 1) and body lengths, namely *Chelostoma florisomne* (7.0–8.0 mm), *C. rapunculi* (8.0–10.0 mm), *Heriades truncorum* (6.0–7.0 mm), *Hoplitis adunca* (11.0–13.0 mm), *O. bicornis* (8.0–12.0 mm), and *Osmia cornuta* (11.0–13.0 mm). Species body sizes are from Amiet et al. (2004) and Scheuchl (2006). We did not ask the students who marked the 2689 bees to also measure body lengths because we wanted to keep bees alive and able to forage after having undergone the capturing and marking procedure; also, as explained in the Introduction, our study goal was not to test correlations between body size and flight distance.

Megachilidae are solitary bees, and the species we investigated are widespread in Europe, Northern Africa and Asia (Scheuchl and Willner 2016). While the two *Osmia* species are polylectic (meaning they forage for pollen on a wide taxonomic variety of plants; Cane and Sipes 2006), the others are oligolectic (they collect pollen at only a few plant families), with *Chelostoma florisomne* specialized on *Ranunculus* (Ranunculaceae), *C. rapunculi* on Campanulaceae, *Heriades truncorum* on Asteraceae,

Species	Body size [mm]	Flight period	Foraging preference
Chelostoma florisomne	∂: 7–9 mm	April–June	Oligolectic on Ranunculus
	♀: 7–8 mm		
Chelostoma rapunculi	∂: 8–10 mm	May–September	Oligolectic on Campanulaceae
	♀: 8–10 mm		
Heriades truncorum	∂: 5–7 mm	May–October	Oligolectic on Asteraceae
	♀: 6–7 mm		
Hoplitis adunca	∂: 11–13 mm	April–September	Oligolectic on Echium
	♀: 11–13 mm		
Osmia cornuta	∂: 11–13 mm	February–June	Polylectic
	♀: 12–15 mm		
Osmia bicornis	∂: 8–12 mm	March-July	Polylectic
	♀: 8–12 mm		

Table 1. The studied species (tribe Osmiini, family Megachilidae) with their male and female body sizes, flight periods, and foraging preferences (Amiet et al. 2004; Scheuchl and Willner 2016).

and *Hoplitis adunca* on *Echium* (Boraginaceae). *Heriades adunca* was tagged in 2017, *Chelostoma florisomne*, *C. rapunculi*, *Heriades truncorum*, and *Osmia bicornis* in 2018, and *O. cornuta* in both 2017 and 2018.

Bee tagging and tracking

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Bees were captured with an insect net near the cavity nest boxes (shown on the garden map in Suppl. material 1: Fig. S1), and the larger species *Osmia cornuta*, *O. bicornis*, and *Hoplitis adunca* were marked using apiarist's tags (Fig. 1). Female bees were mechanically immobilized in a queen marking tube (Fig. 2); male bees were held between the experimenter's fingers such that legs and antennae were hidden from the glue and the mesonotum was freely accessible (Fig. 3). A small amount of nontoxic shellac glue (Liebert 1986) was placed on the bee's thorax with a fine metal stylus and the coloured, consecutively-numbered and slightly concave circular apiarist plastic plates (Opalith Classic from Holtermann, Brockel, Germany) were then attached. Each plate had an average weight of 1.3 mg and a diameter of 2.5 mm. For each species, several colours were used (allowing identification of sex and marking location). The same colours were used for *O. cornuta* and *H. adunca*, which had different flight times, but different colours were used for the two *Osmia* species. Each individual was identifiable by its number/colour combination.

The smaller species *Chelostoma florisomne*, *C. rapunculi* and *Heriades truncorum* with an intertegular distance < 2.5 mm were marked with paint, as apiarists' tags were too big for them. They were cold anesthetized and then marked with two dots of paint. One dot coded for the cavity nest box, one for species and sex. Bees of the same species and sex marked at the same nesting site were therefore indistinguishable in the field. Bees were released directly after being marked, which took two to three minutes per individual.


Figure I. Marked individuals of **A** *Chelostoma florisomne* **B** *C. rapunculi* **C** *Heriades truncorum* **D** *Hoplitis adunca* **E** *Osmia bicornis*, and **F** *Osmia cornuta.*

We searched the garden for bees several hours per day (in both 2017 and 2018) when the weather was warm and dry, and used photography (usually by smartphone) for documenting labelled bees during floral visits. For the four oligolectic species, surveys targeted the relevant food plants. For the two polylectic species, *Osmia bicornis* and *O. cornuta*, relevant flower beds and meadows was searched, and we additionally used a citizen science approach involving garden visitors. During the outdoor season (April to October), the Munich Botanical Garden has about 2000 visitors/day. Posters near the two public entrances and on the Garden's webpage explained our project, and visitors were given three options for informing us about bee sightings: Paper forms with a gridded map of the garden available at the entrance, along with pencils and a box for dropping filled-out forms; via an email account



Figure 2. Marking of an *Osmia cornuta* female (photos: J. Kirndorfer). **a**, **b** A female caught with an insect net is transferred to the queen-marking tube and **c**, **d** pushed with the plunger to immobilize it (**e**, **f** a stylus is used to put glue on the mesonotum **g**, **h** the numbered colour plate is attached and **i** the bee released.

(wildbienen@bio.lmu.de) at which photos could be submitted; or by talking to us directly. Visitors only needed to report the colour and number of a bee's tag and where it had been seen; no special knowledge of bee species or sex was necessary for a 'successful' sighting. For smartphone pictures, GPS tracking was usually available; for oral reports, we were able to ask the visitors to show us the location directly if it was unclear; and for the reports on paper, the position of the sighted bee was directly marked on the gridded garden plan.

Since the nest locations for all individuals included in the analysis were known, we were able to measure the beeline from the respective nest box to the sites where a bee was sighted using the measuring tool of Google Earth.



Figure 3. Marking of an *Osmia cornuta* male (photos: J. Kirndorfer) **a** application of the glue and **b**, **c** attaching of the apiarists' tag **d** a labeled male ready to take off.

Results

Re-sighting rates and flight distances

Summed for the six species, we marked 2689 individuals, including 1808 females and 881 males (Table 2). In all, 450 of the marked individuals were re-sighted (Fig. 4 graphs all re-sightings), although individual bees could be distinguished only in the three number-tagged species (Table 1 and Suppl. material 2: Table S1). Re-sighting rates at flowers were 5.4% for *C. florisomne* females, 4% for *C. rapunculi* females, and 4.8% for *C. rapunculi* males. Of the larger species, we re-sighted 21% of *Heriades truncorum* females, 56% of *Hoplitis adunca* females, 31% of *Osmia bicornis* females, and 24 and 10% of *O. cornuta* females in 2017 in 2018, respectively (Table 2). Males were only re-sighted in *C. rapunculi*, *O. bicornis*, and *O. cornuta* (Table 2), with a 14% re-sighting rate of *O. cornuta* males in 2017 and an 11% rate in 2018. For *O. bicornis*, 24 of 37 tagged females were observed not only on flowers but also at a sand pile at

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Species	Number of tagged	Number of	Number of	Mean flight	Standard	Maximum flight
	individuals	sightings at	re-sightings	distances (m)	deviation	distance (m)
		nest box				
Chelostoma florisomne	♀: 221		Q: 12	82	58.7	174
	්: 0	N/A		N/A	N/A	N/A
	Total: 221					
Chelostoma rapunculi	♀: 248		우: 10	104	45.2	178
	ੈ: 103	N/A	<i>ै</i> :5	59	34.5	119
	Total: 351					
Heriades truncorum	♀: 534		우: 118	73	62.6	298
	ಿ: 0	N/A		N/A	N/A	N/A
	Total: 534					
Hoplitis adunca	♀: 277	우: 100	우: 127	112	77.3	287
	∂ [*] : 92			N/A	N/A	N/A
	Total: 369					
Osmia bicornis	♀: 136	우: 118	♀: 42	121	44.6	250
	ੈ: 38	∂ [*] : 21	∂:6	100	40.3	151
	Total: 174					
Osmia cornuta	2017:					
	♀: 170	♀: 136	♀: 40	106	107.5	724*
	ੈ: 201	♂: 135	ð: 29	96	39.0	225
	Total: 371	우 : 279	♀: 31	107	67.9	226
	2018:	්: 235	<i>ै</i> : 37	77	52.5	215
	♀: 320					
	ී: 349					
	Total: 669					

Table 2. Mean and maximum flight distances of tagged solitary bees in the Munich Botanical Garden in 2017 and 2018 calculated from the 450 values in Suppl. material 2: Table S1. N/A, not applicable, refers to small sample sizes. The asterisk marks a single individual found just outside the 21-ha large garden.

138 m distance from the nest boxes (Suppl. material 2: Table S1), where they collected earth for closing their nests.

In 2017, 77 records of individually numbered *O. cornuta* bees resulted from the citizen science approach and 72 of the 77 could be used for the distance analysis. In 2018, there were 76 records for *O. cornuta* made by citizen scientists of which 70 were usable. For *O. bicornis*, 49 records were made by garden visitors (22 on the form, 2 via email, and 25 via personal communication); all were usable.

Comparison of male and female flight distances

Mean female flight distances in the six species were between 73 and 121 m (Fig. 4; standard deviations and sample sizes in Tables 2 and Suppl. material 2: Tables S1). Mean male flight distances in the three species in which males could be re-sighted were between 59 and 100 m (Tables 2 and Suppl. material 2: Table S1), but sample sizes for males were low (e.g., n = 5 for *Chelostoma rapunculi* and n = 6 in *O. bicornis*).



Figure 4. Mean flight distances (with standard deviations) calculated from the 450 bee re-sightings shown in Suppl. material 2: Table S1, with year of observation given for *Osmia cornuta*, studied in both 2017 and 2018. All remaining data are from 2017. Species body sizes are from Amiet et al. (2004) and Scheuchl (2006). For the smaller species *Chelostoma florisomne*, *C. rapunculi*, and *Heriades truncorum*, which were colour-tagged rather than number-tagged, we cannot exclude repeated observations of the same individual.

Discussion

To our knowledge, this is the largest tagging study of flight distances in solitary small bees in a flower-rich setting. The successful tracking of number and colour-coded tiny bees achieved in this study – 'tracking' because marked bees were not recaptured and hence not accidentally damaged or killed – was achieved through numerous search hours put in by students and citizen scientists in the botanical garden. In this way, we obtained 450 flight distances for six species of body lengths between 6 and 15 mm. These bees flew average distances of 75 to 125 m between their nests and their visited resources, with maximum distances up to seven times larger than mean distances (Table 2), supporting findings in other studies (Gathmann and Tscharntke 2002; Zurbuchen et al. 2010a, b) that did not use individual tagging but instead translocation experiments (e.g., Gathmann and Tscharntke 2002) or mark-recapture studies. Narrow foraging ranges thus appear to be the norm in solitary European bees, and even in the primitively eusocial *Bombus terrestris*, 40% of workers forage within a radius of 100 m around their nests (Wolf and Moritz 2008).

Bee foraging is highly context-dependent (e.g., Osborne et al. 2008; Pope and Jha 2018). For example, most *Hoplitis adunca*, a species in which both sexes prefer

Echium flowers as pollen and nectar sources, were observed on exactly the various *Echium* plants in the garden. Given the context-dependence of bee foraging, a limitation of our study is that it is confined to one site. For the colour-tagged (rather than number-tagged) species, our flight distances also may be pseudo-replicated because the same bee could have been seen several times. Moreover, different plants in the garden are grouped in beds or by topic (Suppl. material 1: Figure S1), which must have influenced bee foraging patterns (but so would any resource distribution anywhere). *Osmia cornuta* is the only species investigated here with different-sized males and females, but the difference is small: Tables 1 and Suppl. material 2: Table S1.

Regardless of these limitations, our results support the correlation between body size and flight distance found with different methods in previous studies (Gathmann and Tscharntke 2002: 16 Central European species; Greenleaf et al. 2007: 62 species worldwide). This correlation implies that females of Central European bees, most of which are between 4.5 and 13.5 mm long (Hofmann et al. 2019), usually may not forage further than 125 to 150 meters from the nest (Gathmann and Tscharntke 2002: 150 to 600 m; our Table 2: 100 m). Despite the six or seven times larger distances that these bees are able to fly when forced to do so (Gathmann and Tscharntke 2002; Zurbuchen et al. 2010a, b), long flights between nests and floral resources have fitness costs in terms of lower offspring number and increased brood parasitism (Peterson and Roitberg 2006; Seidelmann 2006; Zurbuchen et al. 2010b). The persistence of populations therefore requires flower patches and nesting sites at suitable distances, for which we propose a rule-of-thumb of 150 m. This rule of thumb could be used by conservation practitioners planning urban greening measures. Implementing such simple habitat enhancements as flower strips with the appropriate spatial distribution, can greatly increase the connectivity of foraging sites and help bee conservation (Hofmann and Renner 2020).

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Supplementary material I

Figure S1. Map showing the garden lay-out and location of the nest boxes at with bees were tagged

Authors: Michaela M. Hofmann, Andreas Fleischmann, Susanne S. Renner Data type: occurrence

Explanation note: Source: http://www.botmuc.de/en/garden/garden_map.html.

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Link: https://doi.org/10.3897/jhr.77.51182.suppl1

Supplementary material 2

Table S1

Authors: Michaela M. Hofmann, Andreas Fleischmann, Susanne S. Renner

Data type: species data

- Explanation note: Flight distances of 450 males and females from six species (tribe Osmiini, family Megachilidae) re-sighted at flowers or, in the case of *Osmia cornuta* females, also at a sand pile 138 m from the nest, with year of observation given for *Osmia cornuta*, which was studied in both 2017 and 2018.
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RESEARCH ARTICLE



Additions to the knowledge of the genus Allorhynchium van der Vecht, 1963 from China (Hymenoptera, Vespidae, Eumeninae)

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Abstract

In this study, *Halysituberosus* Dong & Wang, 2017 is treated as a synonym of *Allorhynchium* van der Vecht, 1963 (**syn. nov.**). *Halysituberosus yingjiangensis* Dong & Wang, 2017 is a new synonym of *Allorhynchium lugubrinum* (Cameron, 1900) (**syn. nov.**) and *Halysituberosus menglianensis* Dong & Wang, 2017 is transferred to *Allorhynchium* as a new combination (**comb. nov.**). Based on additional *COI* gene sequencing and morphological characters including genitalia characters, both *Allorhynchium diffinis* (Giordani Soika, 1986) and *Allorhynchium radiatum* Li, Barthélémy & Carpenter, 2019 are confirmed to be valid species, and their males of the two species are described for the first time. *Allorhynchium quadrimaculatum* Gusenleitner, 1997 is newly recorded from China. A key to the Chinese species of *Allorhynchium* are also updated.

Keywords

Allorhynchium, Eumeninae, Halysituberosus, new synonym, new record

Introduction

At present, *Allorhynchium* van der Vecht, 1963 contains 20 species and four subspecies worldwide, which are mostly distributed in the Oriental region (Smith 1861; Giordani Soika 1986; Girish Kumar et al. 2016; Tan et al. 2018; Li et al. 2019). Tan et al. (2018)

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revised the genus from Northeast Asia and provided a key to the Oriental species. In our study, the type species of *Halysituberosus* Dong & Wang, 2017 is examined and verified that *Halysituberosus* is a synonym of *Allorhynchium* van der Vecht, 1963 (syn. nov.), *H. yingjiangensis* Dong & Wang, 2017 is a synonym of *Allorhynchium lugubrinum* (Cameron, 1900) (syn. nov.), and *H. menglianensis* Dong & Wang, 2017 should be transferred to *Allorhynchium* (comb. nov.). Meanwhile, seeing that the two related species *A. diffinis* (Giordani Soika, 1986) and *A. radiatum* Li, Barthélémy & Carpenter, 2019 were originally described on a single female specimen and confusing to distinguish, we provided some more morphological characters from both female and male and their *COI* (cytochrome oxidase subunit 1) sequence features. Finally, *A. quadrimaculatum* Gusenleitner, 1997 is newly recorded from China. And some diagnosis and figures of these species and an updated key to the Chinese species of *Allorhynchium* are also given.

DNA barcode was first proposed by Hebert (Hebert et al. 2003), and in his study, a model COI profile, based upon the analysis of a single individual from each of 200 closely allied species of lepidopterans, was 100% successful in correctly identifying subsequent specimens. Hebert's results provided reliable evidences for DNA barcode systems. After that, many scholars began to use DNA barcode technology for species identification, diversity analysis and phylogenetic analysis (Ball et al. 2005; Hajibabaei et al. 2006; Ceccarelli et al. 2012). Herein, with the development of sequencing technology and the reduction of sequencing costs, more scholars conducted in-depth researches on the genome of species and found the use of COI to identify species was a great controversial issue because it's difficult to provide a unified discrimination standard that what's the range of COI sequence variation rate between two different species (Moritz et al. 2004; Dasmahapatra et al. 2010). Thereinto, Consortium for the Barcode of Life (CBOL) initiated scientific research activities using COI for species identification on a global scale, and the data showed that the COI sequences of most species exhibited low intraspecific genetic differences and relatively high interspecific genetic differences (Schindel et al. 2005; Ratnasingham et al. 2007; CBOL Plant Working Group 2009). Research data in recent years have also reflected that the similarity of the same species is above 98%, and the sequence difference between species is greater than 2% (Hebert et al. 2010; Zhang et al. 2011; Schmid-Egger et al. 2017; Abd-El-Samie et al. 2018; Halim et al. 2018; Fernandez-Triana et al. 2019). So, in our work, the intraspecific and interspecific differences of COI between A. diffinis and A. radiatum are analyzed.

Materials and methods

Specimens examined are deposited in Chongqing Normal University (China) and Kunming Institute of Zoology, Chinese Academy of Sciences (China). Descriptions were made under a stereomicroscope (Olympus SZ61). All figures were taken and measured with Keyence VHX-5000 digital microscope. Body length was measured from the anterior margin of head to the posterior margin of metasomal tergum II by KEYENCE-VHX-5000. Photoshop CS6 was used to make the figure plates. For the description of punctures, "sparsely" means that interspaces are larger than one puncture diameter, "moderately" means equal to the diameter, and "densely" means less than one diameter.

A total of 19 dried and pinned specimens belonging to A. diffinis and A. radiatum were examined, among which some were difficult to separate from A. diffinis and A. ra*diatum*. In order to exactly identify these specimens, we selected seven specimens of A. diffinis, A. radiatum and three other species (Allorhynchium argentatum, Allorhynchium chinense, and Anterhynchium flavomarginatum) for molecular identification (Table 1). According to the manufacturer's instructions (https://www.giagen.com), genomic DNAs were extracted from muscle tissues using QIAamp DNA Mini Kit (QIAGEN, Germany). The COI genes were amplified by using standard primers LCO1490 and HCO2198 (Folmer et al. 1994). PCRs were performed with the manufacturer's instructions (https://www.cwbiotech.com). Products of PCRs were sequenced in Sangon Biotech (Shanghai) Co., Ltd. Seven COI sequences newly obtained and the COI seguence of Vespa mandarinia (Sample ID: AAW6949) downloaded from Centre for Biodiversity Genomics (http://v4.boldsystems.org/index.php) were aligned with Clustal W version 1.8 (Altschul et al. 1997) in this study (Table 1). These sequences were checked for stop codons and frame shifts using the invertebrate mitochondrial code and the standard code respectively as implemented in MEGA 6.0 (Molecular Evolutionary Genetics Analysis version 6.0) (Tamura et al. 2013). The maximum likelihood (ML) tree (Felsenstein 1981; Kishino et al. 1990) of the COI sequences was analyzed in PhyML 3.0 (Guindon et al. 2010).

Abbreviations:

- CQNU Chongqing Normal University, Chongqing, China;
- **KIZ** Kunming Institute of Zoology, Kunming, China;
- A1 for antennal segment 1;
- A2 for antennal segment 2;
- T1 for metasomal tergum 1;
- **T2** for metasomal tergum 2;
- **S1** for metasomal sternum 1;
- **S2** for metasomal sternum 2, and so on.

Table 1. The information of <i>COI</i> genes used	l in	this	study.
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Species	Collecting site	Subfamily	Accession number
Al. diffinis	Sichuan (China)	Eumeninae	MT196405
Al. radiatum	Guizhou (China)	Eumeninae	MT188371
Al. A	Guangxi (China)	Eumeninae	MT188373
Al. B	Guangdong (China)	Eumeninae	MT188372
Al. argentatum	Guangxi (China)	Eumeninae	MT178403
Al. chinense	Yunan (China)	Eumeninae	MT178402
An. flavomarginatum	Hubei (China)	Eumeninae	MT178404
Vespa mandarinia	Primorskiy (Russia)	Vespinae	AAW6949

Taxonomy

Allorhynchium van der Vecht, 1963

Allorhynchium van der Vecht, 1963: 57–58. Type species: *Vespa argentata* Fabricius, 1804, by original designation.

Archancistrocerus Giordani Soika, 1986: 143–146. Type species: Archancistrocerus diffinis Giordani Soika, 1986, by original designation.

Halysituberosus Dong & Wang, 2017: 184. Type species: Halysituberosus menglianensis Dong & Wang, 2017, by original designation (syn. nov.).

Diagnosis. Anterior face of pronotum without foveae; tegula longer than wide, emarginated apically and not reaching posterior end of parategula; epicnemial carina present; dorsolateral margin of propodeum somewhat rounded and without teeth-like projections; T1 either evenly rounded or rather rectangular in lateral view, in some species T1 with somewhat transverse carina basally; in some species, S2 of male convex, or protruding medially into a transverse crest in lateral view; S7 of male with flat uplifted area or 1–3 teeth; metasoma sessile (Tan et al. 2018).

Notes. Dong and Wang (2017) established the genus *Halysituberosus* by the three following characters: apical margin of clypeus widely emarginated (Figs 2, 12), vertex without cephalic foveae, and both S2 and S7 with tubercles in male (Figs 6, 7, 16, 17). After our examination of its type species, it is verified that *Halysituberosus* Dong & Wang, 2017 belongs to *Allorhynchium* van der Vecht, and *Halysituberosus yingjiangensis* Dong & Wang, 2017 is a new synonym of *Allorhynchium lugubrinum* (Cameron, 1900) and *Halysituberosus menglianensis* Dong & Wang, 2017 should be transferred to *Allorhynchium*.

Distribution. Oriental, Australian and Palearctic regions.

Allorbynchium menglianensis (Dong & Wang, 2017) comb. nov. Figs 1–9

Halysituberosus menglianensis Dong & Wang, 2017: 184.

Material examined. Holotype, ♂, CHINA, Yunnan Prov., Puer City, Menglian County, 22°19.746'N, 99°35.049'E, 962 m, 13.VI.1989, Dazhi Dong (KIZ 0101842).

Diagnosis. Dong and Wang (2017) reported *Halysituberosus menglianensis* from China (one male). After our examination of the type specimen (Fig. 1), we verify that *Halysituberosus menglianensis* Dong & Wang, 2017 should be transferred to *Allorhynchium*, which is a new combination. It differs from *A. lugubrinum* and other congeners by the combination of the following characters: a yellow square central spot on clypeus (Fig. 2); A13 (Fig. 3) elongate, slightly curved and bent backward beyond the middle of A11; tegula dark black (Figs 4, 5); wings pale brown, without purple



Figures 1–9. *Allorhynchium menglianensis* (Dong & Wang, 2017) comb. nov. **I** habitus (dorsal view) ♂ **2** clypeus, ♂ **3** apex of antenna, ♂ **4** tegula, ♂ **5** mesosoma (dorsal view), ♂ **6** S2, ♂ **7** S7, ♂ **8** metasoma (dorsal view), ♂ **9** information of type specimen.

luster; T1 rather rectangular from lateral view (Fig. 8); apical bands of both T1 and T2 medially interrupted (Figs 1, 8); S2 of male with a large ridge in the middle (Fig. 6); S7 of male with a pair of triangular teeth (Fig. 7).

Distribution. China (Yunnan).

Allorhynchium lugubrinum (Cameron, 1900)

Figs 10-18

Rhynchium lugubrinum Cameron, 1900: 532.
Allorhynchium lugubrinum: van der Vecht, 1963: 60; Giordani Soika 1996: 37; Girish Kumar and Sharma 2015: 21; Girish Kumar et al. 2016: 30.
Halysituberosus yingjiangensis Dong & Wang, 2017: 184–186. (syn. nov.)

Material examined. 1Å, CHINA, Yunnan Prov., Dehong City, Yingjiang County, 24°41.722'N, 97°56.772'E, 844 m, 7.X.1997, Dazhi Dong (KIZ 0101842).

Diagnosis. Dong and Wang (2017) reported *Halysituberosus yingjiangensis* from China (one male). After our examination of the type specimen (Fig. 10), *Halysituberosus yingjiangensis* Dong & Wang, 2017 is identified to be new synonym of *Allorhynchium lugubrinum* (Cameron, 1900). It differs from *A. quadrimaculatum* and other congeners by the combination of the following characters: clypeus rugose-punctate medially, almost yellow (Fig. 12); apex of pronotum with yellow band (Figs 10, 13); tegula reddish brown (Fig. 14); wings pale brown, without purple luster; T1 rather rectangular from lateral view, yellow apical bands of both T1 and T2 medially interrupted (Fig. 15); S2 slightly convex, not protruding medially into a crest in lateral view (Fig. 16); S7 of male with a pair of flat lobe-shaped protuberances (Fig. 17).

Distribution. China (Yunnan); India.

Allorhynchium diffinis (Giordani Soika, 1986)

Figs 20-28

Archancistrocerus diffinis Giordani Soika, 1986: 143–146. *Allorhynchium diffinis* (Giordani Soika, 1986): Tan et al. 2018: 49–64.

Material examined. $6\Im \Im 1$, CHINA, Sichuan Prov., Leshan City, Emeishan County, Shaxi Town, 29°25.083'N, 103°26.913'E, 926 m, 11.VIII.2011, Tingjing Li (CQNU); $2\Im \Im$, CHINA, Sichuan Prov., Yaan City, Lushan County, Taiping Town, Chunguang village, 30°18.794'N, 102°59.351'E, 964 m, 12.VIII.2018, Xue Zhang (CQNU); 1 \Im , CHINA, Sichuan Prov., Yaan City, Lushan County, Shuangshi Town, Xichuan village, 30°16.129'N, 102°53.403'E, 982 m, 11.VIII.2018, Huachuan Wang and Qian Han (CQNU).

Notes. The species *A. diffinis* in the original description was identified on a single female from Sichuan, China (Giordani Soika 1986) and *A. radiatum* Li et al., 2019 was related to it. In this study, some more specimens of *A. diffinis*, including one male were also collected from Sichuan. Meanwhile, some specimens (*Allorhynchium* A, Figs 37–46) from Guangxi, China are similar to both *A. diffinis* and *A. radiatum*, and some other female specimens (*Allorhynchium* B, Figs 47–52) from Guangdong, China are similar to *A. radiatum* by black body (Fig. 47). To precisely classify these specimens, *COI* genes of *A. diffinis*, *A. radiatum*, *Allorhynchium* A and *Allorhynchium* B



Figures 10–18. Allorhynchium lugubrinum (Cameron, 1900) 10 habitus in dorsal view, ♂ 11 apex of antenna, ♂ 12 clypeus, ♂ 13 mesosoma (dorsal view), ♂ 14 tegula, ♂ 15 metasoma (dorsal view), ♂ 16 S2, ♂ 17 S7, ♂ 18 information of type specimen.

are sequenced and analyzed. Four other *COI* sequences of *A. argentatum*, *A. chinense*, *Anterhynchium flavomarginatum* and *Vespa mandarinia* of the same family Vespidae are selected for comparison.



Figure 19. Maximum likelihood tree of eight *COI* sequences (The nodes are shown with their bootstrap values; *Vespa mandarinia* was used as the out-group)

Sequence alignment results display that the same COI sequence occurs in Allorhynchium A, Allorhynchium B and A. radiatum, and 29 different nucleic acids are present in A. radiatum, Allorhynchium A, Allorhynchium B and A. diffinis (Suppl. material 1: Figure S1). ML tree topology reflects that A. diffinis is sister of A. radiatum, Allorhynchium A and Allorhynchium B, with 100% bootstrap value of support for the branch(Fig. 19); the genetic pairwise distance based on K2P (Kimura-2-parameter substitution model) (Kimura 1980) among Allorhynchium A, Allorhynchium B and A. radiatum is 0 and the distance between A. diffinis and A. radiatum, Allorhynchium A, and Allorhynchium B is 4.3% (Table 2). According to Hebert's view that the average difference of COI sequences within the same species is usually less than 2% (Hebert et al. 2003), our results suggest that both Allorhynchium A and Allorhynchium B belong to A. radiatum, and A. diffinis and A. radiatum be valid species, respectively.

First description of male (Fig. 21): sculpture, punctuation, setae, and coloration similar to female (Figs 20, 23, 26); body length 13.5 mm, with large yellow spots and bands (Fig. 21): clypeus (Fig. 24) wholly, wide band along lower inner eye orbit, large inter-antennal spot, scape ventrally, wide anterior band of pronotum, large spot

	(1)	(2)	(3)	(4)	(5)	(6)	(7)
(1) Allorhynchium diffinis							
(2) Allorhynchium radiatum	0.043						
(3) Allorhynchium A	0.043	0.000					
(4) Allorhynchium B	0.043	0.000	0.000				
(5) Allorhynchium chinense	0.152	0.166	0.166	0.166			
(6) Allorhynchium argentatum	0.130	0.146	0.146	0.146	0.064		
(7) Anterhynchium flavomarginatum	0.182	0.176	0.176	0.176	0.192	0.186	
(8) Vespa mandarinia	0.248	0.248	0.248	0.248	0.230	0.229	0.214

Table 2. Genetic distance among eight specimens based on K2P and COI sequences.



Figures 20–28. *Allorhynchium diffinis* (Giordani Soika, 1986) **20** habitus (dorsal view) \bigcirc **21** habitus (dorsal view) \bigcirc **22** genitalia (front view), \bigcirc **23** clypeus, \bigcirc **24** clypeus, \bigcirc **25** apex of antenna, \bigcirc **26** metasoma (dorsal view), \bigcirc **27** S2, \bigcirc **28** S7, \bigcirc .

on mesepisternum, tegula except a central translucent spot, parategula, two spots of metanotum, dorsal and posterior faces of propodeum largely, wide apical band on each of both terga I and II; head and mesosoma coarsely punctate, punctures of metasoma sparser than those of head and mesosoma; A13 (Fig. 25) blunt, short and bent backward not beyond the middle of A11; S2 (Fig. 27) protruding medially into a big and strong crest in lateral view and rounded apically; S7 (Fig. 28) with three distinct teeth at basal area; genitalia as in Fig. 22: apex of penis valve not round in frontal view, apex of volsella slightly narrow in frontal view.

Diagnosis. Body with large yellow markings: clypeus wholly, anterior half of pronotum, propodeum largely, tegula except brown spot, parategula, and wide apical bands on T1–T2; clypeal apex deeply emarginated and forming acute tooth on each lateral side; body with coarse punctures, punctures on both head and mesosoma denser than those on metasoma; A13 short, bent backward, and not beyond the middle of A11; S2 protruding medially into a big and strong crest and rounded apically; S7 with three distinct teeth at basal area.

Distribution. China (Sichuan).

Allorhynchium radiatum Li, Barthélémy & Carpenter, 2019

Figs 29-52

Allorhynchium radiatum Li, Barthélémy & Carpenter, 2019: 139-140.

Material examined. 1913, CHINA, Guizhou Prov., Qiannan City, Libo County, Maolan National Nature Reserve, Dongdai Village, 25°23.408'N, 108°04.374'E, 576 m, 21.VI.2015, Tingjing Li and Yan Peng (CQNU); 299333, CHINA, Guangxi Prov., Guilin City, Longsheng County, Sanmen Town, Huaping National Nature Reserve, 25°37.454'N, 109°54.957'E, 740 m, 16.VII.2018, YanPeng and Xue Zhang (CQNU); 299, CHINA, Guangdong Prov., Shaoguan City, Shixing County, Chebaling National Nature Reserve, 24°43.503'N, 114°15.658'E, 357 m, VI.2018, Feiyue Du (CQNU).

Notes. The species *A. radiatum* was described on a single female from Hong Kong, China (Li et al. 2019). The type specimen is almost wholly black except yellow spots on head. According to the results of *COI* genes in this study (Fig. 19), there are some variations of morphological characters within the species. Among the specimens which are collected from other areas of China, those from Guizhou (Figs 29–36) and Guangxi (Figs 37–46, *Allorhynchium* A) are with more yellow markings than the type specimen (figs 33, 34 of Li et al. 2019) and those from Guangzhou (Figs 47–52, *Allorhynchium* B), and S2 of male protruding medially into a transverse crest or indistinctly convex (Figs 35, 43–45).

First description of male (Figs 30, 38): body length 12.8–13.3 mm, forewing length 12.5–12.9 mm. Sculpture, punctuation, setae, and coloration as in female (Figs 29, 37, 47); the following parts yellow: clypeus wholly or except lateral side (Figs 33, 41), scape ventrally, anterior small separated spots of pronotum, and dorso-



Figures 29–36. *Allorhynchium radiatum* Li et al., 2019 (from Guizhou) **29** habitus (dorsal view), \bigcirc **30** habitus (dorsal view), \bigcirc **31** genitalia (front view), \bigcirc **32** clypeus, \bigcirc **33** clypeus, \bigcirc **34** apex of antenna, \bigcirc **35** metasoma (ventral view), \bigcirc **36** S7, \bigcirc .

lateral spots of propodeum; A3–A12 ventrally dark brown; T1 and T2 almost black or with thin and interrupted apical bands (Figs 30, 38); clypeus almost as wide as long, moderately punctate, apical margin strongly emarginated medially, apical width: emar-



Figures 37–46. *Allorhynchium radiatum (Allorhynchium* A, from Guangxi) **37** habitus (dorsal view), ♀ **38** habitus (dorsal view), ♂ **39** genitalia (front view), ♂ **40** clypeus, ♀ **41** clypeus, ♂ **42** apex of antenna, ♂ **43–45** variations of S2, ♂ **46** S7, ♂.

gination depth = 0.58: 0.21, total width: apical width = 1.8: 0.58; A13 (Figs 34, 42) slightly curved and longer than that of *A. diffinis*; S2 protruding medially into a transverse crest or indistinctly convex (Figs 35, 43–45); S7 with three distinct tubercles at



Figures 47–52. *Allorhynchium radiatum (Allorhynchium* B, from Guangzhou) 47 habitus (dorsal view) ♀ 48 head, (dorsal view) ♀ 49 clypeus, ♀ 50 metasoma (dorsal view), ♀ 51 mesosoma (dorsal view), ♀ 52 metasoma (ventral view), ♀.

basal area (Figs 36, 46); genitalia as in Figs 31, 39, apical tip of penis valve somewhat inflated and round.

Diagnosis. Compared with the related *A. diffinis*, body of *A. radiatum* almost black or just with a few thin yellow markings, A13 elongated and longer than that of *A. diffinis*, punctures on both T2 and S2 distinctly coarser, S2 protruding medially into

a transverse crest or indistinctly convex (in *A. diffinis*, S2 protruding medially into a big and strong crest in lateral view and rounded apically), apex of penis valve round in frontal view (in *A. diffinis*, apex of penis valve not round).

Distribution. China (Hong Kong, Guangdong, Guangxi, Guizhou).

In addition, there was an error that needs to be corrected in the reference (Li et al. 2019): figure 38 of *A. radiatum* in p.138 was misplaced and should be exchanged with figure 89 in page 152.

Allorhynchium quadrimaculatum Gusenleitner, 1997 new record Figs 53–60

Allorhynchium quadrimaculatum Gusenleitner, 1997: 759; 2011: 1362; Tan et al. 2018: 49–64.

Material examined. 299, CHINA, Guangxi Prov., Baise City, Lingyun County, Yuhong Town, Hexiang Village, 24°29.355'N, 106°29.664'E, 791 m, 31.VII.2018, Yan Peng and Zhang Xue (CQNU); 19, CHINA, Guangxi Prov., Baise City, Lingyun County, Yuhong Town, Panxian Village, 24°28.157'N, 106°33.762'E, 964 m, 30.VII.2018, Zhang Xue and Han Qian (CQNU); 1^Q, CHINA, Guangxi Prov., Guilin City, Longsheng County, Sanmen Town, 25°43.789'N, 109°51.905'E, 236 m, 17.VII.2018, Yan Peng and Xue Zhang (CQNU); 1^Q, CHINA, Guangxi Prov., Guilin City, Xingan County, Huajiang Town, Gaozhai Village, 25°50.901'N, 110°28.976'E, 430 m, 19.VII.2015, Tingjing Li (CQNU); 12, CHINA, Guangxi Prov., Fangchenggang City, Shangsi County, Jaoanzhen Town, Shiwandashan National forest park, 22°06.404'N, 107°58.381'E, 280 m, 16.VIII.2017, Xudong Li (CQNU); 1³, Сн-NA, Guangxi Prov., Hechi City, Huanjiang County, Chuanshan Town, Leyi Village, 25°07.015'N, 107°58.820'E, 533 m, 23.VII.2018, Yan Peng (CQNU); 1^Q, Сніла, Sichuan Prov., Pengzhou City, Xiaoyudong Town, Luoyangba Village, 31°11.607'N, 103°45.290'E, 1013 m, 19.VII.2015, Zhang Xue and Han Qian (CQNU); 2♀♀1♂, CHINA, Guizhou Prov., Qiannan City, Libo County, Maolan National Nature Reserve, Dongdai Village, 25°23.408'N, 108°04.374'E, 576 m, 21.VI.2015, Tingjing Li and Yan Peng (CQNU); 1^Q, CHINA, Yunnan Prov., Hekou County, Nanxi Town, 22°37.546'N, 103°56.892'E, 220 m, 19.VII.2015, Liang Wang (CQNU); 1∂, Сні-NA, Yunnan Prov., Hekou County, Nanxi Town, 22°37.546'N, 103°56.892'E, 220 m, 18.VII.2018, Chunfa Chen and Liping Zhao (CQNU).

Diagnosis. Body length 12.2–13.0 mm in female (Fig. 53), 11.9–12.3 mm in male (Fig. 54). Clypeus in female length and width equal, moderately punctate, entirely black, with apical margin strongly emarginate medially, apical width: emargination depth = 0.57: 0.10, total width: apical width = 1.7: 0.57 (Fig. 55); clypeus in male yellow, total width: apical width = 1.5: 0.55, apical margin moderately emarginate medially, apical width: emargination depth = 0.55: 0.12 (Fig. 56); A13 elongate, slightly curved and backward about reaching the middle of A11 (Fig. 57); anterior vertical face of pronotum with smooth; tegula not exceeding parategula; wings dark



Figures 53–60. Allorhynchium quadrimaculatum Gusenleitner, 1997 53 habitus (dorsal view) \bigcirc 54 habitus (dorsal view) \bigcirc 55 clypeus, \bigcirc 56 clypeus, \bigcirc 57 apex of antenna, \bigcirc 58 metasoma (dorsal view), \bigcirc 59 S2, \bigcirc 60 S7, \bigcirc .

brown, with purple luster; (apical yellow bands of T1 and T2 medially interrupted (Figs 53, 58); anterior surface of T1 rectangular in lateral view; S2 in male protruding medially into a transverse crest in lateral view (Fig. 59); S7 of male with pair of triangular teeth (Fig. 60).

Distribution. China (new record: Guangxi, Sichuan, Guizhou, Yunnan); Vietnam; Laos.

Key to the Chinese species of Allorhynchium van der Vecht*

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1	T1 evenly rounded in lateral view and without transverse rim at junction of
_	T1 rather rectangular in lateral view and with transverse rim at junction of
2	anterior and dorsal faces
2	Occipital carina relatively wide laterally; clypeus of male entirely black
	A. chinense (de Saussure, 1862)
_	Occipital carina narrower laterally than the above species; clypeus of male
	with yellow spots
3	T1 and T2 with very small, sparse and thin punctures except lateral and api-
	cal portions
_	T1 and T2 with relatively bigger and denser punctures except lateral and api-
	cal portions A. metallicum (de Saussure, 1852)
4	Emargination of clypeal apex relatively wider and shallower (Figs 2, 12, 55,
	56); S7 of male with two small teeth basally (Figs 7, 17, 60)5
_	Emargination of clypeal apex narrower and deeper, almost semicircular
	(Figs 23, 24, 32, 33, 40, 41, 49); S7 of male with three small teeth basally
	(Figs 28, 36, 46)
5	Tegula reddish brown (Fig. 14); S7 of male with pair of flat lobe-shaped pro-
	tuberances (Fig. 17)
_	Tegula dark black (Figs 4, 5, 53, 54); S7 of male with pair of triangular teeth
	(Figs 7, 60)6
6	Wings dark brown, with purple luster (Fig. 53); S2 of male protruding medi-
	ally into a short and high tuber (Fig. 59)
	A. auadrimaculatum Gusenleitner. 1997
_	Wings pale brown without purple luster (Fig. 1): S2 of male protruding me-
	dially into a transverse high and strong crest (Fig. 6)
	A mongligneneris (Dong & Wong 2017) comb nov
7	Body almost black as with faw vallow markings T1 and T2 without anical
/	body annost black of with new yellow markings, 11 and 12 without apical
	20, 27, 28, (7), A12 is real along to (Figs 24, (2)) \$2 protocoling realized in the state of the
	50, 57, 58, 47; A15 in male elongate (Figs 54, 42); 52 protrucing medially
	into a transverse crest or indistinctly convex (Figs 35, 43–45); apex of volsella
	round in frontal view (Figs 31, 39)
-	Body largely with yellow markings, both T1 and T2 with great wide yellow
	apical bands (Figs 20, 21, 31); A13 in male relatively shorter (Fig. 25); S2 pro-
	truding medially into a big, round and strong crest (Fig. 27); apex of volsella
	not round in frontal view (Fig. 22)

^{*} The characters are applicable to both sexes unless the sex is specified; the female of *A. menglianensis* (Dong & Wang, 2017) is unknown.

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Supplementary material I

Figure S1

Authors: Li Luo, Qiao-Hua Zhang, Bin Chen, Ting-Jing Li

Data type: multimedia

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RESEARCH ARTICLE



Potter wasps of the genus Labus (Hymenoptera, Vespidae, Eumeninae) from Vietnam, with description of two new species

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Abstract

Taxonomy of the potter wasps of the genus *Labus* from Vietnam is reviewed, with six species recorded. Of them, one species previously identified as *L. clypeatus* van der Vecht, 1935 is described as new, namely *L. angulus*, **sp. nov.** Another new species, *Labus obtusus* **sp. nov.**, is also described. In addition, a key to all species of the genus occurring in Vietnam is given.

Keywords

Labus, solitary wasps, new species, Vietnam

Introduction

The genus *Labus* was created by de Saussure (1867), and Bingham (1897) subsequently designated *Labus spiniger* as type. Up to now, the genus contains 16 species, all distributed in the Oriental region (van der Vecht 1935; Giordani Soika 1960, 1973, 1986, 1991; Gusenleitner 1988; Girish Kumar et al. 2014; and Li and Carpenter 2018).

Nguyen et al. (2014) recorded the genus and two species, *Labus clypeatus* van der Vecht, 1935 and *Labus lofuensis* Giordani Soika, 1973 from Vietnam. Careful examination of the specimens of the first taxon show that it is not *Labus clypeatus* but a new species close to it, which shares the character of propodeum posteriorly on each side without a tooth above the apical spine, but it has apical teeth of the clypeus sharper and frontal ocellus larger. Recently, Li and Carpenter (2018) recorded two other species from Vietnam, namely *Labus amoenus* van der Vecht, 1935 and *Labus pusillus* van der Vecht, 1963.

In this paper, based on specimens deposited in the Institute of Ecology and Biological Resources (IEBR), two new species of the genus *Labus* from Vietnam are described and figured. A key to all species occurring in Vietnam is also presented.

Material and methods

All material including the holotype of the new species is deposited in the Institute of Ecology and Biological Resources (**IEBR**), Hanoi, Vietnam. The adult morphological and color characters were observed using pinned and dried specimens under a stereoscopic microscope. Measurements of body parts were made with an ocular micrometer attached to the microscope. "Body length" indicates the length of head, mesosoma and the first two metasomal segments combined. Terminology follows Carpenter and Cumming (1985) and Yamane (1990). Photographic images were made with a Nikon SMZ 800N Digital Stereo Microscope, using Helicon Focus 7 software; the plates were edited with Photoshop CS6.

In the descriptions of adult morphology, the following abbreviations are used: The abbreviations F, S and T refer to numbered flagellomeres, metasomal sterna and metasomal terga, respectively; IED-c and ISD-c refers to collectors of the Insect Ecology Department and Insect Systematic Department, IEBR.

Taxonomic accounts

Genus Labus de Saussure, 1867

Labus de Saussure, 1867, Reise Novara, Zool. 2 (1), Hym: 3, genus.

Type species. Labus spiniger de Saussure, 1867, by subsequent designation of Bingham 1897: 348.

Labus angulus Nguyen & Carpenter, sp. nov. http://zoobank.org/88E70FB5-4FAE-42E6-8962-D224179CD050

Figs 1–7

Labus clypeatus van der Vecht, 1935: Nguyen et al. 2014: 11, misidentification.

Material examined. *Holotype*, female, Vietnam: Dien Bien, 21°56'16.7"N, 102°52'58"E, alt. 500 m, 22 Jul. 2009, Nguyen TPL, Pham HP & Kojima J leg., deposited in IEBR.

Dianosis. This species can be distinguished from all other congeners by the following combination of characters: Propodeum with posterior excavation not margined above; metasomal segment I long and slender, swollen part slightly longer than half the total length of the petiole; TI in dorsal view more than 9 times as long as wide at base; TII with thick lamella, about 1.16 times as long as wide in dorsal view; female frontal fovea much larger than anterior ocellus, oval.

Description. Female (Fig. 7). Holotype: Body length 7.2 mm; fore wing length 6.2 mm.

Head in frontal view subcircular, about 1.1 times as wide as high (Fig. 1). Head with frontal fovea much larger than anterior ocellus, oval, with distinct border (Fig. 2). Gena almost as wide as eye; occipital carina complete, present along entire length of the gena. Inner eye margins strongly convergent ventrally, in frontal view nearly 1.45 times further apart from each other at vertex than at clypeus (Fig. 1). Clypeus in lateral view prominently convex at basal half, then slightly depressed and bent backward to apical margin; in frontal view about 1.18 times as wide as high (Fig. 1), with basal margin emarginated medially, forming a sharp tooth on each side (Fig. 1); width of the emargination about 1/4 width of clypeus between inner eye margin. Mandible with four prominent teeth. Antennal scape about 4.4 times as long as its maximum width, curved; FI about 1.26 times longer than wide, FII–III longer than wide, FIV–IX wider than long, terminal flagellomere bullet-shaped, as long as its basal width.

Mesosoma longer than wide in dorsal view (Fig. 3). Pronotal carina raised, pronotal corner strongly produced to form long and sharp projection (Fig. 2). Mesoscutum weakly convex, 1.2 times as long as wide between tegulae. Scutellum weakly convex, in lateral view at the same level as mesoscutum. Metanotum with a short, tooth-like, sharp tubercle in the middle. Propodeum (Fig. 4) excavated in the middle apically, with posterior excavation not margined above, with a distinct median longitudinal furrow, rounded between posterior and lateral surfaces.

Metasomal segment I much narrower than segment II, swollen part slightly longer than half of the length of the petiole (0.56 times as long as the total length of the petiole) (Fig. 5). TI in dorsal view about 9.35 times as long as wide at base, and 3.45 times as long as wide at apex (Fig. 5); TII with thick lamella, about 1.16 times as long as wide in dorsal view; SII in lateral view almost straight from base to one-third, and slightly convex then straight to apical margin (Fig. 6).

Body covered with short, silver hairs except lower part of propodeum with dense long silver hairs.

Clypeus with dense, coarse punctures in the middle area, punctures sparser and smaller at sides, each puncture bearing a silver bristle. Frons densely covered with very coarse punctures, border between punctures with minute punctures and raised to form reticulations. Vertex and gena with punctures similar to those on frons. Pronotum with punctures coarser than punctures on vertex and gena. Mesoscutum densely and



Figures 1–7. *Labus angulus* sp.nov., holotype, female 1 head, frontal view 2 head, dorsal-frontal view 3 mesosoma, dorsal view 4 propodeum, posterior view 5 TI, dorsal view 6 matasomal segments, lateral view 7 habitus. Scale bars: 0.5 mm.

coarsely covered with punctures similar to those on pronotum, punctures on scutellum dense, coarse and equal than those on mesoscutum, punctures on metanotum smaller. Mesepisternum with punctures similar to those on pronotum posterodorsally, minute

punctures anteroventrally; border between posterodorsal and anteroventral parts indistinct. Dorsal metapleuron with long striae, ventral metapleuron with short striae at inner side, and with sparse shallow punctures. Propodeum with sparse and strong punctures on dorsal and posterior parts, punctures on lateral parts sparser and shallower. TI densely covered with strongly rugose punctures on basal half, with sparse and strong punctures on apical half, TII with sparse and small punctures.

Colour. Body black; following parts orange-yellow: an arcuate transverse band at basal margin of clypeus, large spot on each side of pronotum, two transverse spots on scutellum, spot on apical spine, outer side of tegulae and parategulae, apical band of TI and II. Spot near apical margin of metasomal segment I brown. Legs black; following parts orange-yellow: spot at apical margin of fore and middle femur, fore tibia entirely and outer part of middle tibia.

Male. Unknown.

Distribution. North Vietnam.

Remarks. This species comes close to *Labus clypeatus* van der Vecht in having the propodeum with posterior excavation not margined above, and pronotum with long and sharp projection at the lateral corners, but it is different from the latter by the female head with frontal fovea much larger than anterior ocellus, oval (head with frontal fovea small, slightly larger than anterior ocellus, round in *L. clypeatus*), female clypeus with sharper teeth, and swollen part of the petiole longer than half the total length of the petiole (swollen part shorter than half the total length of the petiole in *L. clypeatus*).

Etymology. The specific name refers to the very sharp and long projecting lateral angle of the pronotum.

Labus obtusus Nguyen & Carpenter, sp. nov.

http://zoobank.org/DC8AE56E-26EE-450E-8947-75D001ED3B39 Figs 8–14

Material examined. *Holotype*, male, Vietnam: Bidoup Nui Ba NP, Da Chais, Lac Duong, Lam Dong, 12°08'403"N, 108°38'56.3"E, alt. 1428 m, 4 Jun. 2013, Nguyen TPL leg., deposited in IEBR. Paratype: 1 male, same data as holotype.

Dianosis. This species can be distinguished from all other congeners by following combination of characters: Propodeum with posterior excavation not margined above; metasomal segment I with swollen part longer than half the total length of the petiole; TI in dorsal view slightly less than 9 times as long as wide at base; TII in dorsal view almost as wide as long.

Description. Male (Fig. 14). Body length 6.9–7.1 mm (holotype 6.9 mm); fore wing length 5.9–6.1 mm (holotype 5.9 mm).

Head in frontal view subcircular, about 1.2 times as wide as high (Fig. 8). Head without frontal fovea. Gena slightly narrower than eye; occipital carina complete, present along entire length of the gena. Inner eye margins strongly convergent ventrally; in frontal view nearly 1.6 times further apart from each other at vertex than at clypeus (Fig. 8). Clypeus in lateral view prominently convex at basal half, then straight to api-

cal margin; in frontal view nearly as wide as long (Fig. 8), with basal margin slightly convex medially and distinctly separated from antennal sockets; apical margin emarginated medially, forming a sharp tooth on each lateral side (Fig. 8); width of the emargination less than 1/4 width of clypeus between inner eye margin. Mandible with four prominent teeth. Antennal scape about 4.2 times as long as its maximum width, curved; FI about 1.8 times longer than wide, FII–III longer than wide, FIV – VIII wider than long, FXI nearly 1.2 times as long as wide, FX small, FXI thin, slightly curved, and long, slightly more than 5 times as long as wide (Fig. 9).

Mesosoma longer than wide in dorsal view (Fig. 10). Pronotal carina raised, pronotal corner slightly produced to form short and blunt projection (Fig. 10). Mesoscutum weakly convex, 1.1 times as long as wide between tegulae. Scutellum weakly convex, in lateral view at the same level as mesoscutum. Metanotum with a short, tooth-like, blunt tubercle in the middle. Propodeum (Fig. 11) excavated in the middle apically, with posterior excavation not margined above, with a distinct median longitudinal furrow except the middle part with short transverse striation, border between posterior and lateral surfaces rounded.

Metasomal segment I much narrower than segment II, swollen part slightly longer than half of the length of the petiole (0.55 times as long as the total length of the petiole) (Fig. 12). TI in dorsal view about 8.8 times as long as wide at base, and 3.1 times as long as wide at apex (Fig. 12); TII with thick lamella, almost as wide as long in dorsal view; SII in lateral view almost straight to one-third from base, then slightly convex and straight to apical margin (Fig. 13).

Body covered with short, silver hairs except clypeus, mandible and lower part of propodeum with dense long silver hairs.

Clypeus with sparse and shallow punctures in the middle area, almost smooth at sides. Frons densely covered with very coarse punctures, border between punctures not raised. Vertex and gena with punctures similar to those on frons. Pronotum with punctures coarser than punctures on vertex and gena, spaces between punctures raised to form reticulation. Mesoscutum densely and coarsely covered with flat-bottomed punctures, punctures on scutellum dense, coarse and equal to those on mesoscutum, punctures on metanotum smaller. Mesepisternum with punctures similar to those on pronotum posterodorsally, minute punctures anteroventrally; border between posterodorsal and anteroventral parts indistinct. Dorsal metapleuron with some long striae, ventral metapleuron with short striae at inner side, and with some sparse shallow punctures. Propodeum with sparse and strong punctures on dorsal and posterior parts, punctures on lateral parts sparser and shallower. TI densely covered with strongly rugose punctures on basal half, with sparse and strong punctures on apical half, TII with sparse and small punctures.

Colour. Body black; following parts yellow: clypeus except black apical margin, large spot on each side of pronotum, two transverse spots on scutellum, spot on apical spine, outer side of tegulae and parategulae; apical band of TI, II and SII. Legs black; following parts yellow: spot at apical margin of middle femur and hind tibia, middle tibia entirely.

Female. Unknown.

Distribution. South Vietnam.


Figures 8–14. *Labus obtusus* sp. nov., holotype male 8 head, frontal view 9 right antenna 10 mesosoma, dorsal view 11 propodeum, posterior view 12 TI, dorsal view 13 metasomal segments, lateral view 14 habitus. Scale bars: 0.5 mm.

Remarks. This species comes close to *Labus angulus* sp. nov. in having the swollen part of metasomal segment I longer than half of the total length of the petiole, and propodeum with posterior excavation not margined above, but it is different from the latter in having the pronotum with short and blunt projections at lateral corners (pronotum with long and sharp projections at lateral corners in *L. angulus*).

Etymology. The specific name refers to the obtuse lateral projections at the corners of the pronotum.

Labus amoenus van der Vecht, 1935

Figs 15, 16

Labus amoenus van der Vecht, 1935, Treubia 15: 159, 161 (key), 162, fig. 1a-f, male, female – "West-Java: ... Buitenzorg" (holotype male Leiden).

Notes. This species has been recorded from Vietnam (Ha Giang province in the northern part of the country) by Li and Carpenter (2018). In our study, the species has been newly recorded from a central province, Quang Nam.

Material examined. VIETNAM: Quang Nam: 1 male, Phuoc My, Phuoc son, 450– 500m, 26 May 2006; 1 male, Phuoc Son, Phuoc Hiep, 300m, 30 Jul. 2004, ISD-c. INDONESIA: West Java: 1 female, Buitenzorg Djasinga, 6.vi.1937, M.A. Lieftinck leg.; 1 male, Tjibarangbang Djasinga, 15.xi.2016, E.v.d.Vecht B leg.

Distribution. India: Meghalaya; Laos; Malaysia; Singapore; Indonesia: Java, Sumatra (including Bangka); Vietnam; China.

Labus clypeatus van der Vecht, 1935

Figs 17, 18

Labus clypeatus van der Vecht, 1935, Treubia 15: 162 (key), 166, male, female, fig. 11-m – "Middle-Java: … Semarang" (holotype male Leiden).

Material examined. VIETNAM: Dak Lak: 1 female, Krong Buk, Pong Giang, Buon Ho, 12°56'56.9"N, 108°16'33.8"E, alt. 706 m, 23 Jul. 2012, Nguyen TPL leg. Distribution. Vietnam; Indonesia: Java.

Labus lofuensis Giordani Soika, 1986

Figs 19, 20

Labus lofuensis Giordani Soika, 1973, Boll. Mus. Civ. Stor. Nat. Venezia 24: 99, male, female – "China: Lofu Mount" (holotype male London).

Notes. This species has been recorded from Vietnam (Bac Giang province) by Nguyen et al. (2014). In our study, the species has been newly recorded from several other provinces in the northern part such as Bac Kan, Lang Son, Hanoi, Hai Phong.

Material examined. VIETNAM: Bac Kan: 2 females, Kim Hy NP, Vu Muon, Bach Thong, 22°15'51"N, 105°58'42"E, 5.viii.2012, Kojima J, Nugroho H &



Figures 15–20. 15, 16 *Labus amoenus*: 15 female head, frontal view 16 male head, frontal view 17, 18 *Labus clypeatus*, female: 17 head, frontal view 18 habitus 19, 20 *Labus lofuensis*: 19 female head, frontal view 20 male head, frontal view. Scale bar: 0.5 mm.

IED-c; **Lang Son**: 3 females, Na Sen, Hoang Dong, 31.x.2014, 21°51'42"N, 106°43'54"E, Nguyen DD, Nguyen LTP & Nguyen PM; 8 males, Na Sen, Hoang Dong, 31.x.2014, 21°51'42"N, 106°43'54"E, Nguyen DD, Nguyen TPL & Nguyen PM; **Ha Noi**: 1 male, Van Hoa, Ba Vi, Ba Vi NP, 3.vi.2001, Nguyen TPL; **Bac Giang**: 2 females, Khe Dan, Tuan Dao, Son Dong, 4.vii.2010, Tran DD; 2 male, Khe Dan, Tuan Dao, Son Dong, 4.vii.2010, Tran DD; 2 male, Khe Dan, Tuan Dao, Son Dong, 4.vii.2010, Tran DD; 1 male, Yen Tu NR, Son Dong, 150 m, 2.viii.2010, Pham HP; 1 male, Thanh Son, Son Dong, 7.vii.2010, Tran DD; **Hai Phong**: 1 female, Cat Ba NP, 11.vi.2006; 1 female, Xuan Dam, Cat Ba, 27.iv.2013, Nguyen DD.

Distribution. China: Guangdong, Macau, Hainan; Vietnam.

Labus pusillus van der Vecht, 1963

Labus pusillus van der Vecht, 1963, Zool. Verh., Leiden 60: 6, fig. 1b, c, female, male – "Deiyannewela, Kandy, Ceylon" (holotype female Basel).

Notes. This species has been recorded from Vietnam (Nghe An province) by Li and Carpenter (2018).

Material examined. No specimen is available for our study.

Distribution. Sri Lanka; India: Andhra Pradesh, Assam, Goa, Himachal Pradesh, Karnataka, Kerala, Maharashtra, Meghalaya, Mizoram, Pondicherry, Sikkim, Tamil Nadu, Uttarakhand, West Bengal; Nepal; Bhutan; Vietnam; China.

Key to species of Labus de Saussure, 1867 from Vietnam

The characters used are applicable to both sexes unless the sex is specified. The characters are taken from the specimens of two new described species in this paper, *L. clypeatus* (female) and *L. amoenus* (male) from Vietnam, *L. amoenus* (female) from Indonesia, and from the description of *L. pusillus* following van der Vecht (1963).

1	Propodeum with posterior excavation not margined above
_	Propodeum with posterior excavation margined above
2	TI with the total length much more than 9 times as long as wide at base,
	pronotum with long and sharp projection at the lateral corners
_	TI with the total length less than 9 times as long as wide at base, pronotum
	with shorter and blunter projection at the lateral corners4
3	Metasoma segment I with swollen part less than half of the total length of the
	petiole, head with frontal fovea slightly larger than anterior ocellus, round,
	border not distinct L. clypeatus van der Vech
_	Metasoma segment I with swollen part slightly more than half of the total
	length of the petiole, head with frontal fovea much larger than anterior ocel-
	lus, oval, border distinct

4 TI in dorsal view less than 7 times as long as wide at base; basal half cover with slightly rugose punctures. Male clypeus with slightly convex basal margin, apical teeth sharp *L. pusillus* van der Vecht TI in dorsal view more than 8 times as long as wide at base; basal half cover with strongly rugose punctures. Male clypeus with strong convex basal margin, apical teeth blunter *L. obtusus* sp. nov. 5 Female head with frontal fovea deep, distinctly defined, and round; punctures on apical half of petiole and TII stronger and denser; the yellow part of scutellum not divergent, transverse and without roundly projecting posterior Female head with frontal fovea shallower, not distinctly defined, and oval; punctures on apical half of petiole and TII weaker and sparser; the yellow part of scutellum with slightly divergent sides and roundly prominent projecting

Acknowledgements

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Two new reared species of Heteropteron Brullé (Hymenoptera, Braconidae, Cardiochilinae) from northwest Costa Rica, with the first definitive host records for the genus

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Abstract

Two new Costa Rican species of the braconid parasitoid wasp subfamily Cardiochilinae, *Heteropteron kidonoi* Dabek & Whitfield and *Heteropteron hasagawai* Dabek & Whitfield, are described and illustrated from dry forest in the Area de Conservacion Guanacastae, along with data on rearing from their hosts. *Heteropteron kidonoi* is a solitary endoparasitoid of *Stenoma cathosiota* (Lepidoptera: Depressariidae) on *Roupala montana* (Proteaceae), while *H. hasagawai* is a solitary endoparasitoid of *Carthara abrupta* (Lepidoptera: Pyralidae) on the same host plant, but typically at slightly higher elevation localities. Diagnostic characters are provided to distinguish these two new species from each other, and also from the three previously decsribed species of *Heteropteron. Heteropteron kidonoi* and *H. hasagawai* are the first species of *Heteropteron* to have any host data, and also are the first to be reported in Costa Rica.

Keywords

Carthara, Depressariidae, Parasitoid, Proteaceae, Pyralidae, Roupala, Stenoma

Introduction

We report here the description of two new reared species of the relatively rare yet large and colorful cardiochiline braconid wasp genus *Heteropteron*, from the Area de Conservacion Guanacaste (ACG) in northwest Costa Rica. The descriptions are notable for adding significantly to our understanding of the geographic distribution, habitat specialization and host natural history of this unusual genus. The specimens and data supporting the descriptions arise from the long -term rearing inventory of ACG (Janzen et al. 2009).

The definition of *Heteropteron* has had a somewhat confusing history, even in recent years. After first being erected by Brullé (1846) for the unusual slender and polished cardiochiline species H. macula Brullé, several other somewhat similar-looking Neotropical genera were later described: Wesmaelella Spinola, (1853) based on W. rubricollis Spinola, Psilophthalmus Szépligeti, (1902) based on P. nigripennis Szépligeti, and Neocardiochiles Szépligeti, (1908) based on N. fasciipennis Szépligeti. Schulz, (1911) synonymized Psilophthalmus under Wesmaelella and this synonymy has been maintained ever since. The remaining three genera were still considered as distinct as recently as Whitfield and Dangerfield (1997), but two years later Dangerfield et al. (1999) synonymized all three with Heteropteron as the senior synonym. Shortly afterward Mercado and Wharton (2003) pulled Wesmaelella (including Psilophthalmus) out of synonymy with Heteropteron, an arrangement agreed with by Papp (2014), with some reservations still due to confusion in the interpretation of some types. Due to museum loan limitations at the relevant museums, it has never been possible to compare all the types with one another simultaneously, but the situation has been clarified considerably in the last 20 years, and Papp's conclusions are adopted here. Heteropteron appears to be relatively early-diverging within Cardiochilinae based on both morphological and molecular evidence (Dangerfield et al. 1999; Murphy et al. 2008).

As a result of this history, *Heteropteron* currently has 3 described species: *H. fasciipennis* (Szépligeti), *H. macula* Brullé, and *H. whitfieldi* Mercado. All are known from the Neotropical Region, ranging from Mexico to Brazil, primarily in wet tropical forest. None of the three has any recorded hosts. The two new species described below most closely resemble *H. fasciipennis* in general appearance, probably belonging to the same color pattern mimicry complex but differing in mesosoma coloration (dark in *H. fasciipennis*, yellowish orange in the two new species) and other less obvious features such as hypopygium shape and slightly more complex spination of the pectinate tarsal claws). Little is known about this mimicry complex, but similar color patterns are found in the same region among some Heteroptera (Hemiptera) as well as among several other subfamilies of Braconidae, especially Braconinae and Agathidinae.

We do have new host data, however, for both species, constituting the first host records for the genus. *Heteropteron kidonoi* sp. nov., described below, attacks caterpillars of *Stenoma cathosiota* (Depressariidae) (Fig. 1A) on the dry forest shrubby evergreen tree *Roupala montana* (Proteaceae); its very similar congener *H. hasagawai* sp. nov., also described below, specializes on the caterpillars of *Carthara abrupta* (Pyralidae)



Figure 1. A live photo of *Stenoma cathosiota* caterpillar, host of *Heteropteron kidonoi* Dabek & Whitfield, sp. nov. **B** live photo of *Carthara abrupta*DHJ02 caterpillar, host of *H. hasegawai* Dabek & Whitfield, sp. nov.

(Fig. 1B) on the same host plant species, usually at slightly lower elevations. *Carthara abrupta*, as currently defined, feeds on a variety of plants; the form that hosts *H. hasa-gawai* is referred to informally as Carthara abruptaDHJ02. *H. kidonoi* spins its cocoon

within that of the host (Fig. 2); presumably *H. hasagawai* does as well, but we do not have direct documentation of that.

There were also no previously described species of *Heteropteron* recorded for Costa Rica.

Methods

Morphological terminology follows that used in Huber and Sharkey (1993) with usage specific to the microgastroid lineage Braconidae from Dangerfield et al. (1999) and Fernandez-Triana et al. 2014. Photographs were taken at the University of Illinois using a Leica M205 C stereo microscope (467 nm resolution) fitted with a five megapixel Leica DFC 425 digital microscope camera. Image stacking was achieved using a motor drive on the scope and the Leica z-stacking software.

Results

Descriptive Taxonomy

Heteropteron kidonoi Dabek & Whitfield, sp. nov. http://zoobank.org/034479D0-3812-4C7A-9303-C0102695C994 Figs 2–5

Material examined. *Holotype*: Female, COSTA RICA: Guanacaste, Area de Conservación Guanacaste, Sector Orosí, Intersección Mata Redonda, el. 565 m, 10.99574, -85.4948, 29-V-2009; 09-SRNP-13270, DHJPAR0062136 (no sequence), host *Stenoma cathosiota* on *Roupala montana*. Deposited in USNM.

Paratypes: 12 females (09-SRNP-13220, 09-SRNP-13321, 09-SRNP-13425, 09-SRNP-13337, 09-SRNP-13380, 09-SRNP-13290, 09-SRNP-13395, 09-SRNP-13322, 09-SRNP-13306, 09-SRNP-13446; 09-SRNP-13265, 09-SRNP-13421), 14 males (09-SRNP-13436, 09-SRNP-13446; 09-SRNP-13265, 09-SRNP-13399, 09-SRNP-13272, 09-SRNP-13267, 09-SRNP-13285, 09-SRNP-13307, 09-SRNP-13409, 09-SRNP-13359, 09-SRNP-13305, 09-SRNP-13391, 09-SRNP-13254, 09-SRNP-13451), all same data as holotype, no successful barcodes. 4 females (96-SRNP-1218, 96-SRNP-1208, 96-SRNP-1211, 96-SRNP-1214), 2 males (96-SRNP-1212, 96-SRNP-1215), same data as holotype except el. 445m, 10.94106, -85.50822, 01-V-1996, no successful barcodes. 1 female (05-SRNP-45258),1 male (05-SRNP-45272), Costa RICA: Guanacaste, Area de Conservación Guanacaste, Sector Orosí, el. 310 m, 10.95045, -85.54173, 24-V-2005, ex *Stenoma cathosiota* on *Roupala montana*. 2 females, Costa RICA: Guanacaste, Area de Conservación Guanacaste, Sector Orosí, Estacion Maritza, el. 570 m, 10.95922, -85.49514, 23-III-2005, ex *Stenoma cathosiota* on *Roupala montana*. Costa RICA: Guanacaste, Area de Conservación Guanacaste, Sector Orosí, Estacion Maritza, el. 570 m, 10.95922, -85.49514, 23-III-2005, ex *Stenoma cathosiota* on *Roupala montana*. Costa RICA: Guanacaste, Area de Conservación Guanacaste, Sector Orosí, Estacion Maritza, el. 570 m, 10.95922, -85.49514, 23-III-2005, ex *Stenoma cathosiota* on *Roupala montana*.



Figure 2. Cocoon of Stenoma cathosiota, cut open to show (opened) cocoon of H. kidonoi spun within.

nacaste, Sector Orosí, Puente Sontoli, el. 245 m, 10.95119, -85.5975, 30-IV-2008, ex Stenoma cathosiota on Roupala montana. 7 females (02-SRNP-13449, 02-SRNP-13488, 02-SRNP-13521, 02-SRNP-13517, 02-SRNP-13470, 02-SRNP-13501, 02-SRNP-13477), 7 males (02-SRNP-13507, 02-SRNP-13461, 02-SRNP-13453, 02-SRNP-13502, 02-SRNP-13500, 02-SRNP-13320, 02-SRNP-13510), Costa Rica: Guanacaste, Area de Conservación Guanacaste, Sector Santa Elena, Quebrada Nance, el. 310 m, 10.86669, -85.64933, 22-VIII-2002, ex Stenoma cathosiota on Roupala montana. 1 female (02-SRNP-13036), COSTA RICA: Guanacaste, Area de Conservación Guanacaste, Sector Santa Elena, Canyon Draga, el. 280 m, 10.87974, -85.65374, 4 -VIII-2002, ex Stenoma cathosiota on Roupala montana. 1 female (04-SRNP-24239), 1 male (04-SRNP-24740), COSTA RICA: Guanacaste, Area de Conservación Guanacaste, Sector El Hacha, Puedra Duende, el. 450 m, 11.011, -85.54459, 16-IX-2004, ex Stenoma cathosiota on Roupala montana; 2 females (11-SRNP-20911, 11-SRNP-20987), 1 male (11-SRNP-20988), same data but 31-V-2011. 1 female (98-SRNP-4871), 1 male (98-SRNP-4862), COSTA RICA: Guanacaste, Area de Conservación Guanacaste, Sector El Hacha, La Guitarra, el. 355 m, 10.99378, -85.52108, 7-VI-1998, ex Stenoma cathosiota on Roupala montana; 1 male (98-SRNP-4537), same data except 24-II-1998. 1 male, COSTA RICA: Guanacaste, Area de Conservación Guanacaste, Sector El Hacha, Estacion Los Almendros, el. 290 m, 11.03226, -85.52776, 9-VII-2013 (host listed as incorrect in database). 1 female (09-SRNP-21074), COSTA RICA: Guanacaste, Area de Conservación Guanacaste, Sector El Hacha, Genova, el. 210 m, 11.02335, -85.60596, 9-IV-2009, ex Stenoma cathosiota on Roupala montana. 2 males, COSTA RICA: Guanacaste, Area de Conservación Guanacaste, Sector El Hacha, Qurebrada Pitahaya, el. 320 m, 11.01182, -85.53168, 11-IX-2013, ex Stenoma cathosiota on Roupala montana. 1 male (06-SRNP-13274), COSTA RICA: Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa, Aguacaliente, el. 250 m, 10.9303, -85.60297, 9-V-2006, ex Stenoma cathosiota on Roupala montana; 1 female (11-SRNP-13207), same data except 9-V-2011; 1 female, same data except 6-III-2005. 1 female (11-SRNP-55002), COSTA RICA: Guanacaste, Area de Conservación Guanacaste, Sector Mundo Nuevo, Cerro Gongora Pelado, el. 740 m, 10.76307, -85.41332, 2-I-2011, ex Stenoma cathosiota on Roupala montana. Deposited in USNM, CNC, INHS, Museo Nacional de Costa Rica, Hymenoptera Institute (116 Franklin Ave, Redlands, CA 92373).

Body length excluding head. Average male, 7.5 mm; average female, 8.0 mm.

Body color (Fig. 3): Mesosoma pale except anterior propleuron dark, head black, metasoma variable with majority (31/42 specimens) with terga 6–8 dark, 1–5 pale. Antenna color: scape, pedicel, and flagellum dark. Coxa, trochanter, trochantellus dark. Forefemur variably pigmented, ventrally dark toward center. Tibia, tarsus, tibial spurs light. Pretarsus and tarsal claws dark, aroliar pad dark (Fig. 5D). Wings alternately banded light and dark (Figs 3A, B, 4C).

Head. Epistomal sulcus present, lightly impressed. Setose except vertex and occiput, sparsely so on clypeus. Setae light yellowish in color. Clypeus weakly and evenly convex. Clypeus $1.9 \times$ broader than high, $2.1 \times$ length of malar space. Clypeal margin truncate. Scape $2 \times$ longer than broad, inner side deeply excised apically, base $2.2 \times$ narrower than broadest point. First flagellomere $2.8 \times$ as long as broad.

Face (Fig. 4A) $1.6 \times$ broader than high. Galea dark, $1.5 \times$ longer than wide. Glossae light, bilobed, similar in shape to galea: semicircular distally. Frons smooth, deeply excavated, excavation extending longitudinally from base of antennae to vertex and transversely from inner margin of left eye to inner margin of right eye. Frons dorsally with Y-shaped shallow ridge, with branches terminating immediately anteriorad median ocellus (Fig. 4B). Ocelli elevated within excavation with some setae. Small ridge evident at antennal base. Antenna with 36–37 flagellomeres.

Mesosoma. Pronotal collar unsculptured except for marginal ridges anteriorly and posteriorly with visible setal pits, lateral pronotum sculptured ventrally, reaching mesopleuron and dark in color, dorsally transitioning to light color with groove reaching subalar depression. Notauli smooth, incomplete, distinct anteriorly, evanescent posteriorly, extending about half length of mesoscutum; mesoscutum smooth, about as broad as long, flattened dorsally in lateral view, medial lobe bulging anteriorly, sparsely covered with brownish yellow setae.

Scutellum triangular, smooth, flat in lateral view, lateral areas bare and smooth. Posterior end of scutellum margined by ridge (Fig. 3A).

Metanotum smooth. Propodeum smooth, areola with complete longitudinal furrow, narrowing anteriorly, margined by weak carinae; pilosity moderate with high abundance in vicinity of spiracles. Setae near areola 10 × longer than distance between adjacent setae; spiracles 1.8 × longer than wide. Sternaulus indistinct, episternal scrobe present, sometimes weakly indented, not extended to sternaulus. Subalar depressions



Figure 3. Heteropteron kidonoi Dabek & Whitfield A dorsal habitus B lateral habitus.

smooth with median carina forming obtuse angle. Subalar prominence tapering posteriorly to pleural sulcus, smooth, convex. Pleural sulcus with double grove. Posterior margin of mesopleuron smooth. Mesopleuron (Fig. 5A) smooth, lightly setose ven-



Figure 4. *Heteropteron kidonoi* Dabek & Whitfield **A** frontal view of face **B** dorsal view of frons and occiput, showing y-shaped ridge **C** wings, showing banding pattern.

trally. Metapleuron with distinct dorsal-ventral groove originating halfway down the dorsal edge of the metapleuron and ending at the posterior end of the ventral margin (forming distinct anterior and posterior separation), dorsoposterior of metapleuron setose, setae yellow.

Legs. Hind tibia gradually broadening distally, distal end $1.8 \times as$ broad as proximal end. Hind femur $5 \times as$ long as broad distally. Hind basitarsus same length as tarsomeres 2–5 combined, inner spur of hind tibia half the length of basitarsus. Second tarsus of fore leg $1.4 \times longer$ than broad, fifth tarsus of foreleg $1.6 \times longer$ than broad;



Figure 5. *Heteropteron kidonoi* Dabek & Whitfield **A** lateral view of mesosoma **B** lateral view of hypopygium tip and ovipositor with sheaths **C** tibial spines **D** last tarsal segment, showing pectinate claws and dark arolium.

second tarsus of mid leg $1.7 \times$ longer than broad, fifth tarsus of mid leg $1.7 \times$ longer than broad; second tarsus of hind leg $1.7 \times$ longer than broad, fifth tarsus of hind leg $1.5 \times$ longer than broad. Tibial spines, up to 12, generally > 6 in two alternating rows, variable in number and pattern. (Fig. 5C).

Wings. Forewing $1.15 \times \text{longer}$ than body. Pterostigma elongate, issuing *r* from its middle. Second submarginal cell long. Color pattern as in Fig. 4C.

Metasoma. First tergite 1.25 × broader posteriorly than long. Third tergite 1.2 × as long as second tergite. Second latero-tergite well visible in dorsal view (Fig. 3A). All tergites polished. Hypopygium narrow laterally, tapering to rounded tip ventrally (Fig. 5B). Exserted ovipositor sheath as long as tarsomeres 1–5 combined, dark on posterior side.

Cocoon. Elongate, silk light tan externally and white internally, spun within the cocoon of its host (Fig. 2).

Host. Caterpillars of *Stenoma cathosiota* (Depressariidae) (Fig. 1A) on *Roupala montana* (Proteaceae).

Etymology. *Heteropteron kidonoi* is named in honor of Dr. Hiroshi Kidono (retired) of Japan International Collaboration Agency (JICA), who first came to ACG in 1992 and has since then, and hopefully many years more, been a major supporter of all aspects of ACG, ranging from financing to Hesperiiidae taxonomy to female parataxonomists to international conservation biopolitics.

Diagnosis. This new species differs from *H. fasciipennis* most obviously in having a yellowish orange (in older specimens occasionally somewhat brownish) mesosoma rather than mostly blackish. From *H. hasegawai*, described below, it can be distinguished by its slightly to significantly darker yellowish portions of the metasoma (Figs 3, 5A), more acutely pointed hypopygium tip (Fig. 5B), more numerous and differently arranged small spines on the mid tibia (Fig. 5C), and the dark tarsal arolia (Fig. 5D).

Heteropteron hasagawai Dabek & Whitfield, sp. nov.

http://zoobank.org/8A5D9EB0-DED0-4042-8B08-F0AABFCB10D8 Figs 6–8

Material examined. *Holotype*: Female, COSTA RICA: Guanacaste, Area de Conservación Guanacaste, Sector Santa Rosa, Finca Jenny, el. 205 m, 10.86333, -85.57443, 29-V-2009; 10-SRNP-15367, host *Carthara abrupta* on *Roupala montana*. Deposited in USNM.

Paratypes: 3 females (10-SRNP-15373, 10-SRNP-15366, 10-SRNP-15356), 8 males (10-SRNP-15370, 10-SRNP-15354, 10-SRNP-15374, 10-SRNP-15351, 10-SRNP-15345, 10-SRNP-15361, 10-SRNP-15368, 10-SRNP-15369), all same data as holotype, no successful barcodes; 1 male, COSTA RICA: Guanacaste, Area de Conservacion Guanacaste, Sector Orosí, Intersección Mata Redonda, el. 565 m, 10.99574, -85.4948, 29-V-2009, host *Carthara abrupta* on *Roupala montana* (09-SRNP-13448, no successful barcode). Deposited in USNM, CNC, INHS, Museo Nacional de Costa Rica, Hymenoptera Institute (116 Franklin Ave, Redlands, CA 92373).

Body length excluding head. Average male, 6.75 mm; average female, 6.5 mm.

Body color (Fig. 6): Mesosoma pale except propleuron dark. Head black, metasoma terga 1–5 pale, 6–8 dark with tergum 5 variable with dark patch medially distinctly triangular or with dusky patch, rarely absent. Antenna color: scape, pedicel, and flagellum dark. Coxa dark, trochanter mostly dark with posterior trochanter small light patch. Medial femur dark (8/13), lacking dark patch (5/13). Tarsus, aroliar pad ventrally white and dorsally black (Fig. 8D). Tarsal claw dark. Wings yellow and alternately banded light and dark (Figs 6, 7C)).

Head. Epistomal sulcus present, very light impression. Setose except vertex and occiput, sparse on clypeus. Setae light yellowish in color. Clypeus weakly and evenly convex. Margin truncate. Clypeus $2.2 \times$ broader than high, $2.4 \times$ length of malar space. Scape $2 \times$ longer than broad, inner side deeply excised apically, base $1.7 \times$ narrower than broadest point. First flagellomere $2.6 \times$ as long as broad.

Face (Fig. 7A) $1.8 \times$ broader than high. Galea dark, $1.2 \times$ wider than long. Anterior tentorial pits very distinct, deep. Glossae light, bilobed. Frons smooth, deeply excavated, excavation extending longitudinally from base of antennae to vertex and transversely from inner margin of left eye to inner margin or right eye. Frons dor-



Figure 6. Heteropteron hasegawai Dabek & Whitfield A dorsal habitus B lateral habitus.

sally with distinct Y-shaped ridge with branches terminating immediately anterior to median ocellus (Fig. 7B). Ocelli elevated within excavation with some setae between. Visible ridge at antennal base. Antenna with 34–36 flagellomeres.

Mesosoma. Pronotum unsculptured except weakly on marginal ridges anteriorly and posteriorly, long light yellow setae anterodorsally. Pronotum light in color later-



Figure 7. *Heteropteron hasegawai* Dabek & Whitfield **A** frontal view of face **B** dorsal view of frons and ocelli, showing y-shaped ridge **C** wings, showing banding pattern.

ally and posterodorsally, dark anteriorly and ventrally. Notauli smooth, incomplete, distinct anteriorly, evanescent posteriorly, extending about half length of mesoscutum; mesoscutum smooth, 1.1 × wider than long, flattened dorsally in lateral view, sparsely covered with yellow setae. Scutellum triangular, smooth, flat in lateral view, lateral areas of scutellum bare and smooth. Posterior end of scutellum lacking ridge at margin (Fig. 6A).

Propodeum smooth, virtually without areola but with complete longitudinal furrow; pilosity abundant in vicinity of spiracles. Setae $6 \times \text{longer}$ then distance between each setae; spiracles $1.4 \times \text{longer}$ than wide.



Figure 8. *Heteropteron hasegawai* Dabek & Whitfield **A** lateral view of mesosoma **B** lateral view of hypopygium tip and ovipositor with sheaths **C** tibial spines **D** last tarsal segment, showing pectinate claws and whitish arolium.

Subalar depression smooth with median carina forming obtuse angle. Subalar prominence tapering posteriorly to pleural sulcus, smooth, convex. Pleural sulcus with double groove. Posterior margin of mesopleuron smooth, moderately setose ventrally with visible setal pits. Mesopleuron smooth (Fig. 8A). Metapleuron with distinct dorsal-ventral groove starting halfway down the dorsal edge of the metapleuron and ending at the posterior end, moderately setose, setae light in color.

Legs. Hind tibia slightly broadening distally, distal end $1.8 \times as$ long as proximal end. Hind femur $2.6 \times as$ long as broad distally, distal end $2.1 \times as$ long as proximal end. Hind basitarsus $1.2 \times the$ length of tarsomeres 2–5 combined, inner spur of hind tibia half the length of basitarsus. Second tarsus of fore leg $1.4 \times longer$ than broad, fifth tarsus of foreleg $1.7 \times longer$ than broad; second tarsus of mid leg $1.3 \times longer$ than broad; second tarsus of hind leg $1.7 \times longer$ than broad; second tarsus of hind leg $1.7 \times longer$ than broad; second tarsus of hind leg $1.7 \times longer$ than broad; second tarsus of hind leg $1.7 \times longer$ than broad; second tarsus of hind leg $1.7 \times longer$ than broad, fifth tarsus of hind leg $1.3 \times longer$ than broad. Tibial spines, generally < 7, variable in number and pattern (Fig. 8C).

Forewing. $1.15 \times \text{longer}$ than body. Pterostigma elongate, issuing *r* from its middle. Second submarginal cell long. Banding pattern as in Fig. 7C.

Metasoma. First tergite 1.4 × broader posteriorly than long. Third tergite 1.4 × as long as second tergite. All tergites polished. Second latero-tergite visible in dorsal view

(Fig. 6A). Hypopygium broad, laterally truncate and rounded at tip (Fig. 8B), irregular blackened spot near tip. Ovipositor sheath as long as mesosoma with white streak at ventral base (Fig. 8B).

Cocoon. Not recorded.

Host. Caterpillars *of Carthara abrupta* (Pyralidae) on *Roupala montana* (Proteace-ae). *Carthara abrupta*, as currently defined, feeds on a variety of plants; the form that hosts *H. hasagawai* is referred to informally as Carthara abruptaDHJ02.

Etymology. *Heteropteron hasegawai* is named in honor of Dr. Motohiro Hasegawa of Japan International Collaboration Agency (JICA), who first came to ACG in 2015 and has since then, and hopefully decades more, been a major supporter of all aspects of ACG, ranging from financing to biomonitoring of a geothermal electricity project with insect thermometers to biodevelopment to DNA barcoding to international conservaton biopolitics.

Diagnosis. This new species differs from *H. fasciipennis* most obviously in having a yellowish orange (in older specimens occasionally somewhat brownish) mesosoma rather than mostly blackish. From *H. kidonoi*, described above, it can be distinguished by its slightly to significantly lighter yellowish portions of the metasoma (Figs 6, 8A), more truncately pointed hypopygium tip (Fig. 8B), less numerous and more linearly arranged small spines on the mid tibia (Fig. 8C), and the whitish tarsal arolia (Fig. 8D).

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RESEARCH ARTICLE



Two new morphologically interesting species of the genus *Ephedrus* Haliday (Hymenoptera, Braconidae, Aphidiinae)

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Abstract

Here we describe two new *Ephedrus* species from the Biologiezentrum Linz's collection: *Ephedrus antennalis* **sp. nov.**, which possesses 12-segmented antennae, a unique character within the genus *Ephedrus*; and *E. carinatus* **sp. nov.**, which represents an additional member of the root aphid parasitoid group within the genus *Ephedrus*.

Keywords

Ephedrus, new species, root aphid parasitoids

Introduction

There are about 40 known species of the genus *Ephedrus* Haliday, 1833 around the world (Akhtar et al. 2011; Kocić et al. 2019). This genus is characterized by the presence of many plesiomorphic characters (e.g., antennae with 11 segments in

both sexes, which is a unique case within the subfamily, a fore wing venation pattern close to the braconid ancestor and long oviposition time), all of which suggest that it is probably one of the basal genera within the subfamily Aphidiinae (Gärdenfors 1986; Belshaw and Quicke 1997; Sanchis et al. 2001). Additionally, black parasitized aphids ("mummies") are specific for *Ephedrus* and very few other genera (e.g., Paralipsis Förster, 1863, some species of Pauesia Quilis, 1931). A single species of the genus Ephedrus, known as an obligatory parasitoid of root aphids (Ephedrus validus (Haliday, 1833)), possesses accompanying adaptations to a subterranean mode of life. This species exhibits features such as small eyes and short and strong legs, along with a densely setose body as a protective trait against the honeydew of waxy root aphids. Interestingly, male specimens are less pubescent, and that character led Gärdenfors (1986) to suspect that males are not in contact with root aphids and that they probably do not follow females beneath the surface of the ground. It is known that Ephedrus plagiator (Nees, 1811), which is a broadly polyphagous species, also occasionally parasitizes the root aphids (Starý 1961; Gärdenfors 1986). Furthermore, while European, African and Central Asian populations of Ephedrus persicae Froggatt, 1904 are biparental (Takada 1979; Gärdenfors 1986), some Far Eastern, Australian and USA populations possess an asexual mode of reproduction (Starý and Schlinger 1967; Takada 1968; Gärdenfors 1986). Based on relevant literature, it is evident that numerous species from the genus *Ephedrus* possess a range of biologically and ecologically complex features.

Recently, the integrative systematic studies, that combine morphological and molecular methods of the subject group, revealed additional members of the genus *Ephedrus*, i.e. *E. tamaricis* Tomanović & Petrović, 2016 and *E. hyadaphidis* Kocić & Tomanović, 2019 (Petrović et al. 2016; Kocić et al. 2019).

After examination of the Biologiezentrum Linz's collection, we discovered two *Ephedrus* species new to science with some unusual morphological traits. Here we describe *Ephedrus antennalis* sp. nov. and *E. carinatus* sp. nov. and discuss their relationships within the genus *Ephedrus*.

Material and methods

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Specimens were collected by sweeping from the Western Caucasus (Russia) and from Austria (before World War II – a historical record). Both specimens are slide-mounted with Berlese medium. Study of the external structure and the measurements was undertaken with a LEICA DM LS phase-contrast microscope (Leica Microsystems GmbH, Wetzlar, Germany). The terminology used in this paper regarding diagnostic characters is based on that of Sharkey and Wharton (1997).

Description of two new species

Ephedrus antennalis Tomanović, sp. nov. http://zoobank.org/6655DBD2-D79A-46A0-839C-760F282FF7CD

Diagnosis. On the basis of fore wing venation (3SR vein shorter than 2SR vein), elongated pterostigma (Fig. 1C), and its short and broad petiole (Fig. 1D), *E. antennalis* sp. nov. belongs to the *persicae* species group (Gärdenfors, 1986). However, the long 12-segmented antennae (Fig. 1A) distinguish the new species from all the members of the *persicae* group, as well as from all other congeneric species.

Female. *Head.* Malar index equal to approximately 0.20 of the longitudinal eye diameter. Clypeus oval with eight long setae. Tentorial index approximately 0.35. Maxillary palps with four, labial palps with two palpomeres. Antennae 12-segmented, filiform, with semierect setae which are shorter than half of the segments' diameter (Fig. 1A). F1 and F2 elongated, 4.25 and 3.6 times as long as wide, respectively (Fig. 1B). F1 subequal to F2. F1 with two, F2 with three (Fig. 1B), F3 and F4 with five longitudinal placodes. Antennae not thickened towards apex, F9 well separated from F10 (whereas in *E. persicae* F8 and F9 are not well separated and form a kind of club).

Mesosoma. Mesoscutum with notaulices distinct in anterior half. Mesoscutal fovea not developed. Propodeum areolated, with seven setae on upper areola and five setae on lower areola. *Fore wing.* Pterostigma approximately 5.7 times as long as wide (Fig. 1C). Vein ratio 3SR/2SR about 0.9 (Fig. 1C).

Metasoma. Petiole subquadrate, 1.33 times as long as wide (Fig. 1D). Ovipositor sheaths elongated, with two long setae on dorsal margin (Fig. 1E).

Colouration. Head light-brown. Mouthparts light-brown. Scape brown, pedicel and F1 yellow to light-brown, remaining parts of antennae brown. Legs brown with light-brown tarsi. Petiole brown, remaining parts of metasoma light-brown to brown. Ovipositor sheath brown.

Body length. 1.8 mm.

Male. Unknown.

Type material. *Holotype*: $1 \, \bigcirc$, Russia, Western Cacausus, E. Krasnaya Polyana, Aibga mt. VII 2000, collected by sweeping, leg. Gurko. Deposited in the Biologiezentrum Linz's collection, Austria.

Distribution and biology. *Ephedrus antennalis* sp. nov. was collected in the Western Caucasus Mountains of Russia, and that is the only locality where the species has been found to date.

Aphid host. Unknown (collected by sweeping).

Etymology. The new species takes its name from an unusual number of antennal segments (12), unique within the genus *Ephedrus*.



Figure 1. *Ephedrus antennalis* sp. nov. Tomanović **A** antenna **B** first and second flagellar segment **C** forewing **D** petiole – dorsal aspect **E** ovipositor sheaths – lateral aspect. Scale bars: 100 μ m.

Ephedrus carinatus Tomanović, sp. nov.

http://zoobank.org/A165E7C3-FD60-4058-A597-201DA76F17F5

Diagnosis. On the basis of fore wing venation (3SR vein longer than 2SR vein) (Fig. 2F), this species belongs to the *plagiator* species group. The new species morphologically resembles *E. validus* in possessing a reticulated petiole (Fig. 2G) and propodeum (Fig. 2E) and a densely setose ovipositor sheath (Fig. 2H), features that point to a subterranean habitat where it probably parasitizes root aphids. However, it differs clearly from *E. validus* in having wide and rugose notaulices along the dorsal side of the mesoscutum (Fig. 2D) (vs. shorter notaulices reaching the first third of the mesoscutum in *E. validus* (Fig. 3A)), second flagellomere approximately 3.2 times as long as wide (Fig. 2C) (vs. 2.7–2.8 times as long as wide in *E. validus* (Fig. 3B)) and a petiole approximately 1.35 times as long as wide at the spiracle level (Fig. 2G) (vs. a more elongated petiole, 1.4–1.6 times as long as wide at the spiracle level in *E. validus* (Fig. 3C)).



Figure 2. *Ephedrus carinatus* sp. nov. Tomanović **A** head **B** antenna **C** first and second flagellar segment **D** mesoscutum – dorsal aspect **E** propodeum – dorsal aspect **F** forewing **G** petiole – dorsal aspect **H** ovipositor sheaths – lateral aspect. Scale bars: 100 μm.

Female. *Head.* Malar space equal to approximately 0.32 of longitudinal eye diameter. Clypeus oval, densely setose with over 20 long setae. Tentorial index approximately 0.48. Maxillary palps with four palpomeres, labial palps with two. Head approximately 1.3 times wider than mesoscutum (Fig. 2A). Antennae 11-segmented, filiform, slightly tickened towards apex, with semierect setae which are shorter than half of diameter of the segments (Fig. 2B). F1 elongated, with a constriction in the



Figure 3. *Ephedrus validus* **A** mesoscutum – dorsal aspect **B** first and second flagellar segments **C** petiole – dorsal aspect. Scale bars: 100 µm.

first half, approximately 5.8 times as long as wide and approximately 1.8 times longer than F2 (Fig. 2C). F2 approximately 3.2 times as long as wide. F1 and F2 with two or three longitudinal placodes (Fig. 2C), F3 and F4 with four longitudinal placodes. F8 and F9 well separated.

Mesosoma. Mesoscutum with notaulices almost reaching the scutellum (Fig. 2D). Mesoscutal fovea absent. Propodeum very rugose, areolated and densely setose (Fig. 2E), with more than 15 and 20 setae on the upper areola and lower areola, respectively (Fig. 2E). Central areola wide and pentagonal.

Fore wing. Pterostigma approximately 4.6 times as long as wide (Fig. 2F). Vein ratios 3SR/2SR and 1SR/3SR approximately 1.30 (Fig. 2F).

Metasoma. Petiole subquadrate, approximately 1.35 times as long as wide at the spiracle level (Fig. 2G). Ovipositor sheaths elongated, densely setose and straight on the dorsal margin (Fig. 2H).

Colouration. Head black. Scape and pedicel yellow to light-brown. F1 yellow, remaining part of antennae brown. Mouthparts light-brown. Petiole light-brown to brown. Legs light-brown with dark apices. Metasoma brown. Remaining body parts brown to black.

Body length. 2.0 mm.

Male. Unknown.

Type material. *Holotype*: $1 \bigcirc$, Austria, Oberösterreich, Lichtenberg, 01 IX 1933., collected by sweeping, leg. J. Kloiber. Deposited in the collection of the Biologiezentrum Linz's collection, Austria.

Distribution and biology. *Ephedrus carinatus* sp. nov. is known only from a historical record from Austria. We assume that it is a parasitoid of root aphid species.

Etymology. The new species takes its name from the developed notaulices on the mesoscutum.

Discussion

Starý (1959) established the subgenus Lysephedrus Stary, 1959, with the nominative species Ephedrus (Lysephedrus) validus. Later on, in a taxonomic and biological revision of Palaearctic species Gärdenfors (1986) divided the genus Ephedrus into three subgenera – Ephedrus Haliday, 1833, Breviephedrus Gärdenfors, 1986 and Lysephedrus Starý, 1958. Davidian (2007; 2018) considers the subgenus Lysephedrus as a separate genus. However, on the basis of molecular markers and morphology, in an integrative study, Kocić et al. (2019) established Ephedrus (Lysephedrus) validus to be nested within species of the subgenus *Ephedrus* and assigned it a status of junior synonym of the subgenus Ephedrus. Here we describe a new Ephedrus species morphologically related to E. validus, with a reticulated propodeum, petiole, and densely pubescent ovipositor sheaths, features which imply that it is another species of root aphid parasitoids within the genus Ephedrus. Long notaulices along the mesoscutum represent a plesiomorphic character absent in almost all other congeneric species, except in E. validus and sometimes E. persicae where they remain shorter, maximally reaching the first third of the mesoscutum. This was confirmed by examination of several available specimens of E. validus, all of which possessed shorter notaulices (Fig. 3A). All these specimens share almost the same cytochrome c oxidase subunit I (COI) gene barcoding sequences (Kocić et al. 2019).

Possession of 11-segmented antennae in both sexes represents a plesiomorphic character state in Ephedrus. Gärdenfors (1986) mentioned that in some "extremely rare" cases some specimens can possess 12-segmented antennae. However, in communication with the author (Gärdenfors, personal communication), we were informed that 12-segmented antennae are present only in specimens where terminal segments are elongated and semi-divided due to developmental instability of these individuals. We also found specimens with the terminal 10th segment elongated and undivided (e.g., aberrant specimens of *E. laevicollis* (Thomson, 1895)). However, with clearly 12-segmented antennae, our Russian specimen of Ephedrus that was discovered in the Biologiezentrum Linz's collection changes diagnostic characters for the genus Ephedrus (from 11-segmented antennae to 11-12-segmented antennae). Possession of 12-segmented antennae represents an apomorphic and very unusual character that was until now unknown for the genus Ephedrus. On the basis of the short fore wing 3SR vein, it can be concluded that E. antennalis sp. nov. belongs to subgenus Fovephedrus Chen, 1986 (recently revised by Kocić et al. 2019) and "persicae" species group. For details of diagnosis and biology, see Gärdenfors (1986), Žikić et al. (2009) and Kocić et al. 2019.

The phylogenetic position of the two species newly described here is unclear and integrative research on them in the future could provide insight about their taxonomic and phylogenetic status and suggest a possible subtribal classification of the genus *Ephedrus*.

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RESEARCH ARTICLE



Revisiting the host use and phylogeny of Colastomion Baker (Hymenoptera, Braconidae, Rogadinae), with a new host record from Japan

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Abstract

We report the solitary parasitism by *Colastomion formosanum* (Watanabe) (Hymenoptera, Braconidae, Rogadinae) on the larva of *Nevrina procopia* (Stoll) (Lepidoptera, Crambidae) feeding on *Turpinia ternata* Nakai (Staphyleaceae) in Amami Ôshima Is., Japan. This is the first host record for the genus *Colastomion* Baker outside of Papua New Guinea. We have also inferred the phylogenetic relationships of *Colastomion* species using Bayesian and maximum likelihood approaches, based on the mitochondrial cytochrome oxidase 1 gene. The results indicate two major clades–solitary and gregarious parasitoids–within *Colastomion*. *Colastomion formosanum* belongs to the clade of solitary parasitoids that specifically parasitize the crambid subfamily Spilomelinae. Plant-host-parasitoid associations and the evolutionary scenario of the host use of *Colastomion* are discussed.

Keywords

Colastomion formosanum, Crambidae, endoparasitoid, mtCO1, mummy, Nevrina procopia

^{*} Contributed equally as the first authors.

Introduction

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The family Braconidae is one of the largest lineages in Hymenoptera, containing 21,221 valid species worldwide (Yu et al. 2016). Braconid wasps are parasitoids of various insects (e.g. Lepidoptera, Coleoptera, and Hymenoptera), including important agricultural pests (Wharton 1993; Quicke 2015; Maeto 2018). Their amazing diversity has resulted from the complicated biological interactions with host insects as well as contrasting lifestyles, e.g. solitary vs. gregarious, ecto- vs. endoparasitic, or idiovs. koinobiont (Shaw 1988). Understanding their biology and phylogeny lends us a greater appreciation of the evolutionary pattern of host-parasitoid systems. Further, from a practical standpoint, the study of Braconidae can also be useful to leverage their parasitic abilities for biological pest control (Quicke 2015).

The subfamily Rogadinae Förster *sensu stricto* contains diverse koinobiont endoparasitoids of Lepidoptera and comprises 63 genera and 1,243 species that are distributed across all zoogeographical regions, except for polar regions (Quicke 2015; Yu et al. 2016). One of the marked biological features of the rogadine parasitoids is the mummification of their host larvae (Chen and He 1997; Zaldívar-Riverón et al. 2008).

Colastomion Baker is an uncommon genus of Rogadinae and comprises 15 species that occur throughout Papua New Guinea, southern East Asia, and Africa (Quicke et al. 2012; Yu et al. 2016). Crambid larvae have been reported to be hosts of *Colastomion* only in Papua New Guinea (Quicke et al. 2012). While the host larvae of *Colastomion* are typically mummified like other rogadine parasitoids, the mummy has been illustrated for only one species of *Colastomion* to date (Zaldívar-Riverón et al. 2008). Also, although the phylogenetic placement of *Colastomion* within Rogadinae has been largely established (Zaldívar-Riverón et al. 2008), the phylogenetic relationships within the genus has not been firmly estimated (Quicke et al. 2012).

Recently, the first and second authors (KS and SS) conducted field studies in Amami Ôshima Is., Kagoshima Pref., Japan, and obtained *Colastomion* specimens from host caterpillars and in a light trap. Here, we identified the *Colastomion* specimens as a species and conducted phylogenetic analyses based on the mitochondrial cytochrome oxidase 1 (*CO1*). These provide the first host record of *Colastomion* outside of Papua New Guinea, detailed mummy morphology, and the evolutionary scenario of host use within *Colastomion*.

Materials and methods

Field collection and rearing

A field study was conducted at Naze-Ôaza-Chinase (28°21'N, 129°26'E, 16 m alt.), Amami Ôshima Is., Kagoshima Pref., southwest Japan on 11 April 2019. The study site was the evergreen broad-leaved forest dominated by *Ficus* spp., *Ligustrum japonicum* Thunb. and *Pittosporum tobira* (Thunb.) W.T.Aiton. KS collected larvae of *Nevrina procopia* (Stoll) (Lepidoptera, Crambidae, Spilomelinae) as they were feeding on *Turpinia ternata* Nakai (Staphyleaceae). The larvae rolled young leaves roughly and hid themselves with the rolled leaves (Fig. 1). Collected larvae were reared in plastic cases under laboratory conditions (25 °C, 16:8 h light:dark). Emerged insects were killed in a freezer.

Further specimen was collected in a field study at Nishinakama (28°15'47.3"N, 129°24'56.1"E, 120 m alt.), Sumiyô Town, Amami Ôshima Is. on 12 July 2019, using High Intensity Discharge light traps by SS.

Specimens examined, repositories and identification

The examined specimens of *Colastomion* from Japan are deposited in the Institute for Agro-Environmental Sciences, NARO, Tsukuba, Japan (NIAES) and Osaka Museum of Natural History, Osaka, Japan (OMNH): 1♀, Naze-Ôaza-Chinase, Amami City, Amami Ôshima Is., Kagoshima Pref. (28°21'N, 129°26'E, 16 m alt.), 11.IV.2019, K. Sakagami leg. (by rearing host) (NIAES) [DDBJ–LC485659]; 1♀, Nishinakama, Sumiyô Town, Amami Ôshima Is., Kagoshima Pref. (28°15'47.3"N, 129°24'56.1"E, 120 m alt.), 12.VII.2019, S. Shimizu leg. (light trap) (NIAES) [DDBJ–LC499982]; 1♀, Mt. Yui-dake, Setouchi Town, Amami Ôshima Is., Kagoshima Pref., 24.VIII.2004, H. Makihara leg. (sweeping net) (OMNH); 1♂, Yona, Kunigami Village, Okinawahontô Is., Okinawa Pref., 29.VI.2013, S. Fujie leg. (sweeping net) (OMNH).

We identified *Colastomion* specimens based on Watanabe (1932, 1934), Tenma (2002), and Quicke et al. (2012): the specimens were morphologically similar to *C. formosanum*. To make sure that *Colastomion* specimens are *C. formosanum*, all the specimens were compared to photos of the Taiwanese specimens of *C. formosanum* deposited in the Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany (SDEI), which include the holotype of the species as follows: holotype ♂, Kankau, Changkou (Koshun), 22.IV.1912, H. Stauter leg.; 1♂, Kankau, Changkou (Koshun), VIII.1912, H. Stauter leg.; 1♀, Kankau, Changkou (Koshun), IV.1912, H. Stauter leg. The photos were provided by Taeger (2020), published online (https://doi.org/10.6084/m9.figshare.11984355.v1).

Morphological observation, photo technique and terms

Morphological observation was conducted using a stereoscopic microscope (SZ61, OLYMPUS, Tôkyô, Japan). Multi-focus photographs were taken using a single lens reflex camera (α 7II, Sony, Tôkyô, Japan) with micro-lens (LAOWA 25 mm F2.8 2.5–5X ULTRA MACRO, Anhui Changgeng Optics Technology Co., Ltd, Hefei, China and A FE 50mm F2.8 Macro SEL50M28, Sony, Tôkyô, Japan). The photos were captured in RAW format and developed using Adobe Lightroom Creative Cloud. Then, they were stacked using Zerene Stacker and edited in Adobe Illustrator 2019. Morphological terms follow those of Quicke et al. (2012).



Figure 1. Leaves of *Turpinia ternata* Nakai rolled by a caterpillar of *Nevrina procopia* (Stoll).

Molecular technique

Part of the mitochondrial protein-coding cytochrome c oxidase 1 (CO1) gene, often referred to as "barcoding gene", of two individuals of C. formosanum was sequenced for phylogenetic analysis. DNA was extracted from the right middle leg using the DNeasy Blood and Tissue Kit (Qiagen, Düsseldorf, Germany). For amplification, the following primers were used: LCO1490 (5'-GGTCAACAAATCATAAAGA-TATTGG-3') and HCO2198 (5'-TAAACTTCAGGGTGACCAAAAAATCA-3') (Folmer et al. 1994). Polymerase chain reactions (PCR) were conducted using KOD FX NEO kit (Toyobo, Ōsaka, Japan), and PCR conditions were 94 °C for 2 min as initial denaturation, followed by 35 cycles of denaturation (10 sec at 98 °C), annealing (30 sec at 48 °C), and extension (30 sec at 68 °C), and then a final extension at 72 °C for 10 min. PCR product was purified using Illustra GFX kit (GE Healthcare Life Sciences, Marlborough, USA). The purified product was amplified with the same primers using the BigDyeTM Terminator v3.1 Cycle Sequencing kit (Applied Biosystems, Waltham, USA). Cycle sequencing products were purified using the 3.0 M sodium acetate, 95% ethanol, 70% ethanol, and Hi-Di formamide. Cycle sequencing reactions were run on an ABI Prism 3100 Genetic Analyzer (Applied Biosystems, Waltham, USA), and the forward and reverse sequences were assembled using the DNA Dynamo Sequence Analyze Software (Blue Tractor Software, North Wales, UK). Finally, we deposited the obtained sequence to DNA Data Bank of Japan (DDBJ).

Phylogenetic analyses

In order to exclude the taxon sampling bias, a single sequence for each species was selected from 42 sequences of *CO1* of the nine *Colastomion* species from Papua New Guinea and Benin deposited in the DNA databases (Quicke et al. 2012). *Megarhogas maculipennis* Chen & He and *Myocron* sp., closely related genera to *Colastomion* (Zaldívar-Riverón et al. 2008), were selected as outgroups. A total of 10 sequences from ingroup and two from outgroups were used for analyses (see Table 1).

Multiple sequence alignment was conducted in MAFFT v7.409 (Katoh and Toh 2008) using the L-INS-I algorithm. The aligned sequences were checked visually. Subsequently, they were manually optimized for phylogenetic analysis.

Using Bayesian Inference (BI) and maximum likelihood (ML) approaches, phylogenetic analyses were performed. Evolutionary models were determined using Kakusan4 v4.0 (Tanabe 2011). The best-fit models were selected based on the lowest corrected Akaike information criterion (AICc) for ML and the lowest Bayesian Information Criterion (BIC) for BI.

For the ML analysis, we used RAxML v8.2.10 (Stamatakis 2014) with 1,000 bootstrap replications, the codon separate model, and GTRGAMMA as a substitution model.

Species	Identifer	Locality	Latitude / longitude	Date	Collector	Accession number
Colastomion crambidiphagus	DLJ Quicke	PNG: Madang, Wanang	5.23088S, 145.182E	16.II.2007	local collector	JF963127
Colastomion formosanum	K Maeto	JPN: Amami-Oshima, Kagoshima	28.3500N, 129.433E	11.IV.2019	K. Sakagami	LC485659
Colastomion gregarius	DLJ Quicke	PNG: Madang, Wanang	5.23088S, 145.182E	24.V.2007	local collector	JF963128
Colastomion maclayi	DLJ Quicke	PNG: East Sepik, Yapsiei	4.62825S, 141.097E	27.I.2004	local collector	JF271312
Colastomion madangensis	DLJ Quicke	PNG: Madang, Wanang	5.23088S, 145.182E	24.V.2007	local collector	JX034716
Colastomion masalaii	DLJ Quicke	PNG: West Sepik, Sandaun, Utai	3.38405S, 141.586E	28.VII.2004	local collector	JF271307
Colastomion parotiphagus	DLJ Quicke	PNG: Madang, Wanang	5.23088S, 145.182E	30.V.2007	local collector	JX034711
Colastomion pukpuk	DLJ Quicke	PNG: East Sepik, Wamangu	3.78713S, 143.652E	3.XI.2005	local collector	JF271303
Colastomion wanang	DLJ Quicke	PNG: Madang, Wanang	5.23088S, 145.182E	29.IV.2005	local collector	JF271302
Colastomion sp.	-	BEN	-	-	-	AY935370
Myocron sp.	-	KEN	-	5.V.2005	R Copeland	JN278218
Megarhogas maculipennis	-	THA: Chanta Bari, Pong Nani Ron	_	-	-	EU979615

Table 1. GenBank and DNA Data Bank of Japan accession numbers and information for specimens used for the phylogenetic analyses.

*BEN, Benin; JPN, Japan; KEN, Kenya; PNG, Papua New Guinea; THA, Thailand.

For the BI analysis, we used MrBayes v3.2.2 (Ronquist et al. 2012) with two independent runs of a Bayesian Markov chain Monte Carlo (MCMC) analyses of eight chains each, heating at 0.1, as well as random starting trees with trees sampled every 1,000th generations for 10,000,000 generations. If the average standard deviation of split frequencies was below 0.01, chain stationarity was checked with Tracer v1.6 (Rambaut and Drummond 2007) and two converged MCMC runs were considered adequate (Ronquist and Huelsenbeck 2003). The anterior half of the generations were discarded as a conservative burn-in and estimates were obtained for the harmonic means of the likelihood scores from the remaining half generations using the sump command. A final check of the convergence of the runs by the value of the potential scale reduction factor was conducted and a majority-rule consensus tree was obtained using the sumt command. The phylogenetic tree was edited using FigTree v1.4.3 (Rambaut 2006–2016) and Adobe Illustrator 2019.

We consider the node to be supported by either the Baysian posterior probabilities (PP) > 0.95 or the bootstrap (BT) > 80%.

Results

Rearing and mummy morphology

One adult female of *Colastomion* emerged from a mummified final instar larva of *N. procopia* on 30 April 2019 (Figs 2, 3). The mummy remained unfixed within rolled leaves. It was mildly hardened, having a posterolateral and irregular, noncircular emergence hole (Fig. 4). Five adults of *N. procopia* emerged from unparasitized pupae, of which two emerged on 30 April, two on 8 May, and one on 9 May 2019.


Figure 2. Female adult wasp of *Colastomion formosanum* (Watanabe) from Amami Ōshima Is., Japan **A** habitus **B** head, frontal view **C** head and mesosoma, lateral view **D** head and mesosoma, dorsal view **E** propodeum, dorsal view **F** metasoma, dorsal view.

Identification and adult morphology

All Japanese *Colastomion* specimens were identified as *C. formosanum* because of yellow face, antennae (although apical segments were brown) and legs (although middle and hind coxae and telotarsi were brown), sharply contrasting with brown mesosoma



Figure 3. Wings of Colastomion formosanum (Watanabe).



Figure 4. A larva of Nevrina procopia (Stoll) mummified by Colastomion formosanum (Watanabe), lateral view.

and metasoma (Fig. 2A, B); epicnemial area finely strigose, precoxal sulcus shallowly impressed and with some rugae, and pleural sulcus crenulate (Fig. 2C); notauli deep and weakly crenulate (Fig. 2D); propodeum rugose and with complete midlongitudinal carina (Fig. 2E); 1st metasomal tergite 1.7–1.8× longer than posteriorly wide; 2nd tergite as long as maximally wide (Fig. 2F); pterostigma entirely dark brown; fore wing cu-a postfurcal to 1-M (Fig. 3); and subquadrate vein 2-SC+R of hind wing (Fig. 3).

A female specimen from Taiwan shows a distinct protuberance on the base of the first metasomal tergite (Taeger 2020), whereas it is absent in males (including holotype) from Taiwan (Taeger 2020) and females and a male from Japan. The protuberance will probably be due to ontogenetic deformation in the individual. On the other hand, the sculpture of epicnemial area and precoxal sulcus tends to be stronger in females than in males, which is most likely a sexual variation.

Phylogeny

The Bayesian majority-rule consensus tree of *Colastomion* obtained from the *CO1* sequences is shown in Figure 5. Both the BI and ML topologies were consistent with each other. *Colastomion formosanum* was identified as a sister group of the well-supported clade (*C. crambidiphagus* and *C. parotiphagus*) by both the BT and PP. Monophyly



Figure 5. Bayesian majority-rule consensus tree of *Colastomion* species based on *CO1*. Posterior probabilities (> 0.80) and bootstrap values (> 50%) are indicated at below of each node (PP / BT). Lifestyles are indicated as shown in Quicke et al. (2012), except for *C. formosanum*.

of the clade of solitary parasitoids (*C. crambidiphagus, C. formosanum, C. maclayi, C. parotiphagus,* and *C. wanang*) plus *C. pukpuk* was good supported only by the PP. On the other hand, the clade of gregarious parasitoids (*C. masalaii, C. gregarius,* and *C. madangensis*) was not fully supported.

Discussion

We have found that *N. procopia* feeding on rolled leaves of *T. ternata* are the host species of *C. formosanum* in Japan. This supports the hypothesis of the host specificity of *Colastomion* to the crambids subfamily Spilomelinae as mentioned by Quicke et al. (2012), whereas the genus *Nevrina* of the tribe Udeini is a new host genus and the Staphyleaceae is a new host plant family for *Colastomion* (Table 2). Interestingly, Quicke et al. (2012) has reported that two solitary species of *Colastomion* use some species of crambid moths on a certain plant: *C. crambidiphagus* parasitizes several species of different tribes of Spilomelinae feeding only on the Convolvulaceae, and *C. parotiphagus* uses various host tribes of moth while mostly feeding on the Rubiaceae. Moreover, all gregarious species (*C. gregarius, C. madangensis, and C. masalaii*) consistently use Margaroniini on the Moraceae (Table 2). These may indicate that adult wasps search the host larvae by plant cues, such as herbivory-induced plant volatiles (Arimura et al. 2009) or oviposition-induced plant volatiles (Hilker and Fatoaros 2015). It is therefore important to understand the specificity of parasitoids not only in host insects but also in host plants.

Species	Host tribe	Host plant family	Lifestyle
C. crambidiphagus	Hydririni, Udeini	Convolvulaceae	Solitary
C. formosanum	Udeini	Staphyleaceae	Solitary
C. gregarius	Margaroniini	Moraceae	Gregarious
C. maclayi	Udeini	Rubiaceae	Solitary
C. madangensis	Margaroniini	Moraceae	Gregarious
C. masalaii	Margaroniini	Moraceae	Solitary/gregarious
C. parotiphagus	Agroterini	Malvaceae	Solitary
ditto	Margaroniini	Rubiaceae	Solitary
ditto	Unidentified	Lauraceae, Ulmaceae	Solitary
C. pukpuk	Unidentified	Rubiaceae	Unknown
C. wanang	Udeini	Myrtaceae, Vitaceae	Solitary

Table 2. Host tribes (Crambidae: Spilomelinae), host plant families, and lifestyles of *Colastomion*. Sources: Quicke et al. (2012), except for *C. formosanum*. Systematics of host tribes follows Mally et al. (2019).

Colastomion formosanum (Figs 2, 3) is a solitary endoparasitoid that forms a hard mummy (Fig. 4). Solitary parasitism in Colastomion is considered the ancestral relative to gregarious parasitism because Megarhogas, which is closely related to Colastomion (and is included as an outgroup in our phylogenetic analyses), and most species in Rogadini are solitary (Quicke and Shaw 2005; Zaldívar-Riverón et al. 2008), while the phylogenetic placement of gregarious species is still unresolved (Fig. 5). The formation of a hard mummy as displayed by C. formosanum remains unusual within Rogadinae, although various types of host mummies appear to act as a protective roll during parasitoid metamorphosing (Zaldívar-Riverón et al. 2008; Maeto 2018). The hosts of most rogadine genera are killed as prepupae within host cocoons, which can protect the parasitoid larvae and pupae, and thus relatively frail mummies are the norm. In contrast, the hosts of genera that form hard mummies are killed in the larval stage, and the hardness of the mummies plays a vitally important protective role. In the case of C. formosanum, the host is killed in the larval stage probably because the immature host caterpillar is large enough for the parasitoid. Host stage of mummifying, which may vary according to relative size of host caterpillars to parasitoids, would therefore be relevant to the hardness of mummies.

Colastomion formosanum was originally described from Taiwan (as Formosa) (Watanabe 1932), later recorded from Hainan Is., China (Chen and He 1997), and was most recently recorded from Okinawa-hontô Is. and Iriomotejima Is., Japan (Tenma 2002). Our collection of *C. formosanum* from Amami Ôshima Is., Japan, has therefore expanded the northernmost border of the genus *Colastomion* as well as the species. It is most likely that *C. formosanum* has advanced northward from the tropics where species of *Colastomion* have highly diversified (Table 1; Fig. 5), although further investigations are needed to reveal the biogeographical history of *Colastomion*. *C. formosanum* is found only in the subtropical islands of China and Japan, whereas its host moth *N. procopia* is distributed much more broadly, from southern Japan to China, India, Papua New Guinea and western Africa (Swinhoe 1916; Chandra 1994; Nasu et al. 2013; Poltavsky et al. 2018). It would be interesting to know whether *C. formosanum* is truly an insular species of East Asia or is also further distributed in continental parts.

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RESEARCH ARTICLE



Characteristics of the meconia of European egg parasitoids of Halyomorpha halys

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Abstract

Halyomorpha halys is a severe invasive Asian pest worldwide and classical biological control is foreseen as the most promising control method. Egg parasitoids appear to be the most important natural enemies of this pest, especially the Asian hymenopteran *Trissolcus japonicus*. In the invaded areas, only a few egg parasitoid species have been able to adopt *H. halys* as a host. *Anastatus bifasciatus* is the most common native egg parasitoid of *H. halys* in Europe, but reaches only low levels of parasitization, while several other native species are only occasionally found. Recently, adventive populations have been found both in the USA and in Europe of *T. japonicus*, and in Italy of a second Asian species, *Trissolcus mitsukurii*. Species identification based on morphological traits by specialists or by molecular analysis is a crucial step in the management of biological control programs. The ability to identify the genus or species within a narrow guild of egg parasitoids based on adult emergence holes and meconium features can be a simple and useful method to support management efforts. We present here detailed descriptions of the meconium of the most frequent parasitoid species attacking *H. halys* in Europe and the characteristics of their emergence holes of the adult wasps.

Keywords

Acroclisoides sinicus, biological control, hyperparasitoid, scanning electron microscopy (SEM), Trissolcus japonicus, Trissolcus mitsukurii

Introduction

Halvomorpha halvs (Stål) (Hemiptera, Pentatomidae) is an invasive stink bug native to Asia which causes significant damage in agriculture in different countries worldwide (e.g. USA, Italy, Switzerland, Georgia) (Leskey and Nielsen 2018). Biological control with egg parasitoids is viewed as the most promising control method for long-term management, and several studies have focused on these natural enemies in the native range of the pest and in the newly invaded countries of USA and Europe (Haye et al. 2015; Herlihy et al. 2016; Roversi et al. 2016; Zhang et al. 2017). Hymenopteran species of Anastatus Motchulsky, Trissolcus Ashmead, Telenomus Haliday and Ooencyrtus Ashmead have been reported to attack eggs of *H. halys* in the native and invaded areas, although with varying degrees of successful development (Zhang et al. 2017; Abram et al. 2017). Unfortunately, in the newly invaded areas, the impact of the native egg parasitoids has not been sufficient to control H. halys (Haye et al. 2015; Abram et al. 2017; Dieckhoff et al. 2017; Costi et al. 2019). In Europe, the most common native egg parasitoid is Anastatus bifasciatus (Geoffroy) (Hymenoptera, Eupelmidae). Although parasitization is sometimes locally high, the overall parasitism by this species on H. ha*lys* egg masses laid naturally in the field is less than 6%–7%, too low to provide significant levels of biological control (Haye et al. 2015; Costi et al. 2019; Stahl et al. 2019a; Moraglio et al. 2020). Other native egg parasitoid species that are reported to attack *H*. halys in Europe include the scelionids Trissolcus kozlovi Ryakhovskii, Trissolcus basalis (Wollaston), Trissolcus semistriatus (Nees von Esenbeck) and Telenomus turesis Walker, all of which are reared infrequently from *H. halys* at low parasitism levels ranging from 0.1-0.7 % (Moraglio et al. 2020).

In the native range of *H. halys*, its most important natural enemy is the egg parasitoid *Trissolcus japonicus* (Ashmead) (Hymenoptera, Scelionidae). This species causes high levels of parasitism (up to 80%) and is considered a classical biological control agent for potential release in the invaded ranges (Yang et al., 2009; Zhang et al. 2017).

Adventive populations of T. japonicus were recently found in Europe (Switzerland and Italy), and a second Asian egg parasitoid species, Trissolcus mitsukurii (Ashmead) (Hymenoptera, Scelionidae), was found also in Italy (Sabbatini Peverieri et al. 2018; Stahl et al. 2019b). The recent discoveries of these species have highlighted the possibility of effective control of *H. halys* in the near future in Europe, and studies aimed at defining the distribution, establishment and impact of the egg parasitoids are of significant interest. Moreover, recent field studies led to the discovery, both in North America and in Europe, of Acroclisoides sinicus (Huang & Liao, 1988) (Hymenoptera, Pteromalidae) (Sabbatini Peverieri et al. 2019). This pteromalid is native to Asia and is thought to be a hyperparasitoid due to its frequent association with Anastatus spp. (e.g. An. bifasciatus in Europe) and Trissolcus spp. (e.g. T. japonicus in Europe and Asia) within the same parasitized host egg masses (Clarke and Seymour 1992; Grissell and Smith 2006; Sabbatini Peverieri et al. 2019). All known egg parasitoids of H. halys are solitary idiobionts, with generally only one adult egg parasitoid emerging from each host egg. Monitoring the field occurrence of egg parasitoids by collecting and rearing host egg masses, followed by the identification or characterization of emerged

parasitoids by taxonomists and molecular biologists (e.g. Talamas et al. 2017) are crucial steps for successful biological control programs. When adult egg parasitoids have already emerged from host eggs prior to their collection, identification by molecular analysis of their DNA remaining in the host eggs is still possible (Gariepy et al. 2014; Stahl et al. 2019c). However, a rapid visual method for species or genus identification is also desirable. For example, the characteristic exit holes of the different species of the *H. halys* egg parasitoid guild in Europe (i.e. *T. japonicus, T. mitsukurii, Ac. sinicus* and *An. bifasciatus*) were recently described (Sabbatini Peverieri et al. 2019).

In this paper we describe the meconia of the most frequently recorded species of egg parasitoids of *H. halys* in Europe. Meconium is the waste material (feces) excreted by the larvae prior to pupating in the host egg (Gullan and Cranston 2010). Within an egg parasitoid guild, different egg parasitoids produce different kinds of meconia. The meconium can often be clearly seen within the emptied host egg through the exit hole or by dissection if necessary. The morphological analysis of meconia has previously been proposed for species identification within the parasitoid guild of different agricultural and forest pests (Schmidd and Kitt 1994; Mirchev et al. 2004; Sands and Liebregts 2005; El-Heneidy and Adly 2009).

Materials and methods

Collection and rearing of the insects

Halyomorpha halys egg masses (n = 75) were collected from the field at sites in Northern Italy during the 2019 growing season. In the laboratory, single egg masses were reared in glass vials held in a climatic chamber at 26 °C, 65% RH and 16:8 L:D conditions. After parasitoid emergence, egg masses were labelled with site data and preserved in a dry condition until the next step of analysis. Emerged egg parasitoids were separated and transferred to glass vials and labelled with their egg mass origin. The parasitoids were fed with honey and used to establish a lab-reared generation of adults (F1). Parental specimens emerged from field-collected egg masses and adults of the F1 generations were identified to species level with the keys of Talamas et al. (2017) for *Trissolcus* species, Kalina (1981) and Askew and Nieves-Aldrey (2014) for *An. bifasciatus*, and the redescription of *Ac. sinicus* in Sabbatini Peverieri et al. (2019).

To ensure that the meconium-species associations were correct and exclude the possibility of multiparasitism, initial analyses were performed with eggs produced in the laboratory with isolated individual F1 generation female wasps. Fresh egg masses of *H. halys* (< 24 h old) were used to produce the laboratory-reared F1 generation of *T. japonicus*, *T. mitsukurii* and *An. bifasciatus*. For rearing *Ac. sinicus*, due to its hyperparasitoid biology, *H. halys* egg masses previously parasitized by *T. japonicus* and *T. mitsukurii* were offered. Subsequent analyses and identifications of meconia to parasitoid species or genus were performed using egg masses collected in the field.

Ooencyrtus telenomicida (Vassiliev) (Hymenoptera, Encyrtidae) and *Gryon penn-sylvanicum* (Ashmead) (Hymenoptera, Scelionidae) were also studied for comparison.

Oencyrtus telenomicida attacks various European pentatomid species and is also able to attack and successfully develop in *H. halys* fresh sentinel eggs in Italy (Roversi et al. 2016), while *G. pennsylvanicum* is known to be a natural enemy of *Leptoglossus occidentalis* Heidemann (Hemiptera, Coreidae) (Roversi et al. 2011). *Gryon obesum* has been recorded from *H. halys* in the U.S.A. (Tillman et al. 2020) and other *Gryon* species attack pentatomid hosts in North America and Asia (Felipe-Victoriano et al. 2019; Martel et al. 2019). *Ooencyrtus telenomicida* and *G. pennsylvanicum* originated from the permanent colonies maintained at CREA facilities on egg masses of *H. halys* and *L. occidentalis* as hosts, respectively (Sabbatini Peverieri et al. 2012; Roversi et al. 2016).

Microscope observations

Examination of the egg masses from which parasitoids emerged and meconium structure was conducted using a stereomicroscope (SMZ25) equipped with a digital camera (DS-Ri2) and the image acquisition software NIS-Elements (all from Nikon Corporation, To-kyo, Japan). Image postprocessing utilized Gimp (v. 2.10.04, GNU Image Manipulation Program). The samples of meconium were also analyzed by scanning electron micros-copy (SEM) to obtain different details; images were taken with a JEOL NEO-SCOPE JCM-5000 equipped with an imaging system. Samples of meconium were prepared following the technique of Raafat et al. (2014). The mounted samples were coated with a thin layer of gold with a JEOL JFC-1300 Sputter Coater. Images were then taken under high vacuum at 10 kv with an enlargement ranging from 60X to 130X.

Results and discussion

A total of 12 egg masses of *H. halys* were collected in the field (298 eggs) which were partially or completely parasitized by at least one of the species of the egg parasitoid guild. Of these, 7.72% emerged in the field prior to collection, 8.05% of the eggs hatched to produce first instar *H. halys* nymphs, and 23.18% eggs died without any emergence. Overall, the parasitized egg masses produced 47 specimens of *T. japonicus*, 89 *T. mitsukurii*, 20 *An. bifasciatus* and 22 *Ac. sinicus*.

Adults that emerged from the collected egg masses were used to establish lab-reared colonies. From these reared colonies, a total of 21 parasitized egg masses of *H. halys* ware randomly selected for further analysis (four egg masses parasitized by *T. japonicus*, four by *T. mitsukurii*, five by *Ac. sinicus*/*T. japonicus*, three by *Ac. sinicus*/*T. mitsukurii* and five from *An. bifasciatus*). In total, 351 parasitized eggs were analyzed which included 104 adults of *T. japonicus*, 105 of *T. mitsukurii*, 97 *Ac. sinicus* (68 associated with *T. mitsukurii* and 29 associated with *T. japonicus*) and 45 *An. bifasciatus*.

Observation of parasitized egg masses revealed the presence of at least one type of meconium in each *H. halys* egg from which an egg parasitoid emerged, and in some cases the meconium (and pupae) could be observed through the intact egg chorion



Figure 1. *Halyomorpha halys* eggs parasitized by *Trissolcus mitsukurii*: red eye spots (**A**) and meconium (arrows) (**B**) are clearly visible through the chorion.



Figure 2. Exit holes of egg parasitoids of *Halyomorpha halys* in Europe and hyperparasitoids: *Acroclisoides sinicus* (**A**), *Trissolcus mitsukurii* (**B**), *Anastatus bifasciatus* (**C**), *Acroclisoides sinicus* partly emerged (**D**), *Trissolcus japonicus* (**E**), *Ooencyrtus telenomicida* (**F**, only from sentinel eggs); hatched *Halyomorpha halys* egg (**G**).

prior to emergence of the adult (Fig. 1). According to the descriptions in Sabbatini Peverieri et al. (2019), different features of exit holes of the parasitoid guild of *H. halys* in Europe can be useful for species identification (Fig. 2). Unparasitized *H. halys* eggs that produced nymphs exhibited semitransparent white chorions with partially removed or absent operculae and egg bursters often present; these egg shells were clearly empty (Figs 2G, 3A, B).



Figure 3. Hatched Halyomorpha halys egg with black egg burster visible (A) and empty egg shell (B).

Meconium description

Anastatus bifasciatus produced meconium with generally elongate brown or dark brown pellets packed in a compact mass where single fecal pellets were still clearly observable (Figs 4A, 5A, 6A, 7A). The meconium was frequently recognizable through the circular exit holes; however, for more detailed observation partial or full dissection of the host egg is required (Fig. 5A).

In contrast, the meconium of *T. japonicus* and *T. mitsukurii* appear very different from the packed fecal pellets of *An. bifasciatus*. The meconium of these *Trissolcus* species appeared as a crescent-shaped mass of a creamy brownish or dark-grey in color (Figs 4B, C, 5B, C, 6B, C, 7B, C) and individual fecal pellets were not clearly recognizable. In a few cases, after dissection of the meconium and with careful lighting, it was possible to observe the shape of individual fecal pellets pressed together to form the whole mass (Fig. 6F). Apparently, mature *Trissolcus* larvae produce feces of a more liquid consistency than those of *An. bifasciatus*, although the meconium tends to harden with time. Slight movements of the mature larvae or pre-pupae inside the host egg is perhaps responsible for pushing the semiliquid meconium to the borders of the egg and molding it to the shape of the egg wall. This aspect of meconium may be common in scelionids, since meconia of *G. pennsylvanicum* display the same features and similarly assumes part of the shape of its host egg (*Leptoglossus occidentalis*) (Fig. 8A–C).

Meconia of *Ac. sinicus* appear as droplet-like fecal pellets (similar to sesame seeds), brown or dark grey in color (Figs 4D, 5D, 6D, E, 7D, E). In contrast with *Trissolcus* species or *An. bifasciatus*, pellets of *Ac. sinicus* do not form a single compact mass but are instead more loosely distributed along a transverse line on the inner of the egg shell, forming a discontinuous layer of feces. The meconium of *Ac. sinicus* is thus clearly distinguishable from that of the primary parasitoids of *H. halys* considered here. In all cases when *Ac. sinicus* emergence holes were investigated, its meconium was associated



Figure 4. Adult exit holes and meconium (arrows) of egg parasitoids of *Halyomorpha halys: Anastatus bi-fasciatus* (**A**); *Trissolcus mitsukurii* (**B**); *Trissolcus japonicus* (**C**); *Acroclisoides sinicus* on previous parasitized egg by *Trissolcus mitsukurii* (**D**); *Ooencyrtus telenomicida* (**E**).



Figure 5. Meconium (arrows) of egg parasitoids of *Halyomorpha halys* visible through partially dissected host eggs: *Anastatus bifasciatus* (**A**); *Trissolcus mitsukurii* (**B**); *Trissolcus japonicus* (**C**); *Acroclisoides sinicus* on previous parasitized egg by *Trissolcus mitsukurii* (**D**); *Ooencyrtus telenomicida* (**E**).



Figure 6. Halyomorpha halys egg parasitoid meconium extracted from the host egg: Anastatus bifasciatus (**A**); Trissolcus japonicus (**B**); Trissolcus mitsukurii (**C**); Acroclisoides sinicus (red arrows) on meconium of Trissolcus japonicus (**D**); Acroclisoides sinicus (red arrows) on meconium of Trissolcus mitsukurii (**E**); detail of meconium of T. japonicus (view from the bottom (**F**); Ovencyrtus telenomicida (**G**). Scale bars: 500µm.



Figure 7. Meconium of *Halyomorpha halys* egg parasitoid at SEM: *Anastatus bifasciatus* (**A**); *Trissolcus japonicus* (**B**); *Trissolcus mitsukurii* (**C**); *Acroclisoides sinicus* (red arrow) on meconium of *Trissolcus japonicus* (**D**); *Acroclisoides sinicus* (red arrow) on meconium of *Trissolcus mitsukurii* (**E**); *Ooencyrtus telenomicida* (**F**).

strictly with the presence of the meconium of *Trissolcus* specimens: the meconium is not randomly voided in the host egg, but is placed onto the meconium of the primary parasitoid (i.e. its "host"). This suggests that hyperparasitism of *Trissolcus* by *Ac. sinicus*



Figure 8. *Leptoglossus occidentalis* eggs parasitized by *Gryon pennsylvanicum* (A) and meconium recognizable in the host egg (B) and its SEM image (C). Scale bar: 500µm (B).

occurs during a late stage of development of its host, when the larvae were mature, during the larvae-pupae transition, or at the pupal stage.

The meconium of *O. telenomicida* is different from all the other species of egg parasitoids previously considered, appearing as a mass of feces comprised of amber-brown discs that are randomly distributed inside the egg host (Figs 2, 4E, 5E, 6G, 7F). In contrast with the meconium of the egg parasitoids described above, the individual pellets of *O. telenomicida* can easily be separated by breaking apart the mass with a brush (Fig. 6G).

Our results show that the meconia produced by different species within the egg parasitoid guild of *H. halys* in Europe are family-specific. Because a limited number of genera can develop in *H. halys* eggs, this can be used to help identify the parasitoids responsible for parasitism in the absence of an adult specimen. Surveys have identified three species of egg parasitoids that emerge with the greatest frequency from H. halys eggs in Europe (one eupelmid and two scelionids). The comparative rarity of other species means that most identifications will be of Trissolcus and Anastatus, which can be distinguished from each other based on the meconium. Although the meconia of T. japonicus and T. mitsukurii are similar in appearance, distinguishing between the two is facilitated by features of the emergence hole (Sabbatini Peverieri et al. 2019). The characteristics of the meconia reported here for T. japonicus, T. mitsukurii, and Ac. sinicus were comparable to those of meconia observed in representative specimens of parasitized H. halys eggs used to rear T. japonicus, T. cultratus and T. mitsukurii in USDA-ARS laboratory culture in Newark, DE, USA, in reared material from Asian field collections of T. japonicus, T. mitsukurii, T. cultratus, Anastatus spp., and Ac. sinicus, and in several Anastatus species that attack H. halys in the USA. However, a definitive species identification can be provided only by a taxonomist based upon adult specimens or through molecular analysis. Furthermore, the species-level identity of parasitoids that attacked host eggs but did not mature can be obtained only through molecular analysis.

In summary, the exit holes and meconia of *H. halys* egg parasitoids are easily recognizable, and examination of parasitized eggs from which adult wasps have already emerged can be helpful for identifying the parasitoid that emerged from the host eggs. Although definitive species identifications within genera require molecular analysis of insect remnants, by considering the relatively short list of common egg parasitoids of *H. halys* reported in the invaded areas in Europe, a rapid view of the probable parasitoid complex can be obtained. Moreover, by monitoring egg parasitoids in *H. halys* biological control programs, the cumulative impact of the egg parasitoids on eggs or egg masses of the pest can be defined even if some of the adults have already emerged in the field prior to collection.

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A new species of genus *Rhinotorus* Förster (Ichneumonidae, Ctenopelmatinae) parasitizing *Pristiphora erichsonii* (Hymenoptera, Tenthredinidae) and a key to Eastern Palaearctic species

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Abstract

A new species of Ctenopelmatinae, *Rhinotorus nigrus* Sheng, Li & Sun, **sp. nov.** reared from cocoons of *Pristiphora erichsonii* (Hartig) in Jilin Province, China, is described and illustrated. A key to Eastern Palaearctic species of *Rhinotorus* is provided.

Keywords

Key, new species, Rhinotorus, Mesoleiini, taxonomy

Introduction

The larch sawfly, *Pristiphora erichsonii* (Hartig) (Hymenoptera, Tenthredinidae), has been a significant pest of *Larix* spp. in China and other countries (Xiao 1992; Zhou et al. 1995). It is distributed in the Palaearctic and Nearctic regions (Coppel and Leius 1955; Wong 1974; Richmond et al. 1975; Taeger et al. 2018). Parasitoids of this sawfly include Diptera and Hymenoptera (Muldrew 1967; Zinnert 1969; Pschorn-Walcher

and Zinnert 1971; Drooz 1975; Richmond et al. 1975; Drooz and Thompson 1986). The parasitism rates of *Olesicampe nematorum* (Tschek) for *P. erichsonii* about 61% to 87% (Muldrew 1967), and the parasitism rate of *Olesicampe benefactor* Hinz for *P. erichsonii* reached over 90% in Minnesota (Kulman et al. 1974). In China, there are about 16 species of parasitoids of this sawfly (Sheng and Chen 2001; Li et al. 2014; Yang et al. 2015). The parasitism rates of parasitoids range from 15.9% to 31.5% (Li et al. 2014). Parasitoids are playing an important role in terminating larch sawfly outbreaks. In the present research a new parasitoid of *Pristiphora erichsonii* (Hartig), belonging to the genus *Rhinotorus* Förster, 1869, was found.

Rhinotorus Förster (Hymenoptera, Ichneumonidae, Ctenopelmatinae) comprises 15 species (Reshchikov 2016; Yu et al. 2016), of which three are from the Eastern Palaearctic Region (also found in the Western Palaearctic) (Meyer 1936; Townes et al. 1965; Reshchikov 2016), 14 from the Western Palaearctic (Reshchikov 2016), and one from the Nearctic Region (Yu et al. 2016).

The species of *Rhinotorus* Förster were revised by Reshchikov (2016). Prior to the present study the genus has not been recorded in China, nor from the Oriental Region.

The diagnostic characters of *Rhinotorus* were described by Townes (1970) and expanded upon by Reshchikov (2016).

Nineteen host species of *Rhinotorus* from ten genera of Tenthredinidae have been recorded, 17 of them belong to subfamily *Nematinae* (Yu et al., 2016). In the present research parasitism of the genus *Rhinotorus* Förster, 1869 *Pristiphora erichsonii* (Hartig) is recorded for the first time.

Material and methods

Institutional abbreviations

- **GSFGPM** General Station of Forest and Grassland Pest Management, National Forestry and Grassland Administration, P. R. China;
- NHMUK Natural History Museum, London, United Kingdom;
- **ZISP** Zoological Institute of the Russian Academy of Sciences, St. Petersburg, Russia.

Specimen collection and rearing

Cocoons of sawflies were collected under naturally infested trees in Mt. Maoer, belonging to the branch of Mt. Changbai (42°50'N, 129°28'E, elevation 375 to 400 m), Jilin Province. The forest stand is composed of mixed deciduous angiosperms mainly *Quercus mongolica* Fischer ex Ledebour and shrubs, with evergreen conifers – *Pinus koraiensis* Siebold et Zuccarini, *P. tabuliformis* Carr., and with deciduous conifers – *Larix gmelinii* (Rupr.) Kuzen., *L. kaempferi* (Lamb.) Carr., *L. principis-rupprechtii* Mayr. The detail methods according to Li et al. (2014). Images were taken using a Leica M205A stereo microscope with LAS Montage MultiFocus. Morphological terminology is mostly based on Broad et al. (2018). Type specimens are deposited in the Insect Museum, GSFGPM.

Taxonomy

Rhinotorus Förster, 1869

Rhinotorus Förster, 1869: 211. Type-species: Spudaea longicornis Schmiedeknecht.

Key to the Eastern Palaearctic species of Rhinotorus

Rhinotorus nigrus Sheng, Li & Sun, sp. nov.

http://zoobank.org/CF23EC1D-BA28-4317-BD9D-5CFBAD9BA84A Figures 1–9

Etymology. The specific name is derived from the entirely black mesosoma and metasoma.



Figures 1–9. *Rhinotorus nigrus* Sheng, Li & Sun, sp. nov. Holotype, female I habitus and host's cocoon, lateral view 2 head, anterior view 3 head, lateral view 4 head, dorsal view 5 head, dorsoanterior view 6 mesosoma, lateral view 7 propodeum 8 metasoma, dorsal view 9 apical portion of metasoma, lateral view.



Figures 1–9. Continued.

Material examined. Holotype, female, reared from cocoon of *Pristiphora erichsonii* (Hartig) in Mt. Maoer, Yanji, Jilin Province, China by Tao Li on 24 May 2009. Paratypes: 3 females, same data as holotype except 25 May–5 June 2009.

Diagnosis. Postocellar line as long as ocular-ocellar line. Area petiolaris of propodeum high (Fig. 7) with strong median longitudinal carina and irregular oblique longitudinal wrinkles. First and second tergites (Fig. 8) with distinct subposterior transverse depressions. First tergite approximately 0.8 × as long as posterior width. Head except clypeus, mesosoma, metasoma (Fig. 8), and hind leg (Fig. 1) black, except that basal 0.3 of hind tibia brownish and its spurs white.

Description. Body length 6.0–7.0 mm. Fore wing length 6.0–6.5 mm.

Head. Inner orbits parallel. Face (Fig. 2) approximately $1.9 \times as$ wide as long, slightly evenly convex, lateral portion shagreened, upper-median portion with distinct punctures; lower-median portion with indistinct punctures; upper margin with median small tubercle. Clypeus approximately $2.4 \times as$ wide as long, smooth, shiny, with sparse shallow indistinct punctures, apical median portion convex; median section of apical margin distinctly depressed. Basal portion of mandible with dense indistinct punctures; upper tooth sharper and slightly longer than lower tooth. Malar area and vertex (Fig. 4) shagreened. Malar space approximately $0.5 \times as$ long as basal width of mandible. Postocellar line approximately same length as ocular-ocellar line. Gena (Fig. 3) with fine punctures. Frons (Fig. 5) slightly convex medially, with dense fine punctures. Antenna with 31 flagellomeres; ratio of length from first to fifth flagellomeres approximately: 6.5:4.0:3.5:3.5:3.0. Occipital carina reaching hypostomal carina slightly above base of mandible.

Mesosoma. Along anterior margin of pronotum (Fig. 6) with dense fine punctures; lateral concavity with weak oblique transverse wrinkles; upper-posterior portion with dense fine punctures. Mesoscutum, scutellum and postscutellm with fine punctures. Notauli reaching beyond middle. Scutoscutellar groove almost shiny. Mesopleuron (Fig. 6) slightly shagreened, upper-median portion with fine transverse wrinkles; speculum shiny, smooth. Upper end of epicnemial carina approximately reaching to 0.6 distance to subtegular ridge. Metapleuron evenly convex, with dense punctures; lower posterior portion with oblique wrinkles. Ratio of length of hind tarsomeres from first to fifth approximately: 10.0:5.0:3.5:2.0:2.5. Wings hyaline. Fore wing with vein 1cu-a slightly distal to M&RS. Postnervulus intercepted at lower 0.4. Hind wing vein 1-cu approximately 1.5 × as long as cu-a. Propodeum (Fig. 7) with complete strong median longitudinal carinae and area petiolaris shiny, remain areae with dense distinct punctures; area petiolaris with strong median longitudinal carina and irregular oblique longitudinal wrinkles. Propodeal spiracle small, circular, located at basal 0.25.

Metasoma. First three tergites (Fig. 8) with dense punctures. Subposterior portions of first and second tergites with weak transverse depressions. First tergite approximately $0.8 \times as$ long as posterior width, with irregular short wrinkles; dorsal median carina reaching to 0.6 length of first tergite; dorsolateral and ventrolateral carinae complete; postpetiole strongly convex; spiracle small, circular, convex, located approximately at anterior 0.4 of first tergite. Second and third tergites (Fig. 8) approximately $0.5 \times$ as long as posterior width. Fourth and subsequent tergites with relatively sparse fine punctures. Ovipositor sheath (Fig. 9) approximately $2.3 \times$ as long as its maximum width, from middle evenly narrowed posteriorly.

Colouration (Fig. 1). Black, except for following: clypeus, maxillary palpi, labial palpi, malar area, upper-posterior corners of pronotum, tegulae yellowish brown; mandible except base and teeth, fore and middle femora, tibiae and tarsi, apexes and bases of hind femora red brown; ventro-basal portions of hind tibiae brownish yellow; antennae, pterostigma and veins brownish black. Second and third metasomal sternites black brown.

Male. Unknown. Distribution. China (Jilin). Host. Pristiphora erichsonii (Hartig).

Differential diagnosis

The new species is similar to *Rh. jussilai* Reshchikov, 2016, but can easily be distinguished from it by the following combinations of characters: occipital carina reaching hypostomal carina slightly above base of mandible; area petiolaris of propodeum with strong median longitudinal carina; hind femur black. *Rhinotorus jussilai*: occipital carina reaching hypostomal carina distinctly above base of mandible; area petiolaris of propodeum with ut median longitudinal carina; hind femur brownish red.

Discussion

The new species is the only species of *Rhinotorus* recorded in the southeastern part of the Eastern Palearctic Region. The genus is not recorded in this part of Russia, in Korea and Japan. Nevertheless in the collections from the boreal and oriental part of China there are unidentified species of this genus. *Rhinotorus* need in further taxonomical research.

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Discovery of a non-native parasitoid, Marlattiella prima Howard (Hymenoptera, Aphelinidae) and its non-native host, Lopholeucaspis japonica Cockerell (Hemiptera, Diaspididae) in Central Texas

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Abstract

Sampling of crapemyrtle trees (*Lagerstroemia* L.) in central Texas yielded the discovery of an invasive scale pest, *Lopholeucaspis japonica* Cockerell, and its parasitoid natural enemy, *Marlattiella prima* Howard. These discoveries expand the known range of both the scale insect and the parasitoid wasp in the United States. *Marlattiella prima* was not recovered in the absence of *L. japonica*. Of the two counties sampled, Brazos County yielded 26 *M. prima* individuals and Tarrant County yielded neither *M. prima* nor *L. japonica*.

Keywords

biologivcal control, Marlattiella, Marlattiella prima, Lopholeucaspis japonica

Introduction

Members of the genus *Marlattiella* Howard (Hymenoptera: Aphelinidae) are known to parasitize only armored scale insects (Hemiptera: Diaspididae). Two species have been described worldwide (Viggiani 1985; Rehmat et al. 2011): *M. prima* Howard and *M. maculata* Hayat. *Marlattiella prima* is a parasitoid of *Lopholeucaspis japonica* Cockerell (Japanese maple scale) in China and Japan (Rosen and DeBach 1970) and *M. maculata* is a parasitoid of *Aonidiella orientalis* Newstead (Oriental yellow scale) in India (Rehmat et al. 2011). Viggiani (1985) identified chalcidoid wasps collected from sticky traps in Africa and uncovered a possible third species, extending the geographical range of the *Marlattiella* genus to the Ethiopian region.

Marlattiella prima adults closely resemble adults in the genus *Aphytis* Howard, and other genera in the tribe Aphytini (Kim and Heraty 2012). *Marlattiella* spp. individuals are distinguished from the other members of Aphytini by their antennal formula: scape, pedicel, no funicle segments or anelli, and a long, unsegmented clava (Figure 1). Species of *Eretmocerus* Haldeman, a similar and closely related genus (Kim and Heraty 2012), share this antennal formula but have four-segmented tarsi while *Marlattiella* spp. have five-segmented tarsi. Additional recognition characteristics include a short propodeum in *Marlattiella* spp. lacking the marginal crenulae found in *Aphytis* spp. (Rosen and DeBach 1970) (Figure 1).

Lopholeucaspis japonica (Hemiptera: Diaspididae) was first reported in the United States in Connecticut in 1914 (Miller et al. 2005). Currently the reported distribution of this scale in the United States includes Connecticut, Delaware, Georgia, Kentucky, Louisiana, Maryland, New Jersey, New York, North Carolina, Pennsylvania, Rhode Island, Tennessee, Virginia, and Washington DC (Frank et al. 2013; Jeger et al 2018). It has a host range of approximately 97 plant species from 35 families (Knox et al. 2012; Harsur et al. 2018; Jeger et al. 2018). In the United States, *M. prima* has been reported in Maryland, only one of the fifteen states in which *L. japonica* has been reported (Krombein et al. 1979). This paper describes the first reported occurrences of *L. japonica* and *M. prima* in Texas. This is important because it expands the range of a pervasive pest of 97 tree species as well as the range of one of its known parasitoids.

Methods

Foliage samples were collected from 40 plants of the 'Natchez' (*Lagerstroemia indica* L.) crapemyrtle cultivar and 60 plants of other crapemyrtle cultivars in Brazos County and Tarrant County, Texas. Tarrant County is 190 km north of Brazos County, and Brazos County is approximately 158 km NE of Houston, Texas. Ten 30 cm long branch tips randomly distributed along the canopy perimeter of three-meter to five-meter-tall trees were collected using a telescoping pruner with a 2.7 m reach. Branch tips were immediately placed in Sure Fresh rectangular storage containers, 10 cm × 35 cm (Greenbrier International, Inc., 1509 Sam's Circle Store No 502 Chesapeake, VA 23320-4694



Figure 1. *Marlattiella prima* Howard adult female recovered from *Lopholeucaspis japonica* Cockerell on *Lagerstroemia indica* L. trees. This specimen is in the TAMU insect collection (TAMUIC) as TAMU Vouchers #746. The photograph was taken by JBW with a Macropod system (https://macroscopicsolutions.com) using 20× microscope objective, a 200 mm tube lens, and a Canon EOS 5D Mark III camera.

United States, www.dollartree.com, SKU: 236854). Storage containers were labelled by tree. Each tree was given a unique number and GPS data was collected using a cell-phone application (GPS Status & Toolbox Pro version 9.0.183 2019, EclipSim). The GPS coordinates were recorded for the purpose of using the same trees every season from spring 2018 to winter 2018.

The plastic containers containing branch samples were placed in cold storage for 24 to 120 hours at 6 °C to slow down arthropods during the sample processing period. Containers removed from cold storage were opened and branches were carefully examined with the aid of a stereo microscope (Olympus SZ-6045). Scale insects were counted and identified to the lowest taxon possible.

Branches were subsequently placed in sealed, white paper bags (Uline white grocery bags, uline.com model no. S-11541, 19.685 cm \times 12.065 cm \times 40.64 cm) to allow for parasitoid emergence. After three months, the bags were opened and the contents were shaken into a petri dish containing 70% ethanol. Using a stereo microscope (Olympus SZ-6045), parasitoids were then counted and identified to the lowest taxonomic level possible before being placed in labelled vials with 70% ethanol for preservation. Voucher specimens have been deposited in the TAMU Insect Collection (TAMUIC) as TAMU Vouchers #746.

Collection	Trees with L. japonica ⁴	Trees with <i>M. prima</i> present (range of <i>M. prima</i> recovered) ^b	Number of M. prima present
Spring 2018	Data Not Recorded	4 (1-2)	6
Summer 2018	29	4 (1-3)	6
Fall 2018	23	1 (1)	1
Winter 2018	25	5 (1–5)	13

Table 1. Numbers of Lagerstroemia indica trees with L. japonica and M. prima present.

^aA total of 100 trees were sampled for each collection and a total of 35 trees across all collections hosted *L. japonica*. Values within the column are the number of trees infested with *L. japonica* within a collection. ^bRange represents the minimum and maximum of *M. prima* recovered from trees infested by *L. japonica* within a collection.

Results

A total of 26 *M. prima* individuals were recovered from 400 *L. indica* samples in Brazos County (Table 1). Most were recovered from samples collected during winter of 2018. All of the *L. indica* twigs from which *Marlattiella* individuals were recovered contained *Lopholeucaspis japonica* individuals, with the exception of those collected in the spring of 2018, for which there are no data on scale presence. *Lopholeucaspis japonica* were frequently recovered from the same locations and trees across all four seasons. No *L. japonica* or *M. prima* were recovered from 400 samples taken in Tarrant County.

Discussion

Our collections represent the first occurrence of both *L. japonica* and *M. prima* individuals in Texas. The range of *L. japonica* around Brazos County may be indicative of a population existing prior to our detection. The fact that it was recovered from the same trees at the same locations may imply that it is not rapidly spreading, though only *L. indica* plants were sampled and it is known that *L. japonica* has a wide host range (Knox et al. 2012; Harsur et al. 2018; Jeger et al. 2018). *Acer* spp. L. (Sapindales: Sapindaceae), *Alnus* spp. Miller (Fagales: Betulaceae), *Ilex* spp. L. (Aquifoliales: Aquifoliaceae), *Liquidambar* spp. L. (Saxifragales: Altingiaceae) and, *Magnolia* spp. L. (Magnoliales: Magnoliaceae) are among the native Texas trees (Texas A&M Department of Horticulture 2019) that *L. japonica* individuals in Texas.

Conclusion

Surveys from Brazos County, TX document the presence of *Lopholeucaspis japonica* and *Marlattiella prima*, which have not previously been reported for Texas. This record expands the range of both organisms. The population of *L. japonica* is apparently not spreading, as it remained localized on a set number of trees in Brazos County and was not found in Tarrant County.
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RESEARCH ARTICLE



Discovery and description of the first known fossil Signiphoridae (Hymenoptera, Chalcidoidea)

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Abstract

Chartocerus azizae **sp. nov.** is described as the first known fossil from the family Signiphoridae, based on two inclusions in the same piece of Eocene Baltic amber (36.7–48.5 million years ago). Implications of the morphology of *C. azizae* are discussed, indicating that it should be placed in *Chartocerus*.

Keywords

Baltic amber, extinct, new species

Introduction

The family Signiphoridae is a monophyletic group (Heraty et al. 2013) of primary and secondary parasitoids of a variety of hosts, classified into four genera (Woolley 1988, 1997; Woolley and Dal Molin 2017). Although two subfamilies, Signiphorinae (for *Signiphora* Ashmead) and Thysaninae (for *Chartocerus* Motschulsky, *Thysanus* Walker

and *Clytina* Erdös), have been proposed in the past, Woolley (1988, 1997) suggested that Thysaninae is paraphyletic with respect to Signiphorinae. Changes resulting in monophyly would have required formation of a weakly justified and plesiomorphic subfamily to contain only *Chartocerus* (Woolley 1988).

Molecular data (28S and 18S ribosomal DNA) indicated that *Clytina giraudi* Erdős rendered *Chartocerus* paraphyletic, thus reinforcing that Thysaninae would be problematic if recognized (Munro et al. 2011). Combined data (Heraty et al. 2013) agreed with these results but did not include enough taxa to test monophyly of *Chartocerus*.

Extant Signiphoridae possess many features that are presumably apomorphic within Chalcidoidea, including long, unsegmented antennal clava, the anelliform shape and size of all preclaval flagellomeres, lack of external indication of notauli, transverse shape of the mesoscutellum, lack of external indication of axillae, lack of or reduced number of fore wing disc setae, presence of a triangular median area defined on the propodeum, presence of internal anterior projections on metasomal sterna 3–6, and presence of a separate epipygium (metasomal tergum 9) in females and most males (Woolley 1997). Some of these features are shared most notably with Azotidae, which is the sister group of Signiphoridae supported by most recent analyses (Woolley 1988, Heraty et al. 2013).

No fossil Signiphoridae have been previously described, but similarly small-bodied Chalcidoidea such as Aphelinidae and Trichogrammatidae are known from Eocene Baltic amber (Burks et al. 2015). The discovery of a Baltic amber signiphorid establishes the minimum age of Signiphoridae in the Eocene, but does not pinpoint that age with great accuracy because of uncertainty over which stratum the fossils came from (Ritzkowski 1997). Therefore, we choose a cautious estimate of 36.7–48.5 million years ago for this species.

Methods

The holotype belongs to the American Museum of Natural History (AMNH B-JWJ-73, UCRCENT00237907). Stereoscope photographs were taken using Leica Imaging System Software with a Z16 APO A microscope, a Keyence VHX-6000 digital microscope equipped with NHZ20R 20–200× zoom lens and VH-250R/W/T 250–2500× zoom lens, and a Macropod Pro macrophotography system (https://macroscopicsolutions.com) using Mitutoyo planapochromat objectives. Serially focused images were focus-stacked using Zerene Stacker (Build T2019-10-07-1410 or earlier versions) using the PMax algorithm, and subsequently processed in Adobe Lightroom to adjust brightness and contrast and to bring out image details, and Adobe Photoshop to add scale bars. In some cases, backgrounds were removed using Topaz ReMask. Images were annotated in Adobe InDesign. Terminology follows that of Woolley (1988), with some additional terms following Gibson (1997) and sculptural terms following Eady (1968). For the Macropod images, the amber piece was submerged in glycerin in an optical cuvette, with the surface closest to the specimen placed as close as possible

to the crystal optical surface. Illumination was entirely indirect: twin Yognou flashes were directed not at the specimen but at a white plastic diffuser on the front of the microscope objective. For the Keyence images, specimens were submerged in glycerin in a small petri dish, and lighting was performed using diffusers on the Keyence lenses. Best results with the Keyence were generally obtained with the Depth Up/Fine Depth Composition algorithm.

Results

Generic placement

Chartocerus is defined by features that are presumably plesiomorphic in Signiphoridae (Woolley 1988), including a narrowly rounded occipital margin of the head (instead of broadly rounded or sharp), presence of 4 anelli in females (instead of 3 or fewer in other genera) and 3 anelli in males, presence of five dorsal setae on the anterior edge of the marginal vein (instead of four), a rounded posterior hind wing margin (instead of nearly straight), lack of a comb of setae on the protibial spur, three or four long mesofemoral spines (instead of one), lack of a lamelliform process on the median elevation of the propodeum, and the lack of an epipygium in males (Woolley 1988). Chartocerus azizae possesses most characters used by Woolley (1988) and Woolley and Dal Molin (2017) to define *Chartocerus*, including a curved and bifid foretibial spur, without a comb of fine setae (Fig. 10), and metasomal terga 8 and 9 combined to form a syntergum (Fig. 13: syn). However, C. azizae has two mesofemoral spines instead of three or four (Fig. 13), and one anellus in males instead of three (Fig. 4). The median area of the propodeum could not be assessed. Chartocerus azizae also possesses a posteriorly emarginate subgenital plate, but its exact shape is also not clearly discernable in these specimens (Fig. 11: Ms_o). The fore wing venation setae in C. azizae correspond to that those in extant *Chartocerus* (Fig. 7). The raised surface sculpture of the fore wing (Fig. 7) is much stronger and more conspicuous than the hardly visible fore wing sculpture of other Chalcidoidea. Recently, an unusual new species has been described in Chartocerus, C. kartiniae Polaszek and Schmidt (Schmidt et al. 2019). This species has two anelli in females, a large discal seta in the fore wing, and light coloration on the mesosoma (both previously unknown in *Chartocerus*).

Description

Chartocerus azizae Burks, Woolley, Kesbeh, Eldridge & Dal Molin, sp. nov. http://zoobank.org/0A161559-185B-44CB-AC7D-53EF17055711 Figs 1–13

Male (n = 2). Body length 0.67–0.75 mm.



Figures 1–6. 1 Whole fossil showing the holotype and paratype (Leica Z16 Apo A) **2** holotype, dorsal habitus (Macropod) **3** paratype, lateral habitus (Keyence) **4** paratype, head and antennae (anl: anellus) (Keyence) **5** holotype, head and antennae (man: mandible) (Macropod) **6** holotype, mesosoma (Macropod).

Type material. The Baltic amber piece containing the holotype and paratype contains two inclusions, both males of this species [AMNH B-JWJ-73, UCR-CENT00237907]. The amber was not cut to separate the specimens, because fractures in the piece would endanger the inclusions (Fig. 1). The holotype (Fig. 1: Holotype, Figs 2, 5–7, 9, 11, 12) is the specimen with one wing folded over the body. The paratype (Fig. 1: Paratype, Figs 3, 4, 8, 10, 13) is the specimen with both wings raised, near a fractured edge in the amber. Types deposited in AMNH.

Diagnosis. Fore wing venation with setae M1, M2b, and M6 present, thus fore wing venation with a total of 10 dorsal setae, with 7 on the marginal vein (Fig. 7). Male

antenna with one anellus (Fig. 4: anl). Mesofemur with 2 stout ventral setae subapically (Fig. 13: mfs). Fore wing with strong raised surface sculpture (Fig. 7).

Color and sculpture. Head and antenna. Head dark brown, pedicel, funicle and clava brown.

Body. Mesosoma and metasoma uniformly as dark brown as head; patchy light areas are visible on the holotype, however these appear to be artifacts of preservation in amber. Fore wings hyaline except for infuscate area below marginal vein and at wing base, hind wings hyaline. Profemur dark with light areas at apex, protibia dark; mesofemur and mesotibia dark, mesobasitarsus light, metafemur and metatibia dark.

Head (Figs 4, 5). Clava about 5× as long as broad, with about 40 MPS (Fig. 4); one anellus present (Fig. 4: anl). Scape inserted slightly ventral to lower eye margin, about 0.55× clava length; pedicel 0.3× clava length. Mandible small, with two short teeth (Fig. 5: man) of equal length. Face with shallow coriaceous sculpture; antennal scrobe distinctly margined dorsally, rounded interantennal elevation present. Vertex narrowly rounded. Postgenae posteriorly separated (therefore subforaminal bridge similar to that in Burks and Heraty. 2015: fig. 6h).

Mesosoma (Figs 2, 6–10). Pronotum short. Mesoscutum shallowly sculptured (transversely coriaceous), with sparse, scattered, minute setae, only slightly longer than mesoscutellum. Mesoscutum:mesoscutellum 1.43, number of setae on mesoscutum not visible. Mesoscutellar sculpture nearly isodiametric. Metascutellum with transverse sculpture with meshes longer than those on the mesoscutum. One pair of setae visible on mesoscutellum, mesoscutellum:metascutum 2.33.

Prosternum and lower mesepisternum transversely sculptured. Prepectus dorsally short, shallowly sculptured. Mesepisternum short, with sulcus-like mesodiscrimen, with mesofurcal pit near mesocoxal insertions. Mesopleural sulcus indicated. Foretibial spur curved and bifid, without a comb of fine setae (Fig. 10: fls). Mesotibia expanded apically, with two stout dorsal spines; mesotibial spur stout, setose. Mesobasitarsus:mesofemur 0.36, mesotibial spur:mesobasitarsus 0.88, 6 spines on mesotibial spur. Metafemur stout, less than twice as long as broad.

Fore wing length:width 1.82, with long marginal fringe, the longest fringe setae slightly longer than parastigma, longest fringe:width of fore wing 0.23; parastigma strongly sinuate (Fig. 7), discal seta absent; linea calva not present, but a smooth unsculptured area on fore wing extends basally from stigmal vein almost to posterior margin (Figs 7, 8). Fore wing and hind wing with raised surface sculpture (Figs 7, 8); fore wing with two setae on submarginal vein and with setae M1, M2b, and M6 present. A small seta appears to be present in the basal area of the wing, but the location is different from the discal seta in other Signiphoridae. Posterior margin of hind wing rounded (not nearly parallel with anterior margin, Fig. 8). Hind wing with sculpture like that of fore wing, fringe slightly longer than that of fore wing, hind wing length:width 4.00, marginal setae:width hind wing 0.67, discal seta present on hind wing below apex of marginal vein.

Metasoma (Figs 11–13). Metasomal terga 8 and 9 combined to form a syntergum (Fig. 13: syn). Terga and sterna with coriaceous sculpture. Male genitalia with diver-



Figures 7–13.7 Holotype, wings showing surface sculpture (ssmv: setae submarginal vein, setae M1–M6). (Macropod) **8** paratype, fore wing and hind wing (Leica Z16 Apo A) **9** holotype, wing venation (Macropod) **10** paratype, legs (fts: foretibial spur) (Macropod) **11** holotype, dorsal metasoma and genitalia (Ms₇: metasomal sternum 7, Ms₈: metasomal sternum 8) (Macropod) **12** Holotype, ventral metasoma and subgenital plate (dg: digitus) (Keyence) **13** Paratype, apex of metasoma, lateral (mfs: mesofemoral spines) (Macropod).

gent digiti, each with 1 apical digital spine (Fig. 12), and possibly a pair of median denticles (one median denticle visible in 2010). Subgenital plate (Ms₈) deeply emarginate medially (Fig. 11, Ms₉). Metasomal sternum 7 broadly truncate (Fig. 11, Ms₉).

Etymology. The species name is a noun in genitive case, the gender is feminine. The species is named after SOK's grandmother, Aziza Meetab. Aziza means "precious" in Arabic, recognizing the precious nature of this fossil.

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