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## Bees of Maine, with a State Species Checklist

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and John S. Ascher<sup>5</sup>

**Abstract** - We present a new county checklist developed from bee research in Maine since the 1800s. The list contains 278 bee species in 37 genera and 6 families, of which all but 8 are native, with  $\geq 50$  taxa each in *Andrena* and *Lasioglossum*. Data for 16 counties from publications, museum collections, and recent surveys varied in number of species from 8 (Androscoggin) to 197 (Hancock). Research since 1930 on *Vaccinium angustifolium* (Lowbush Blueberry) led to many records. Twenty-one species are considered unusual, including 3 first recorded in 2016: *Epeoloides pilosulus*, *Melitta melittoides*, and *Holcopasites calliopsidis*. Maine records provide evidence of declines in *Bombus affinis*, decline in *B. terricola* followed by partial recovery, and increase in *B. impatiens*. Crops that should be studied regarding associated bees are *Malus pumila* (Apple), *Vaccinium corymbosum* (Highbush Blueberry), *Vaccinium macrocarpon* (American Cranberry), and Curcubitaceae (cucurbits). Montane, sandy, and island habitats were identified as priorities for future sampling. We discuss records of bee species from New England relevant to understanding the Maine fauna, bee diversity, changes in abundance, cleptoparasitism, pesticide impacts, habitat requirements, and climate change.

### Introduction

In Maine, native bees have received attention due to their role as pollinators, in particular of native, insect-dependent *Vaccinium angustifolium* Aiton (Lowbush Blueberry). This crop is designated in the industry as “wild blueberry” and also known as Low Sweet Blueberry. It is unusual in that large monocultural stands of a wild shrub are managed commercially (Hall et al. 1979). Extensive studies of Lowbush Blueberry since the 1960s (Boulanger et al. 1967; Bushmann and Drummond 2015; Drummond and Stubbs 1997a, 1997b, 2003; Stubbs et al. 1992) have identified that the most important pollinators for this crop are native bees including *Bombus* (bumble bees), *Andrena* (mining bees), *Halictus* and *Lasioglossum* (sweat bees), *Megachile* (leaf-cutter bees), and *Osmia* (mason or orchard bees). Of particular interest to researchers and growers are the alternate forage plants visited by bees for pollen and nectar before and after the bloom period for the Lowbush Blueberry crop (Bushmann and Drummond 2015, Stubbs et al. 1992). Other research foci within the Lowbush Blueberry pollination system are the effects of pesticides, pests, and diseases on native bees (Bushmann et al. 2012, Drummond 2012a).

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Collecting for purposes other than to understand pollination of Lowbush Blueberry has been less intensive despite the longstanding importance of orchard crops and research on invasive plant pollination since the early 1990s (Stubbs et al. 2007). Procter (1938, 1946) included bees in a general survey of the Mount Desert Region, and in recent decades several bee surveys have been conducted that were not related to Lowbush Blueberry (Dibble et al. 1997; Droege 2010; Stubbs et al. 1996, 2007). Diverse bees also visit other native blueberry species including *Vaccinium corymbosum* L. (Highbush Blueberry), common in Maine wetlands, and also *V. myrtilloides* Michx. (Common Blueberry), which often grows intermixed with Lowbush Blueberry.

In Maine, the study of native bees and their collection has been uneven across time and geographic locale (Table 1). The earliest scientific studies of Maine bees include reports of an entomological collecting trip to northern parts of Penobscot and Piscataquis Counties by Alpheus S. Packard Jr. (1861). There is also a description by Cresson (1863) of 2 currently valid *Nomada* species from unknown localities in Maine: *N. depressa* and the poorly known *N. proxima*; both are from the collection of Edward Norton, and their type specimens are deposited in the Academy of Natural Sciences Philadelphia. Another collector, Frederick Allen Eddy, collected bees in the early 1880s from the vicinity of Orono, Penobscot County, many of which are deposited in the University of Maine Collection.

John H. Lovell made the most important historical contribution to the study of Maine bees by documenting the bee fauna of Waldoboro in Lincoln County where he lived and by making broader studies of regional bees and their floral associations (Covell 1972; Lovell 1900, 1905a, 1905b, 1907, 1908, 1910, 1911, 1913, 1922a, 1922b, 1924, 1925a, 1925b, 1925c; Lovell and Cockerell 1905, 1906, 1907a, 1907b; Lovell and Lovell 1932; Pellett 1939). His collections, which consist of about 16,000 specimens of bees and other flower-visiting insects, were brought to the University of Louisville insect collection (renamed as the Lovell Insect Museum). Most of Lovell's type specimens of New England bees, including those from Maine, are in the National Museum of Natural History, with lectotype designations provided by Covell (1972), and have been databased and imaged. However, the types of 4 additional species described from New England by Lovell (1909) and originally deposited in the Museum of the Boston Society of Natural History, were overlooked by Covell (1972). These types are now in the Museum of Comparative Zoology at Harvard University (Moure and Hurd 1987). In all, Lovell described from New England 15 currently valid bee species (2 of questionable validity; 8 with coauthor T.D.A. Cockerell) and 18 additional names now placed in synonymy, with Waldoboro the type locality of 10 valid species and an additional 14 taxa now considered to be junior synonyms. Lovell made important contributions to what is known about pollination ecology, flower morphology, and the honey plants of North America (see the biography of John Lovell at <https://www.encyclopedia.com/doc/1G2-2830902685.html>). His work was of particular importance as a foundation for regional investigations of floral specialization (oligolecty), complementing investigations of bees in the Midwestern United States by the pioneering

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Table 1. Chronological list of selected collectors of bees in Maine, including those having more than 10 records in available sources, with approximate years of activity, collecting localities, comments and citation if known, and repository if known. det. = determined by. County abbreviations are in Figure 1. Other abbreviations: American Museum of Natural History (AMNH), Maine Department of Agriculture, Conservation and Forestry, Augusta (ME DACF), University of Connecticut Entomological Collection (UCMS). [Table continued on following 2 pages.]

Collectors	Collection years	Collection localities and/or study focus	Comments and citation if known	Repository, if known
Packard, A.S., Jr.	1861	Northern PE and PI	Report to Maine Board of Agriculture	Unknown
Zabriskie, J.L.	1898–1900	Little Deer Isle (HA), Casco Bay (CU)		AMNH
Lovell, J.H.	1904–1907	Waldoboro (LI)	Types catalogued by Covell (1972)	Lovell Insect Museum at the University of Louisville; type specimens in the National Museum of Natural History and the Museum of Comparative Zoology at Harvard; some specimens in AMNH
Eddy, F.A.	1881–1884	Assumed PE	Locale info patchy; “Orono Hill”, “Carre Woods”, “Odlin Road”; red ink	ME DACF
Franklin, H.J.	1911–1913	Orono (PE)	<i>Bombus</i>	Unknown
Woodruff, L.B.	1915	Camden (KN)	<i>Bombus</i>	AMNH
Viereck, H.L.	1922	Mount Desert Island (HA)	Viereck 1922	Unknown
Schwarz, H.F.	1925	Rangeley (FR)	Schwarz (1926)	AMNH
Procter, W.	1938–1946	Mount Desert Island (HA)	Part of a general natural history survey; Procter (1938, 1946)	Sawtell Museum Archives, Acadia National Park at McFarland Hill, Bar Harbor, ME
Borror, D.J.	1940	LI	Academic insect collection	Ohio State University
Brower, A.E.	1933–1960	Bar Harbor (HA), Augusta (KE), Katahdin (PI)	Maine Forest Service, specialized in Lepidoptera	ME DACF, in part

Table 1, continued.

Collectors	Collection years	Collection localities and/or study focus	Comments and citation if known	Repository, if known
Unknown	1927–1929, 1937	N. Gray (CU)	“Maine Agric Exp Sta” “Entomological Museum”	ME DACF
Phipps, C.R.	Late 1920s	CU, HA, WN	With O. Dirks, studied insects associated with blueberry crop	ME DACF
Plath, O.E.	1935	Caribou (AR)		University of Connecticut
Klots, W.B.	1954	Oxford (OX)		AMNH
Wygodzinsky, P.	1964	Skowhegan (KE)		AMNH
Osgood, E.A.	1960s–1980s	Alternate forage for Lowbush Blueberry, including <i>Rubus</i> , <i>Viburnum</i> (PE, WN, YO)	Specimens det. by TB. Mitchell, W.E. LaBerge, and, for <i>Bombus</i> , H.E. Milliron	ME DACF
Boulanger, L. W.	1961–1965	Lowbush Blueberry pollinators (WD, WN, YO)	With E.A. Osgood; also sampled New Brunswick, Canada	ME DACF
Favreau, M.	1974	WD		AMNH
Heinrich, B.	1970s–1980s	Farmington area (FR)	<i>Bombus</i> biology and foraging behavior	Unknown
Miliczky, E.R. (student of E.A. Osgood)	1970s	Blueberry pollinators	Some <i>Dialictus</i> det. by S.W. Batra; Masters thesis 1978	ME DACF
Hansen, R. (student of E.A. Osgood)	1982	HA, WN	Bees on spruce, T34 (HA) and Washington County, T4 ND, (n. HA) and WN, sent specimens to M. Arduser; <i>Dialictus</i> and <i>Erythraeus</i> det. by G.C. Eickwort	ME DACF
Dibble, A.C.	Early 1990s–present	Conservation of bee diversity on <i>Amelanchier</i> (HA, PE); bee/host plant relationships (AR, HA, PE, PI, WN)	Dibble and Drummond 1997, Dibble et al. 1997; <i>Andrena</i> det. by W.E. LaBerge, Halictidae by G.C. Eickwort and J. Gibbs, <i>Nomada</i> by S. Droege, <i>Bombus</i> by L. Richardson, various by J.S. Ascher and M. Veit	School of Biology and Ecology, University of Maine, Orono, ME

Table 1, continued.

Collectors	Collection years	Collection localities and/or study focus	Comments and citation if known	Repository, if known
Stubbs, C.S., F.A. Drummond, and H. Ginsberg	1990s–2010	Pollinators on Lowbush Blueberry, invasive plants (HA, PE, WD, WN)	<i>Nomada</i> det. by S. Droege	Acadia National Park Collection
Droege, Sam	2010	Schoodic Peninsula, Winter Harbor (HA); Bradley (PE)	Hymenoptera Bioblitz, Acadia National Park; bee diversity study, Penobscot Experimental Forest, Bradley	US Geological Survey
Loose, J., F.A. Drummond, and C.S. Stubbs	Late 1990s	WN	Lowbush Blueberry research (Deblois and Cherryfield), det. by S.W. Batra, updates by M. Veit	ME DACE, in part
Ascher, J.S.	2001	Monhegan Island, Port Clyde (KN)	American Museum of Natural History and University of Singapore	AMNH
Maier, C.T.	2001–2004	Steuben (WN)	Connecticut Agricultural Experiment Station, New Haven, CT	
Bushmann, S.	2010–present	HA, WD, WN	Blueberry pollinators confirmed or det. by S. Droege, J. Gibbs, R. Jean	School of Biology and Ecology, University of Maine, Orono, ME
Veit, M.	2006–2016	HA, KE, PE, SO, WD, YO	General bee surveying	Personal collection, Pepperell, MA

mellitologists Sigmund Graenicher (1905, 1911, 1914, 1927, 1935) and Charles Robertson (1929).

Other earlier scientists who contributed to what is known of Maine bees include Franklin (1911, 1912), who made the first extensive studies of Maine bumble bees (*Bombus sensu lato*, including *Psithyrus*), and cited Orono, ME, among the syntype localities in his description of *Psithyrus fernaldae* Franklin, 1911. This taxon is now cited as *Bombus (Psithyrus) fernaldae* or treated as a synonym of the Palearctic *B. (P.) flavidus* Eversmann (see Cameron et al. 2007). Viereck (1922) described from Mount Desert Island 2 *Andrena* species now in synonymy. Herbert F. Schwarz (1926) reported bees collected at Rangeley in Franklin County and deposited voucher specimens in the American Museum of Natural History. William Procter (1938, 1946) included bees in his general biological survey of Mount Desert Island in Hancock County. In Washington, Hancock, Cumberland, Knox, and Lincoln counties and perhaps elsewhere in the late 1920s, Clarence R. Phipps (1930) inventoried insects associated with blueberry species and *Gaylussacia baccata* (Wangenh.) K. Koch (Black Huckleberry). Auburn E. Brower, a well-known microlepidopteran specialist, collected Maine bees among other insects from the early 1930s for almost 50 years, in the Augusta area of Kennebec County and many other Maine locales (Davis and Hevel 1995).

Interest in Lowbush Blueberry prompted many research projects since the work of Phipps (1930). From early times, a high priority was given to documenting bee fauna and obtaining expert identification of specimens, as correct determination to the level of species is a crucial aspect in understanding ecological patterns (see discussion in Cane 2001). In 1961–1965, bees and other insect visitors to Lowbush Blueberry were documented in 3 Maine counties and 4 Canadian provinces (Boullanger et al. 1967). Eben A. Osgood (1972, 1989) examined the nesting biology of *Andrena* and contributed to the identification of 2 *Osmia* species (Rust and Osgood 1993). His students and others extended this research by investigating native plants as floral resources and the response of the bee communities to pesticides applied to control *Choristoneura fumiferana* (Clemens) (Spruce Budworm) outbreaks (Hansen and Osgood 1983; Miliczky and Osgood 1979a, b; Stubbs et al. 1992, 1996).

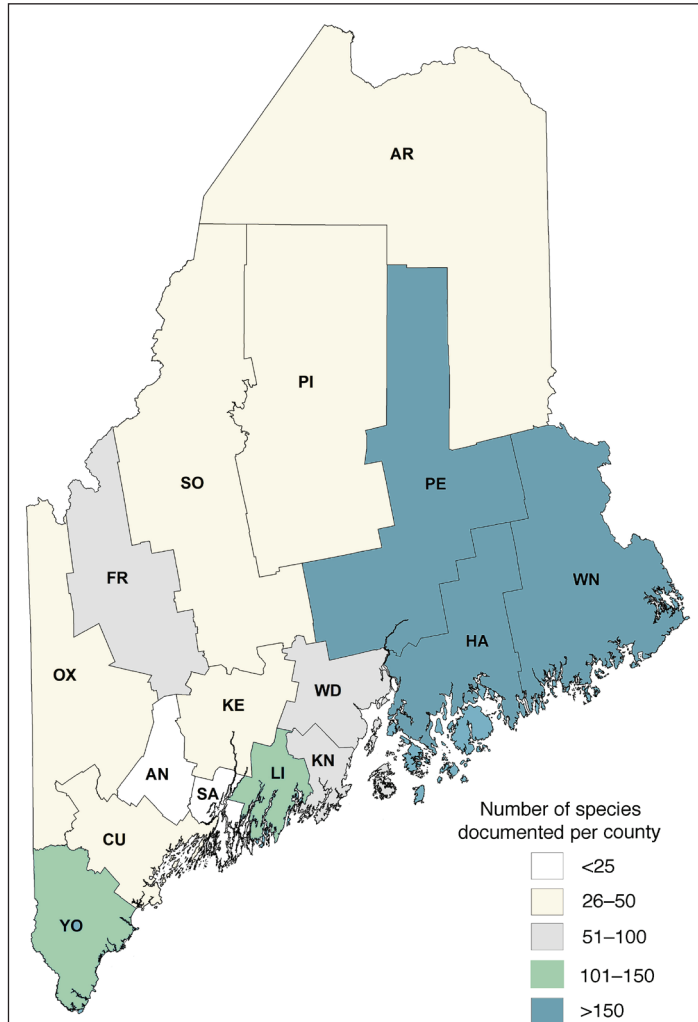
Bernd Heinrich has been internationally recognized for his research on the ecological physiology of bee and moth thermoregulation, and for his numerous writings in natural history (Heinrich 1971, 1976b, 1979, 1993, 1994, 1995, 2004; Heinrich and Chavarría 2001; Heinrich and Heinrich 1983a, 1983b; Heinrich et al. 1977). Heinrich conducted important research on the behavior and biology of *Bombus* in the Farmington, ME, area. Starting in the 1970s, he elucidated the ecological physiology of bumble bee energy budgets for optimal foraging and thermoregulation (Heinrich 1972a, 1972b, 1972c, 1972d, 1973, 1974a, 1974b, 1975, 1976a, 1976c, 1979, 1995, 2004).

These and additional researchers, natural historians, and collectors who have provided baseline information on Maine's bee fauna and bee biology are listed chronologically and annotated in Table 1. Identification of some Maine bee specimens to species was conducted by resident scientists, especially S. Bushmann and

C.S. Stubbs, and most identifications were by taxonomic specialists on Northeastern bees, including T.B. Mitchell (1960, 1962), G.C. Eickwort, and W.E. LaBerge. More recently the specialists who determined Maine bees have included J. Gibbs, S. Droege, T. Griswold, J.S. Ascher, L. Richardson, and M. Veit.

This report on bee diversity in Maine includes a state checklist of species occurrence by county (Table 2, Fig. 1) based on all available data, including specimens examined by the authors, taxonomic catalogs, revisions, other literature, and digitized specimen records. The latter include specimens from multiple collections in the northeastern United States, including the American Museum of Natural History (AMNH), Cornell University, the University of Connecticut, and other collaborating institutions, compiled using open-source Arthropod Easy Capture (AEC; Seltmann 2013) (see [http://biodiversity-informatics-training.org/wp-content/uploads/2014/03/D2\\_P6\\_CW\\_AEC2.pdf](http://biodiversity-informatics-training.org/wp-content/uploads/2014/03/D2_P6_CW_AEC2.pdf)) and made publicly accessible through the biodiversity portals Discover Life (<http://www.discoverlife.org>)

Figure 1. State of Maine, showing approximate boundaries of the 16 counties, and number of bee species known. County names are abbreviated as: AN = Androscoggin, AR = Aroostook, CU = Cumberland, FR = Franklin, HA = Hancock, KE = Kennebec, KN = Knox, LI = Lincoln, OX = Oxford, PE = Penobscot, PI = Piscataquis, SA = Sagadahoc, SO = Somerset, WD = Waldo, WN = Washington, YO = York.





and iDigbio (<https://www.idigbio.org/portal/recordsets/8919571f-205a-4aed-b9f2-96ccd0108e4c>). The citizen-science website Bugguide ([www.bugguide.net](http://www.bugguide.net)) was also consulted as a source for recent records for the subset of species identifiable from digital images. The checklist, while preliminary, provides insight into the state of knowledge of bee species for each of Maine's 16 counties (Fig. 1) and provides a baseline for future assessment of native bee community health and diversity in Maine. For example, a 5-year bumble bee survey initiated in 2015 (<http://mainebumblebeeatlas.umf.maine.edu/>) will likely expand upon the baseline for bumble bees reported here (Bickerman-Martens et al. 2017).

## Methods

### Checklist

We compiled records for Maine bees from collections we examined (University of Maine Entomological Museum, American Museum of Natural History, Cornell University, Museum of Comparative Zoology, Maine Forest Service Entomological Collection, Acadia National Park, The Peabody Museum of Natural History at Yale University, and several private collections), published bee research conducted in Maine (Boulanger et al. 1967; Bushmann and Drummond 2015; Dibble and Drummond 1997; Dibble et al. 1997; Miliczky 1978; Procter 1938, 1946; Stubbs et al. 1992, 2007), and additional graduate theses and widely disseminated reports (e.g., Dearborn et al. 1983, Droege 2012). We consulted historical literature for Maine records and ranges of bee taxa, including taxonomic revisions by Bouseman and LaBerge (1978), LaBerge (1956, 1961, 1967, 1971, 1973, 1977, 1980, 1985, 1987, 1989), LaBerge and Bouseman (1970), LaBerge and Ribble (1972, 1975), McGinley (1986), Michener (1947), and Ribble (1968). Species distribution information was also derived from recent taxonomic publications such as Gibbs (2010, 2011), Gibbs et al. (2013), Rightmyer et al. (2010), and Sheffield et al. (2011). Published and unpublished databases were consulted including iDigbio; records from specimens integrated by Discover Life from the United States Geological Survey through efforts of S. Droege and displayed using its global mapper tool; the Maine Forest Service Entomological Museum (see Dearborn et al. 1983) with updates (C. Donohue, Maine Forest Service, Augusta, ME, pers. comm.); and the Maine Bumble Bee Atlas (hosted by the Maine Department of Inland Fisheries and Wildlife with the University of Maine). State records for Maine were also obtained from critical review of Mitchell (1960, 1962), and from taxonomic revisions that also served as a basis for updating all scientific names to current usage, following Ascher and Pickering (2017) and a pending update of the World Bee Checklist in the Integrated Taxonomic Information System (<http://www.itis.gov>). New records based on specimens collected since 1992 by A.C. Dibble and from 2009 to 2015 by S. Bushmann, F.A. Drummond, B. DuClos, and M. Veit are also reflected in the checklist.

Many vouchers, especially in older collections, have labels with minimal data regarding localities and collecting events. By contrast, collections made for various research projects in Maine may have voucher specimens with detailed ecological

and collecting-effort information recorded. Most of these vouchers were obtained in one of the following ways: (1) as an individual bee captured directly on flowers, (2) using sweep nets on flowers of known plants in a repeatable manner, (3) using malaise traps set up at a known plant, (4) using small tent-like nets set up over bee burrows, or (5) using bowl traps with a liquid solution in which insects drown when they arrive to investigate a visual trap mimicking a highly attractive floral resource (Droege 2010). Catch rates for bee groups differ between capture methods (Bushman and Drummond 2015, Drummond and Stubbs 1997b), but important and complementary data were obtained in Maine by each of the sampling methods. For instance, bowl traps captured large numbers of sweat bees but were ineffective at reliably capturing bumble bees. Hand capture and netting were, by contrast, highly effective for some large and noticeable bees (Bushman 2013).

The compilation of the checklist by county (Table 2) includes only taxa where historical reports are consistent with species ranges as currently understood and are otherwise considered to be reliable (for some of these, county-level information was unavailable) or for which a specimen is known to us. Additional bee taxa that could be in Maine based on reports that we regard as yet unconfirmed but potentially valid are excluded from the checklist table but are discussed below.

Table 2. Checklist of the bees of Maine by county including selected sources. “Unknown county” means that a locality label or literature source does not include county or town but is from Maine. County abbreviations are explained in Figure 1. Superscripts following county records are representative sources, and are not comprehensive. Numbers refer to sources that are records in the literature or specimens in collections, lower case letters refer mostly to museum specimens (see Source Legend at end of checklist). \* = introduced species. [Table continued on the following 10 pages.]

Scientific name	Counties (selected sources)
<i>Andrena (Andrena) carolina</i> Viereck, 1909	AR <sup>n</sup> , CU <sup>13</sup> , HA <sup>1,8</sup> PE <sup>1,4,14,53</sup> , PI <sup>12</sup> , WN <sup>8,9,12,26,61,n</sup> , YO <sup>k</sup>
<i>Andrena (Andrena) clarkella</i> (Kirby, 1802)	HA <sup>1,25</sup> , PE <sup>1,10,12,19,n</sup> , WN <sup>1</sup> , YO <sup>±</sup>
<i>Andrena (Andrena) frigida</i> Smith, 1853	AN <sup>a</sup> , HA <sup>1,8,25</sup> , PE <sup>1,12,14,18,n</sup> , WD <sup>8</sup> , WN <sup>1,8,10,12,61</sup>
<i>Andrena (Andrena) mandibularis</i> Robertson, 1892	HA <sup>1,8,18</sup> , PE <sup>14</sup> , WN <sup>c</sup>
<i>Andrena (Andrena) milwaukeensis</i> Graenicher, 1903	HA <sup>25</sup> , KE <sup>12</sup> , PE <sup>1,12,n</sup> , PI, WN <sup>9</sup>
<i>Andrena (Andrena) rufosignata</i> Cockerell, 1902	AR <sup>n</sup> , HA <sup>8</sup> , KE <sup>12</sup> , LI <sup>m</sup> , PE <sup>1,14,n</sup> , SO <sup>2</sup> , WN <sup>8,10,12,26,54,61,c,n</sup> , YO <sup>k</sup>
<i>Andrena (Andrena) thaspii</i> Graenicher, 1903	AR <sup>a</sup> , FR <sup>a</sup> , HA <sup>8,25</sup> , PE <sup>1,18</sup> , WN <sup>9,24,n</sup> , YO <sup>61,c</sup>
<i>Andrena (Callandrena s.l.) asteris</i> Robertson, 1891	HA <sup>25,a,o</sup> , KN <sup>p</sup> , LI <sup>m</sup> , WN <sup>c</sup> , YO <sup>c</sup>
<i>Andrena (Callandrena s.l.) braccata</i> Viereck, 1907	YO <sup>29</sup> , PE <sup>1</sup>
<i>Andrena (Callandrena s.l.) placata</i> Mitchell, 1960	CU <sup>a,g</sup> , HA <sup>g</sup> , KN <sup>g</sup> , OX <sup>n</sup> , PE <sup>1,n</sup> , SO <sup>a</sup>
<i>Andrena (Cnemidandrena) canadensis</i> Dalla Torre, 1896	CU <sup>g</sup> , FR <sup>a</sup> , HA <sup>1,g</sup> , LI <sup>1</sup> , PE <sup>1</sup> , SO <sup>a,i</sup>
<i>Andrena (Cnemidandrena) hirticincta</i> Provancher, 1888	FR <sup>a</sup> , HA <sup>1,25,a,c,g</sup> , LI <sup>c</sup> , OX <sup>q</sup> , PE <sup>k,n</sup> , PI <sup>a</sup> , SO <sup>c</sup> , YO <sup>a,k</sup>
<i>Andrena (Cnemidandrena) nubecula</i> Smith, 1853	CU <sup>a,g</sup> , FR <sup>a</sup> , HA <sup>1,25,a,g</sup> , KE, KN <sup>c</sup> , LI <sup>m</sup> , PE <sup>1,n</sup> , SO <sup>c</sup> , WD <sup>2</sup>
<i>Andrena (Conandrena) bradleyi</i> Viereck, 1907	AR <sup>n</sup> , HA <sup>8</sup> , PE <sup>1,14</sup> , WD <sup>8</sup> , WN <sup>8,10,12,61</sup>
<i>Andrena (Euandrena) algida</i> Smith, 1853	HA <sup>1</sup> , PE <sup>1,14,n</sup> , WN <sup>8,12</sup>
<i>Andrena (Euandrena) nigrihirta</i> (Ashmead, 1890)	FR <sup>a</sup> , HA <sup>25</sup> , KN <sup>7</sup> , PE <sup>1,2,14,n</sup> , WN <sup>9,12</sup> , YO <sup>k</sup>

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Scientific name	Counties (selected sources)
<i>Andrena (Gonandrena) integra</i> Smith, 1853	HA <sup>8</sup> , PE <sup>1,12</sup>
<i>Andrena (Gonandrena) persimulata</i> Viereck, 1917	WD <sup>2</sup>
<i>Andrena (Holandrena) cressonii</i> Robertson, 1891	CU <sup>18</sup> , HA <sup>1,8</sup> , PE <sup>1,14,26,n</sup> , WD <sup>a</sup> , WN <sup>1,9,10</sup>
<i>Andrena (Larandrena) miserabilis</i> Cresson, 1872	HA <sup>1,25</sup> , PE <sup>1,2,12,14,n</sup> , WD <sup>8</sup> , WN <sup>10</sup> , YO <sup>2</sup>
<i>Andrena (Leucandrena) barbilabris</i> (Kirby, 1802)	HA <sup>25</sup> , PE <sup>12,n</sup>
<i>Andrena (Leucandrena) erythronii</i> Robertson, 1891	PE <sup>19</sup> , Unknown county <sup>29</sup>
<i>Andrena (Melandrena) carlini</i> Cockerell, 1901	CU <sup>12,13</sup> , HA <sup>1,8,25</sup> , KN <sup>12</sup> , PE <sup>1,4,10,12,14,19,k,n</sup> , WD <sup>a</sup> , WN <sup>4,10,12,45,61,n</sup> , YO <sup>o</sup>
<i>Andrena (Melandrena) commoda</i> Smith, 1879	HA <sup>1,25</sup>
<i>Andrena (Melandrena) dunningi</i> Cockerell, 1898	HA <sup>1</sup> , PE <sup>1,12,14,19,k,n</sup> , WN <sup>8,9,61</sup>
<i>Andrena (Melandrena) nivalis</i> Smith, 1853	AR <sup>n</sup> , HA <sup>8</sup> , KE <sup>c</sup> , OX <sup>a,k</sup> , PE <sup>1,2,14</sup> , PI <sup>k</sup> , WN <sup>1,2,9,10,61</sup> , YO <sup>12</sup>
<i>Andrena (Melandrena) pruni</i> Robertson, 1891	WN <sup>n</sup>
<i>Andrena (Melandrena) regularis</i> Malloch, 1917	HA <sup>8</sup> , KN <sup>12</sup> , PE <sup>1,12,14,16,n</sup> , WN <sup>4,9,10,12,61</sup>
<i>Andrena (Melandrena) vicina</i> Smith, 1853	CU <sup>j</sup> , HA <sup>1,8,20,25</sup> , KE <sup>12</sup> , KN <sup>12</sup> , LI <sup>56,a,p</sup> , OX <sup>k,p</sup> , PE <sup>1,8,14,19,n</sup> , WN <sup>1,8,9,10,12,61</sup> , YO <sup>12</sup>
<i>Andrena (Micrandrena) melanochoera</i> Cockerell, 1898	HA <sup>1</sup> , KN <sup>n</sup> , OX <sup>c</sup> , PE <sup>1,12,14,45,n</sup> , WD <sup>2</sup> , WN <sup>10,12,61</sup> , YO <sup>k</sup>
<i>Andrena (Micrandrena) salictaria</i> Robertson, 1905	HA <sup>1,25</sup> , LI <sup>45</sup> , PE <sup>45</sup> , WN <sup>12</sup>
<i>Andrena (Plastandrena) crataegi</i> Robertson, 1893	HA <sup>1,25,a,o</sup> , KN <sup>12</sup> , LI <sup>m</sup> , OX <sup>a</sup> , PE <sup>1,4,10,12,14,n</sup> , PI <sup>h</sup> , WN <sup>10,12,61,c,h</sup> , YO <sup>2,12,o</sup>
<i>Andrena (Rhacandrena) brevipalpis</i> Cockerell, 1930	HA <sup>8</sup> , PE <sup>2</sup>
<i>Andrena (Rhacandrena) robertsonii</i> Dalla Torre, 1896	KN <sup>m</sup> , LI <sup>m</sup> , PE <sup>12</sup> , WN <sup>12</sup>
<i>Andrena (Scrapteropsis) alleghaniensis</i> Viereck, 1907	HA <sup>1</sup> , PE <sup>14,n</sup> , WN <sup>8,10,12,61</sup> , YO <sup>2</sup>
<i>Andrena (Scrapteropsis) imitatrix</i> Cresson, 1872	HA <sup>1</sup> , KE <sup>12</sup> , PE <sup>12,n</sup> , WN <sup>8,10,61</sup>
<i>Andrena (Scrapteropsis) kalmiae</i> Atwood, 1934	AR <sup>n</sup> , CU <sup>13</sup> , HA <sup>8</sup> , WN <sup>8,c</sup> , YO <sup>2</sup>
<i>Andrena (Simandrena) nasonii</i> Robertson, 1895	HA <sup>1</sup> , KN <sup>12</sup> , PE <sup>1,12,14,n</sup> , WN <sup>8,9,10,12</sup>
<i>Andrena (Simandrena) wheeleri</i> Graenicher, 1904	AR <sup>n</sup> , HA <sup>1,25</sup> , KN <sup>12</sup> , PE <sup>1,12,13,14</sup> , PI <sup>h</sup> , WD <sup>12,a,d</sup> , WN <sup>9,10,12,61</sup> , YO <sup>12,o</sup>
* <i>Andrena (Taeniandrena) wilkella</i> (Kirby, 1802)	AR <sup>n</sup> , CU <sup>g</sup> , FR <sup>a</sup> , HA <sup>1,25,a,o</sup> , LI <sup>m</sup> , OX <sup>a</sup> , PE <sup>1,12,18,n</sup> , PI <sup>h,k</sup> , SA <sup>i</sup> , SO <sup>c</sup> , WD <sup>8</sup> , WN <sup>1,5,8,12,61</sup> , YO <sup>a,c</sup>
<i>Andrena (Thysandrena) bisalicensis</i> Viereck, 1908	CU <sup>12</sup> , HA <sup>8</sup> , PE <sup>1,12</sup> , YO <sup>13</sup>
<i>Andrena (Thysandrena) w-scripta</i> Viereck, 1904	HA <sup>25,a</sup> as <i>A. lata</i> , KE <sup>12</sup> , PE <sup>1,12,14</sup> , PI <sup>h</sup> , WN <sup>9</sup> as <i>A. lata</i> , 10,12
<i>Andrena (Trachandrena) ceanothi</i> Viereck, 1917	HA <sup>1</sup> , PE <sup>1,12</sup> , WN <sup>8</sup> , YO <sup>12</sup>
<i>Andrena (Trachandrena) forbesii</i> Robertson, 1891	HA <sup>8</sup> , PE <sup>1,12,14,k,n</sup> , PI, WD <sup>a</sup> , WN <sup>12</sup>
<i>Andrena (Trachandrena) hippotes</i> Robertson, 1895	PE <sup>1,12,16,19,n</sup> , PI <sup>h</sup> , WD <sup>a</sup>
<i>Andrena (Trachandrena) miranda</i> Smith, 1879	AR <sup>n</sup> , FR <sup>a,n</sup> , HA <sup>1,25</sup> , LI <sup>n</sup> , PE <sup>1,2,14,n</sup> , PI <sup>h</sup> , WN <sup>9,12,61</sup> , YO <sup>c</sup>
<i>Andrena (Trachandrena) nuda</i> Robertson, 1891	PE <sup>66</sup> , YO <sup>66</sup>
<i>Andrena (Trachandrena) rugosa</i> Robertson, 1891	HA <sup>1,8</sup> , LI <sup>m</sup> , PE <sup>1,2</sup> , WN <sup>8,10</sup> , YO <sup>k</sup>
<i>Andrena (Trachandrena) sigmundi</i> Cockerell, 1902	HA <sup>1,20,25</sup> , KN <sup>12,n</sup> , LI <sup>a</sup> , PE <sup>1,12,14,n</sup> , WN <sup>1,4,10,12,61,n</sup> , YO <sup>12</sup>
<i>Andrena (Trachandrena) spiraeana</i> Robertson, 1895	PE <sup>12,46</sup>
<i>Andrena (Trachandrena) virginiana</i> Mitchell, 1960	CU <sup>c,g</sup> , HA <sup>1,8,g</sup> , OX <sup>n</sup> , PE <sup>1</sup> , WD
<i>Andrena (Tylandrena) erythrogaster</i> (Ashmead, 1890)	CU <sup>k</sup> , PE <sup>f,n</sup>
<i>Andrena (Tylandrena) perplexa</i> Smith, 1853	PE <sup>10</sup>
<i>Calliopsis (Calliopsis) andreniformis</i> Smith, 1853	HA <sup>8,25</sup> , KE <sup>56,k</sup> , YO <sup>2</sup>
<i>Perdita (Perdita) octomaculata</i> (Say, 1824)	CU <sup>c,g</sup> , HA <sup>2,g</sup> , KN <sup>g</sup> , LI <sup>56,a,p</sup> , WN <sup>5</sup>
<i>Pseudopanurgus aestivalis</i> (Provancher, 1882) (= <i>P. nebraskensis</i> )	WN <sup>1</sup> , Unknown county <sup>43</sup>

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<i>Pseudopanurgus andrenoides</i> (Smith, 1853)	FR <sup>57,a</sup> , HA <sup>1,2,c</sup> , KN <sup>c</sup> , LI <sup>56</sup> , PE <sup>1</sup> , SO <sup>a</sup>
<i>Anthophora (Clisodon) terminalis</i> Cresson, 1869	HA <sup>25</sup> , OX <sup>q</sup> , PE <sup>1</sup> , SO <sup>2</sup> , YO <sup>k</sup>
<i>Anthophora (Melea) bomboides</i> Kirby, 1837	Unknown county <sup>28</sup>
* <i>Apis (Apis) mellifera</i> L., 1758	AR <sup>4</sup> , AN <sup>4</sup> , CU <sup>13</sup> , HA <sup>1,4,25,63</sup> , KE <sup>4</sup> , KN <sup>4,70</sup> , LI <sup>4,70</sup> , OX <sup>4,n</sup> , PE <sup>1,4,12,69,63,70,k</sup> , WD <sup>4,8,63,70,q</sup> , WN <sup>1,4,5,9,10,61,63,70</sup>
<i>Bombus (Bombus) affinis</i> Cresson, 1863	CU <sup>j,i</sup> , FR <sup>27</sup> , HA <sup>25</sup> , KE <sup>k</sup> , LI <sup>h,m</sup> , PE <sup>12,n,p</sup> , PI <sup>a</sup> , WD <sup>4,12</sup> , WN <sup>12</sup> , YO <sup>a</sup>
<i>Bombus (Bombus) terricola</i> Kirby, 1837	AR <sup>1,4,8,p</sup> , CU <sup>4,a,g,o</sup> , FR <sup>1,4,27,57,63,a,o</sup> , HA <sup>1,4,18,25,63,70,a,f,g,q</sup> , KE <sup>4,k</sup> , KN <sup>4,70,a,g</sup> , LI <sup>o</sup> , OX <sup>a</sup> , PE <sup>1,4,12,13,14,18,63,69,70,k</sup> , PI <sup>a,h,k</sup> , SA <sup>4</sup> , SO <sup>4,i</sup> , WD <sup>4,63,70,p,q</sup> , WN <sup>1,4,5,9,12,61,63,70</sup> , YO <sup>4,73,a,k,r</sup>
<i>Bombus (Cullumanobombus) griseocollis</i> (DeGeer, 1773)	HA <sup>1,63</sup> , PE <sup>1,63</sup> , PI <sup>a</sup> , WN <sup>b</sup>
<i>Bombus (Cullumanobombus) rufocinctus</i> Cresson, 1863	AR <sup>j,n</sup> , HA <sup>1</sup> , PE <sup>1,63,b</sup> , WN <sup>5</sup>
<i>Bombus (Thoracobombus) fervidus</i> (Fabricius, 1798)	HA <sup>1,25,m</sup> , KE <sup>k,n</sup> , LI <sup>p</sup> , PE <sup>1,12</sup> , OX <sup>q</sup> , PI <sup>a</sup> , SO <sup>2</sup> , WN <sup>4,61</sup> , YO <sup>a,r</sup>
<i>Bombus (Thoracobombus) pensylvanicus</i> (DeGeer, 1773)	YO <sup>29,32,66</sup>
<i>Bombus (Psithyrus) ashtoni</i> (Cresson, 1864)	CU <sup>a,n</sup> , FR <sup>57,a</sup> , HA <sup>1,25,k,o,q</sup> , KE <sup>k,n</sup> , LI <sup>o</sup> , OX <sup>a</sup> , PE <sup>1,2,n</sup> , YO <sup>a,r</sup>
<i>Bombus (Psithyrus) citrinus</i> (Smith, 1854)	AR <sup>8</sup> , CU <sup>r</sup> , HA <sup>25,63,k,p</sup> , KE <sup>k</sup> , KN <sup>a</sup> , LI <sup>p</sup> , OX <sup>k</sup> , PE <sup>p</sup> , WD <sup>p</sup> , WN <sup>c</sup> , YO <sup>73</sup>
<i>Bombus (Psithyrus) fernaldae</i> (Franklin, 1911)	FR <sup>57,a</sup> , HA <sup>2,25,p</sup> , PE <sup>1</sup> , PI <sup>12</sup> , WD <sup>63</sup> , WN <sup>1,4,5,63</sup>
<i>Bombus (Psithyrus) insularis</i> (Smith 1861)	FR <sup>a</sup> , HA <sup>n</sup> , PE <sup>1</sup>
<i>Bombus (Pyrobombus) bimaculatus</i> Cresson, 1863	AR <sup>8</sup> , HA <sup>1,25,63</sup> , KE <sup>2</sup> , KN <sup>63</sup> , LI <sup>6j</sup> , PE <sup>1,2,63,b</sup> , WD <sup>5,63</sup> , WN <sup>1,4,61,63</sup> , YO <sup>2</sup>
<i>Bombus (Pyrobombus) impatiens</i> Cresson, 1863	AR <sup>8</sup> , CU <sup>1,13</sup> , FR <sup>4,8</sup> , HA <sup>1,4,8,63,m</sup> , KE <sup>4,k,n</sup> , KN <sup>4,63,g</sup> , LI <sup>4</sup> , OX <sup>n</sup> , PE <sup>1,2,4,12,63,b</sup> , PI <sup>a,m</sup> , SA <sup>i</sup> , WD <sup>4,63</sup> , WN <sup>1,4,61,63</sup> , YO <sup>1,73,a</sup>
<i>Bombus (Pyrobombus) perplexus</i> Cresson, 1863	AR <sup>2,8</sup> , HA <sup>1,2,25,63,a,j,q</sup> , KE <sup>k</sup> , LI <sup>m</sup> , KN <sup>63,a</sup> , PE <sup>1,2,12,14,63,m</sup> , PI <sup>h,k</sup> , WD <sup>63,q</sup> , WN <sup>1,5,12,63,b</sup> , YO <sup>r</sup>
<i>Bombus (Pyrobombus) sandersoni</i> Franklin, 1913	AN <sup>b</sup> , AR, FR <sup>a</sup> , HA <sup>63,a</sup> , KE <sup>b</sup> , KN <sup>a</sup> , PE <sup>1,63</sup> , PI <sup>k,m</sup> , WN <sup>1,4,5,63,b</sup> , YO <sup>q</sup>
<i>Bombus (Pyrobombus) ternarius</i> Say, 1837	AR <sup>1,2,8</sup> , CU <sup>a,g,r</sup> , FR <sup>4,57,a,o</sup> , HA <sup>1,4,25,63,a,g,k,m,n,p,q</sup> , KE <sup>4,m,n</sup> , KN <sup>4,63a</sup> , LI <sup>j,o,p,q</sup> , OX <sup>n</sup> , PE <sup>1,4,12,18,63,k</sup> , PI <sup>a,h,k</sup> , SA <sup>4</sup> , SO <sup>aj</sup> , WD <sup>4,63,k,p,q</sup> , WN <sup>1,4,5,9,61,63,a,b</sup> , YO <sup>a,r</sup>
<i>Bombus (Pyrobombus) vagans vagans</i> Smith, 1854	AR <sup>1,4</sup> , CU <sup>13,g,p,r</sup> , FR <sup>4,57,a</sup> , HA <sup>1,19,25,63,a,k,q</sup> , KN <sup>63,a</sup> , LI <sup>m</sup> , PE <sup>1,2,10,63,m,n</sup> , PI <sup>a,h</sup> , SO <sup>2</sup> , WD <sup>63,k,q</sup> , WN <sup>1,4,5,9,10,61,63</sup> , YO <sup>a</sup>
<i>Bombus (Subterraneobombus) borealis</i> Kirby, 1837	AR <sup>1,2,4,8</sup> , FR <sup>4,57,a</sup> , HA <sup>1,2,25</sup> , KN <sup>63,e</sup> , LI <sup>p</sup> , OX <sup>q</sup> , PE <sup>1,63,b</sup> , WD <sup>5,8,63,q</sup> , WN <sup>1,4</sup>
<i>Habropoda laboriosa</i> (Fabricius, 1804)	LI <sup>m</sup>
<i>Melissodes (Apomelissodes) apicatus</i> Lovell & Cockerell, 1906	LI <sup>48,m,p</sup> , WD <sup>48</sup>
<i>Melissodes (Eumelissodes) agilis</i> Cresson, 1878	LI <sup>47,a</sup>
<i>Melissodes (Heliomelissodes) desponsus</i> Smith, 1854	LI <sup>a</sup> , PE <sup>1</sup>
<i>Melissodes (Eumelissodes) druriellus</i> (Kirby, 1802)	AN <sup>47,o</sup> , AR <sup>47</sup> , CU <sup>47,c</sup> , HA <sup>1,25,a</sup> , LI <sup>47</sup> , PE <sup>1,47</sup>
<i>Melissodes (Eumelissodes) illatus</i> Lovell & Cockerell, 1906	FR <sup>a,o</sup> , HA <sup>1,2,8,25,47,a</sup> , KE <sup>47</sup> , KN <sup>a</sup> , LI <sup>47</sup> , PE <sup>1,n</sup> , SO <sup>a</sup> , WN <sup>1,4,5,7,12,b,c</sup> , YO <sup>47,o</sup>

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<i>Melissodes (Eumelissodes) subillatus</i> LaBerge, 1961	CU <sup>47</sup> , HA <sup>47</sup> , LI <sup>47,m</sup>
<i>Melissodes (Eumelissodes) trinodis</i> Robertson, 1901	LI <sup>62,a</sup>
<i>Melissodes (Melissodes) b. bimaculatus</i> (Lepeletier, 1825)	Unknown county <sup>66</sup>
<i>Peponapis (Peponapis) pruinosa</i> (Say, 1837)	CU <sup>1</sup> , HA <sup>1</sup> , PE <sup>4</sup>
<i>Holcopasites calliopsidis</i> (Linsley, 1943)	WA <sup>1</sup>
<i>Holcopasites illinoiensis</i> (Robertson, 1891)	PE <sup>41</sup>
<i>Epeolus americanus</i> Cresson, 1878 [= <i>lanhami</i> Mitchell, 1962]	WN <sup>40,c</sup>
<i>Epeolus autumnalis</i> Robertson, 1902	HA <sup>1</sup>
<i>Epeolus pusillus</i> Cresson, 1864	Unknown county <sup>66</sup>
<i>Epeolus scutellaris</i> Say, 1824	CU <sup>6,a</sup> , HA <sup>1,25,a,g</sup> , KN <sup>a,g</sup> , WN <sup>1</sup>
<i>Epeoloides pilosulus</i> (Cresson, 1878)	LI <sup>m</sup> YO <sup>2</sup>
<i>Triepeolus donatus</i> (Smith, 1854)	HA <sup>25</sup> , LI <sup>56,a,m</sup>
<i>Triepeolus pectoralis</i> (Robertson, 1897)	CU <sup>g</sup> , HA <sup>c</sup> , KN <sup>a</sup>
<i>Nomada armatella</i> Cockerell, 1903	WN <sup>66</sup>
<i>Nomada articulata</i> Smith, 1854	CU <sup>n</sup> , HA <sup>8</sup> , LI <sup>m</sup> , PE <sup>14</sup> , PI <sup>k</sup>
<i>Nomada bella</i> Cresson, 1863	PE <sup>14,16</sup> , WD <sup>2</sup>
<i>Nomada bethunei</i> Cockerell, 1903	HA <sup>8</sup> , WN <sup>8</sup>
<i>Nomada composita</i> Mitchell, 1962	HA <sup>a</sup> , PE <sup>14</sup> , WN <sup>10,45</sup>
<i>Nomada cressonii</i> Robertson, 1893	AN <sup>m</sup> , HA <sup>1,25</sup> , PE <sup>1,14,16</sup> , WD <sup>2</sup> , WN <sup>9,10,45</sup> , YO <sup>2</sup>
<i>Nomada cuneata</i> (Robertson, 1903)	HA <sup>25</sup>
<i>Nomada denticulata</i> Robertson, 1902	PE <sup>18</sup> , YO <sup>2</sup>
<i>Nomada depressa</i> Cresson, 1863	OX <sup>q</sup> , PE <sup>14</sup> , WN <sup>8,9</sup>
<i>Nomada dreisbachi</i> Mitchell, 1962	Unknown county <sup>29</sup>
<i>Nomada florilega</i> Lovell and Cockerell, 1905	AN <sup>m</sup> , LI <sup>29,Lovell and Cockerell, 1905,p</sup>
<i>Nomada gracilis</i> Cresson, 1863	HA <sup>as N. inepta</sup> , PE <sup>1</sup> , WN <sup>8,10</sup>
<i>Nomada illinoensis</i> Robertson, 1900	Unknown county <sup>58</sup>
<i>Nomada imbricata</i> Smith, 1854	HA <sup>8</sup> , PE <sup>1,14</sup> , WN <sup>8,10</sup>
<i>Nomada lepida</i> Cresson, 1863	PE <sup>14</sup> , WD <sup>2</sup>
<i>Nomada louisianae</i> Cockerell, 1903	Unknown county <sup>71</sup>
<i>Nomada luteoloides</i> Robertson, 1895	HA <sup>1</sup> , PE <sup>14</sup> , WD <sup>8</sup> , WN <sup>1,10,45</sup>
<i>Nomada maculata</i> Cresson, 1863	HA <sup>8</sup> , PE <sup>14</sup> , WN <sup>8</sup> , YO <sup>2</sup>
<i>Nomada ovata</i> (Robertson, 1903)	PE <sup>14,17,29</sup>
<i>Nomada perplexa</i> Cresson, 1863	HA <sup>25</sup> , LI <sup>m</sup> , PE <sup>14</sup>
<i>Nomada proxima</i> Cresson, 1863	Unknown county <sup>28,Cresson 1863</sup>
<i>Nomada pygmaea</i> Cresson, 1863	HA <sup>5</sup> , PE <sup>1,2,14</sup> , WN <sup>9,10</sup>
<i>Nomada sayi</i> Robertson, 1893	HA <sup>1</sup> , PE <sup>14</sup> , WN <sup>9,10</sup>
<i>Nomada subrutula</i> Lovell & Cockerell, 1905	LI <sup>Lovell and Cockerell, 1905,p</sup>
<i>Nomada valida</i> Smith, 1854	HA <sup>8</sup> , WN <sup>10</sup>
<i>Nomada vicina</i> Cresson, 1863	HA <sup>g</sup>
<i>Nomada vincta</i> Say, 1837	PE <sup>n</sup>
<i>Nomada xanthura</i> Cockerell, 1908	Unknown county <sup>29</sup>
<i>Ceratina (Zadontomerus) calcarata</i> Robertson, 1900	HA <sup>1,2,25,o</sup> , LI <sup>m</sup> , PE <sup>1,2,12,14</sup> , SA <sup>i</sup> , WD <sup>2</sup> , WN <sup>1,8,61</sup> , YO <sup>2</sup>
<i>Ceratina (Zadontomerus) dupla</i> Say, 1837	HA <sup>1,25,o</sup> , KN <sup>12</sup> , LI <sup>m</sup> , PE <sup>1,10,12,14,n</sup> , SA <sup>i</sup> , WN <sup>9</sup>
<i>Ceratina (Zadontomerus) mikmaqi</i> Rehan & Sheffield, 2011	HA <sup>1,8</sup> , SO <sup>a</sup> , WD <sup>a</sup> , WN <sup>8</sup>
<i>Xylocopa (Xylocopoides) virginica</i> (L., 1771)	HA <sup>1</sup>
<i>Colletes americanus</i> Cresson, 1868	WN <sup>1</sup>
<i>Colletes compactus</i> Cresson, 1868	HA <sup>1</sup> , PE <sup>18</sup> , YO <sup>a</sup>
<i>Colletes consors</i> Cresson, 1868 [ssp. <i>mescocopus</i> Swenk]	HA <sup>8,25,a</sup> , LI <sup>a</sup> , WN <sup>12,17</sup>

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<i>Colletes hyalinus</i> Provancher, 1888	FR <sup>a</sup>
<i>Colletes impunctatus</i> Nylander, 1852 [ssp. <i>lacustris</i> Swenk]	PI <sup>29,39</sup>
<i>Colletes inaequalis</i> Say, 1837	HA <sup>1,8</sup> , KE <sup>k</sup> , PE <sup>1,12,16,18,19</sup> , WN <sup>8,10,12,61,n</sup>
<i>Colletes kincaidii</i> Cockerell, 1898	SO <sup>i</sup> , WN <sup>1</sup>
<i>Colletes latitarsis</i> Robertson, 1891	Unknown county <sup>72</sup>
<i>Colletes simulans</i> Cresson, 1868	HA <sup>2,25</sup> , KN <sup>c</sup> , LI <sup>1,a</sup> , PE <sup>1,n</sup> , SO <sup>a</sup> , WN <sup>1,5,12</sup>
<i>Colletes validus</i> Cresson, 1868	YO <sup>12</sup> , Unknown county <sup>29</sup>
<i>Hylaeus (Hylaeus) annulatus</i> (L., 1758)	AR <sup>4</sup> , FR <sup>a,s</sup> , HA <sup>2,4,25,s</sup> , KN <sup>a</sup> , PE <sup>1,4,12</sup> , PI <sup>4</sup> , WD <sup>4</sup> , WN <sup>1,4,5,9</sup>
<i>Hylaeus (Cephalylaeus) basalis</i> (Smith, 1853)	FR <sup>a</sup> , LI <sup>38</sup> , WN <sup>9</sup>
<i>Hylaeus (Hylaeus) mesillae</i> (Cockerell, 1896) [ssp. <i>cressoni</i> (Cockerell, 1907)]	CU <sup>a</sup> , HA <sup>1,25,a</sup> , LI <sup>38,m</sup> , PE <sup>1</sup> , SO <sup>a</sup> , WN <sup>1,8</sup> , YO <sup>2</sup>
<i>Hylaeus (Hylaeus) saniculae</i> (Robertson, 1896)	LI <sup>a</sup>
<i>Hylaeus (Hylaeus) verticalis</i> (Cresson, 1869)	HA <sup>8</sup> , LI <sup>m</sup> , PE <sup>1</sup> , PI, WN <sup>9</sup>
<i>Hylaeus (Metziella) sparsus</i> (Cresson, 1869)	HA <sup>25</sup>
<i>Hylaeus (Paraprosopis) floridanus</i> (Robertson, 1893)	Unknown county <sup>33</sup>
<i>Hylaeus (Prosopis) affinis</i> (Smith, 1853)	CU <sup>a</sup> , FR <sup>a</sup> , HA <sup>1,2,8,25,a</sup> , KN, LI <sup>a</sup> , PE <sup>1,2,12,o</sup> , WN <sup>8</sup>
<i>Hylaeus (Prosopis) illinoisensis</i> (Robertson, 1896)	Unknown county <sup>29</sup>
<i>Hylaeus (Prosopis) modestus modestus</i> Say, 1837	FR <sup>57</sup> , HA <sup>1,25</sup> , PE <sup>1,2,12,14</sup> , PI, WN <sup>1,9</sup>
<i>Dufourea novaeangliae</i> (Robertson, 1897)	HA <sup>25</sup> , LI, WN <sup>42</sup>
<i>Augochlora (Augochlora) pura</i> (Say, 1837)	FR <sup>c</sup> , HA <sup>1,8,25</sup> , KN <sup>m</sup> , PE <sup>1</sup> , WD <sup>k</sup> , WN <sup>9,61</sup>
<i>Augochlorella aurata</i> (Smith, 1853)	CU <sup>a</sup> , HA <sup>1,25,a</sup> , KE <sup>n</sup> , LI <sup>a,m</sup> , OX <sup>q</sup> , PE <sup>1,12,14,n</sup> , SO <sup>a</sup> , WD <sup>8,12,a</sup> , WN <sup>1,4,5,9,10,12,61</sup> , YO <sup>2,f,k</sup>
<i>Augochloropsis (Paraugochloropsis) metallica</i> (Fabricius, 1793)	WD <sup>8</sup>
<i>Agapostemon (Agapostemon) sericeus</i> (Förster, 1771)	OX <sup>q</sup>
<i>Agapostemon (Agapostemon) splendens</i> (Lepelletier de Saint Fargeau, 1841)	PE <sup>n</sup> , SA <sup>i</sup>
<i>Agapostemon (Agapostemon) texanus</i> Cresson, 1872	HA <sup>1,8</sup> , OX <sup>q</sup> , PE <sup>12</sup> , WN <sup>58</sup> , YO <sup>12</sup>
<i>Agapostemon (Agapostemon) virescens</i> (Fabricius, 1775)	HA <sup>1,8,25</sup> , LI <sup>m</sup> , PE <sup>1,12,19</sup> , WN <sup>8</sup> , YO <sup>c</sup>
<i>Halictus (Odontalictus) ligatus</i> Say, 1837	HA <sup>1,8</sup> , LI <sup>m</sup> , PE <sup>1,12,14,16,n</sup> , WD <sup>8</sup> , WN <sup>1,5,8,12</sup> , YO <sup>2</sup>
<i>Halictus (Seladonia) confusus confusus</i> Smith, 1853	AR <sup>i</sup> , FR <sup>a,s</sup> , HA <sup>1,8,25,a,s</sup> , KE <sup>12</sup> , KN <sup>a</sup> , PE <sup>1,14,s,n</sup> , WD <sup>2,a</sup> , WN <sup>1,8,9</sup> , YO <sup>2</sup>
<i>Halictus (Protohalictus) rubicundus</i> (Christ, 1791)	CU <sup>ja,±</sup> , FR <sup>a,s</sup> , HA <sup>1,2,8,25,a,s</sup> , LI <sup>a,m</sup> , PE <sup>1,12,14,19,s</sup> , WD <sup>2,a</sup> , WN <sup>1,5,8,10,12,61</sup>
<i>Lasioglossum (Dialictus) admirandum</i> (Sandhouse, 1924)	HA <sup>1,8</sup>
<i>Lasioglossum (Dialictus) albipenne</i> (Robertson, 1890)	HA <sup>1,8,a</sup> , KE <sup>8</sup> , WN <sup>1,8</sup> , YO <sup>12</sup>
<i>Lasioglossum (Dialictus) anomalum</i> (Robertson, 1892)	HA <sup>8</sup> , WD <sup>8</sup> , WN <sup>8</sup>
<i>Lasioglossum (Dialictus) atwoodi</i> Gibbs, 2010	PE <sup>1,14</sup>
<i>Lasioglossum (Dialictus) coeruleum</i> (Robertson, 1893)	WN <sup>61</sup>
<i>Lasioglossum (Dialictus) cressonii</i> (Robertson, 1890)	FR <sup>o</sup> , HA <sup>1,8,25</sup> , LI <sup>a,m</sup> , PE <sup>1,12,14,n</sup> , PI <sup>a</sup> , WN <sup>1,5,8,9,10,12</sup> , YO <sup>12,k</sup>
<i>Lasioglossum (Dialictus) ellisiae</i> (Sandhouse, 1924)	HA <sup>1</sup> , PE <sup>1</sup> , WN <sup>5</sup>
<i>Lasioglossum (Dialictus) ephialtum</i> Gibbs, 2010	HA <sup>8</sup> , SO <sup>a</sup> , WN <sup>8</sup>
<i>Lasioglossum (Dialictus) heterognathum</i> (Mitchell, 1960)	HA <sup>8</sup> , PE <sup>12,14</sup> , SO <sup>a</sup> , WD <sup>8</sup> , WN <sup>1,8</sup>
<i>Lasioglossum (Dialictus) hitchensi</i> Gibbs, 2012	HA <sup>1,8</sup> , PE <sup>1,n</sup> (as <i>L. atlanticum</i> ), WN <sup>1</sup>
<i>Lasioglossum (Dialictus) imitatum</i> (Smith, 1853)	HA <sup>1</sup> , LI <sup>a</sup> , SO <sup>a</sup> , PE <sup>1,n</sup> , WD <sup>8</sup> , WN <sup>1,8,10</sup>
<i>Lasioglossum (Dialictus) katherineae</i> (Gibbs, 2011)	HA <sup>8</sup> , WN <sup>66</sup> , YO <sup>66</sup>
<i>Lasioglossum (Dialictus) laevissimum</i> (Smith, 1853)	FR <sup>a</sup> , HA <sup>1,2,8,25</sup> , KE <sup>12</sup> , PE <sup>1,12</sup> , WN <sup>9</sup>
<i>Lasioglossum (Dialictus) leucocomum</i> (Lovell, 1908)	HA <sup>1,8</sup> , LI <sup>a</sup> , PE <sup>1,15</sup> , WD <sup>8</sup> , WN <sup>8,45</sup> , YO <sup>12</sup>

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Scientific name	Counties (selected sources)
<i>Lasioglossum (Dialictus) lineatulum</i> (Crawford, 1906)	PE <sup>n</sup> , WD, WN <sup>8</sup> , YO <sup>4</sup>
<i>Lasioglossum (Dialictus) nigroviride</i> (Graenicher, 1911)	FR <sup>a</sup> , HA <sup>1,8</sup> , KN <sup>a</sup> , LI <sup>m</sup> , PE <sup>1,12,n</sup>
<i>Lasioglossum (Dialictus) novascotiae</i> (Mitchell, 1960)	KN <sup>a</sup>
<i>Lasioglossum (Dialictus) oblongum</i> (Lovell, 1905)	HA <sup>1,25,o</sup> , LI <sup>m,o</sup> , PE <sup>1,14</sup> , WN <sup>1</sup>
<i>Lasioglossum (Dialictus) oceanicum</i> (Cockerell, 1916)	HA <sup>25</sup> , WN <sup>8</sup>
<i>Lasioglossum (Dialictus) obscurum</i> (Robertson, 1892)	LI <sup>m</sup> , PE <sup>m</sup>
<i>Lasioglossum (Dialictus) paradmirationum</i> (Knerer & Atwood, 1966)	HA <sup>8</sup> , WN <sup>8</sup>
<i>Lasioglossum (Dialictus) perpunctatum</i> (Ellis, 1913)	HA <sup>1,8</sup> , PE <sup>1</sup> , WN <sup>1,8</sup> , YO <sup>12</sup>
<i>Lasioglossum (Dialictus) pilosum</i> (Smith, 1853)	HA <sup>1,2</sup> , YO <sup>12</sup>
<i>Lasioglossum (Dialictus) planatum</i> (Lovell, 1905)	FR <sup>a</sup> , HA <sup>1,2,8</sup> , LI <sup>a</sup> , PE <sup>1</sup> , WD <sup>8</sup> , YO <sup>2</sup>
<i>Lasioglossum (Dialictus) smilacinae</i> (Roberson, 1899)	HA <sup>1,8</sup> , SO <sup>c</sup> , PE <sup>12,19</sup> , WD <sup>8</sup> , WN <sup>8</sup> , YO <sup>12</sup>
<i>Lasioglossum (Dialictus) subversans</i> (Mitchell, 1960)	FR <sup>a</sup> , HA <sup>2,8</sup> , WD <sup>8</sup>
<i>Lasioglossum (Dialictus) subviridatum</i> (Cockerell, 1938)	HA <sup>8</sup> , WN <sup>8</sup>
<i>Lasioglossum (Dialictus) taylorae</i> (Gibbs, 2010)	HA <sup>8</sup> , PE <sup>1</sup>
<i>Lasioglossum (Dialictus) tenax</i> (Sandhouse, 1924)	FR <sup>a</sup> , HA <sup>2</sup> , WN <sup>9</sup>
<i>Lasioglossum (Dialictus) timothyi</i> (Gibbs, 2010)	HA <sup>8</sup> , WN <sup>8,10</sup> , YO <sup>24</sup>
<i>Lasioglossum (Dialictus) versans</i> (Lovell, 1905)	HA <sup>1,2,8,a</sup> , LI <sup>a</sup> , PE <sup>1,n</sup> , WD <sup>a</sup> , WN <sup>8,9</sup>
<i>Lasioglossum (Dialictus) versatum</i> (Robertson, 1902)	HA <sup>1,2,8,25</sup> , PE <sup>1,n</sup> , SO <sup>a</sup> , WN <sup>8</sup>
<i>Lasioglossum (Dialictus) viridatum</i> (Lovell, 1905)	FR <sup>a</sup> , HA <sup>1,25,a</sup> , KE, LI <sup>m</sup> , PE <sup>1,m</sup> , WD <sup>8</sup> , WN <sup>1,9</sup>
<i>Lasioglossum (Dialictus) weemsi</i> (Mitchell, 1960)	HA <sup>8</sup> , WD <sup>8</sup> , WN <sup>8</sup>
<i>Lasioglossum (Dialictus) zephyrum</i> (Smith, 1853)	HA <sup>25</sup>
<i>Lasioglossum (Evylaeus) cinctipes</i> (Provancher, 1888)	HA <sup>8,25,c</sup> , KE <sup>2,c</sup> , LI <sup>a,m</sup> , PE <sup>1,n</sup> , WD <sup>2</sup> , WN <sup>1,8,a</sup> , YO <sup>2</sup>
<i>Lasioglossum (Hemihalictus) birkmanni</i> (Crawford, 1906) (former <i>L. macoupinense</i> sensu auct.)	HA <sup>8,25</sup> , WN <sup>1</sup>
<i>Lasioglossum (Hemihalictus) foxii</i> (Robertson, 1895)	HA <sup>1,25,a,n</sup> , PE <sup>1,n</sup> , WN <sup>1,9</sup>
<i>Lasioglossum (Hemihalictus) inconditum</i> (Cockerell, 1916)	FR <sup>a</sup> , HA <sup>a,1</sup> , PE <sup>1</sup> , WD <sup>8</sup> , WN <sup>1,9</sup>
<i>Lasioglossum (Hemihalictus) macoupinense</i> (Robertson, 1895) [non auct.; = <i>divergens</i> (Lovell, 1905)]	HA <sup>8,25</sup> , PE <sup>14</sup> , WN <sup>9</sup>
<i>Lasioglossum (Hemihalictus) nelumbonis</i> (Robertson, 1890)	HA <sup>8</sup>
<i>Lasioglossum (Hemihalictus) pectorale</i> (Smith, 1853)	HA <sup>1,8</sup> , PE <sup>1,14</sup> , WN <sup>1</sup> , YO
<i>Lasioglossum (Lasioglossum) acuminatum</i> McGinley, 1986	HA <sup>1,8</sup> , LI <sup>a,m</sup> , PE <sup>1</sup> , WN <sup>1,8,61</sup> , YO <sup>10</sup>
<i>Lasioglossum (Lasioglossum) athabascense</i> (Sandhouse, 1933)	HA <sup>8,25</sup> , PE <sup>1</sup> , WN <sup>8,9</sup>
<i>Lasioglossum (Lasioglossum) coriaceum</i> (Smith, 1853)	FR <sup>o</sup> , HA <sup>1,2,8,25</sup> , LI <sup>m</sup> , PE <sup>1,n</sup> , WD <sup>2,8</sup> , WN <sup>1,8,61</sup>
* <i>Lasioglossum (Lasioglossum) zonulum</i> (Smith, 1848)	FR <sup>a</sup> , HA <sup>a</sup> , KN <sup>a</sup> , LI <sup>a,c</sup> , PE <sup>15,n</sup> , WN <sup>8</sup>
* <i>Lasioglossum (Leuchalictus) leucozonium</i> (Schrank, 1781)	FR <sup>s</sup> , HA <sup>1,2,8,25,a,s</sup> , SO <sup>a</sup> , WD <sup>8</sup> , WN <sup>8</sup>
<i>Lasioglossum (Sphecodogastra) comagenense</i> (Knerer & Atwood, 1964)	SO <sup>2</sup> , WN <sup>1,2</sup> (Veit det., with "?")
<i>Lasioglossum (Sphecodogastra) quebecense</i> (Crawford, 1907)	HA <sup>1,8</sup> , KE <sup>c</sup> , PE <sup>14</sup> , PI <sup>c</sup> , WD <sup>8</sup> , WN <sup>26,45,c</sup> , YO <sup>a,o</sup>
<i>Lasioglossum (Sphecodogastra) truncatum</i> (Robertson, 1901)	HA <sup>1,2,25</sup> , WD <sup>8,a</sup>
<i>Sphecodes atlantis</i> Mitchell, 1956	FR <sup>a</sup>
<i>Sphecodes clematidis</i> Robertson, 1897	CU <sup>a</sup> , HA <sup>9,25,a</sup> , PE <sup>1</sup>
<i>Sphecodes confertus</i> Say, 1837	PI <sup>c</sup> , WN <sup>61</sup>
<i>Sphecodes coronus</i> Mitchell, 1956	HA <sup>2</sup> , PI <sup>c</sup> , YO <sup>61</sup>

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<i>Sphecodes cressonii</i> (Robertson, 1903)	HA <sup>25</sup> , LI <sup>a</sup>
<i>Sphecodes davisii</i> Robertson, 1897	HA <sup>1</sup> , PE <sup>1,14</sup> (as <i>S. persimilis</i> ) <sup>k</sup> , SO <sup>a</sup> , WN <sup>1,9,61</sup> , YO <sup>2</sup>
<i>Sphecodes dichrous</i> Smith, 1853	HA <sup>1,25</sup> , KN <sup>c</sup> , WN <sup>1</sup>
<i>Sphecodes johnsonii</i> Lovell, 1909	HA <sup>25</sup> , WN <sup>1</sup>
<i>Sphecodes levis</i> Lovell and Cockerell, 1907	FR <sup>a</sup> , LI <sup>p</sup> , PE <sup>1,14</sup> , YO <sup>k</sup>
<i>Sphecodes mandibularis</i> Cresson, 1872	PE <sup>14,a</sup> , WN <sup>61</sup>
<i>Sphecodes minor</i> Robertson, 1898	KE <sup>12</sup>
<i>Sphecodes prosporus</i> Lovell and Cockerell, 1907	HA <sup>10</sup> , KN <sup>a</sup> , LI <sup>a,p</sup> , SO <sup>2</sup>
<i>Sphecodes ranunculi</i> Robertson, 1897	FR <sup>a</sup> , HA <sup>1,25</sup> , PE <sup>14,16</sup> , WD <sup>a</sup> , WN <sup>12,61</sup> , YO <sup>67</sup>
<i>Sphecodes solonis</i> Graenicher, 1911	FR <sup>a</sup> , PE <sup>14</sup> , SO <sup>2</sup>
* <i>Anthidium</i> ( <i>Anthidium</i> ) <i>m. manicatum</i> (L., 1758)	HA <sup>1</sup> , LI <sup>1</sup> , PE <sup>1</sup>
<i>Dianthidium</i> ( <i>Dianthidium</i> ) <i>simile</i> (Cresson, 1864)	YO <sup>a</sup>
<i>Stelis</i> ( <i>Dolichostelis</i> ) <i>louisae</i> Cockerell, 1911	Unknown county <sup>30</sup>
<i>Stelis</i> ( <i>Stelis</i> ) <i>foederalis</i> Smith, 1854	LI <sup>m</sup> , WN <sup>9,61</sup>
<i>Stelis</i> ( <i>Stelis</i> ) <i>lateralis</i> Cresson, 1864	HA <sup>25</sup> , LI <sup>29,51,m</sup> , PE <sup>1</sup>
<i>Stelis</i> ( <i>Stelis</i> ) <i>nitida</i> Cresson, 1878	WN <sup>61</sup>
<i>Coelioxys</i> ( <i>Boreocoelioxys</i> ) <i>funeraria</i> Smith, 1854	Unknown county <sup>31</sup>
<i>Coelioxys</i> ( <i>Boreocoelioxys</i> ) <i>moesta</i> Cresson, 1864	HA <sup>8</sup> , KN <sup>a</sup> , PI <sup>4</sup> , WN <sup>9,61</sup>
<i>Coelioxys</i> ( <i>Boreocoelioxys</i> ) <i>octodentata</i> Say, 1824	PE <sup>1</sup> , YO <sup>c</sup>
<i>Coelioxys</i> ( <i>Boreocoelioxys</i> ) <i>porterae</i> Cockerell, 1900	HA <sup>1,2</sup> , OX <sup>q</sup> , PE <sup>1,4</sup> , PI <sup>4</sup> , WN <sup>61</sup>
<i>Coelioxys</i> ( <i>Boreocoelioxys</i> ) <i>rufitarsis</i> Smith, 1854	HA <sup>a</sup> , KN <sup>a</sup> , PE <sup>1</sup> , YO <sup>2</sup>
<i>Coelioxys</i> ( <i>Coelioxys</i> ) <i>sodalis</i> Cresson, 1878	HA <sup>1,25</sup> , PI <sup>1</sup>
* <i>Megachile</i> ( <i>Callomegachile</i> ) <i>sculpturalis</i> Smith, 1853	AR <sup>1</sup> , HA <sup>1</sup> , PE <sup>1</sup>
* <i>Megachile</i> ( <i>Eutricharaea</i> ) <i>rotundata</i> (Fabricius, 1793)	PE <sup>1</sup> , WD <sup>4</sup> , WN <sup>14,9,61</sup>
<i>Megachile</i> ( <i>Litomegachile</i> ) <i>brevis</i> Say, 1837	CU <sup>c</sup> , HA <sup>25</sup> , LI <sup>59</sup>
<i>Megachile</i> ( <i>Litomegachile</i> ) <i>mendica</i> Cresson, 1878	HA <sup>25</sup> , WN <sup>9</sup> , YO <sup>b,c</sup>
(*?) <i>Megachile</i> ( <i>Megachile</i> ) <i>centuncularis</i> (L., 1758)	HA <sup>1,25,a</sup> , PE <sup>1</sup> , WN <sup>c</sup>
<i>Megachile</i> ( <i>Megachile</i> ) <i>inermis</i> Provancher, 1888	FR <sup>a</sup> , HA <sup>4,25</sup> , LI <sup>59</sup> , PE <sup>1,2,4</sup> , SO, WD <sup>4</sup> , WN <sup>9,61</sup>
<i>Megachile</i> ( <i>Megachile</i> ) <i>montivaga</i> Cresson, 1878	PE <sup>17</sup>
<i>Megachile</i> ( <i>Megachile</i> ) <i>lapponica</i> Thomson, 1872 [= <i>nivalis</i> Friese, 1903]	Unknown county <sup>35</sup>
<i>Megachile</i> ( <i>Megachile</i> ) <i>relativa</i> Cresson, 1878	AR <sup>4</sup> , CU <sup>c</sup> , FR <sup>a</sup> , HA <sup>1,2,4,25,a,o</sup> , LI <sup>59</sup> , PE <sup>1,2,4</sup> , PI <sup>4</sup> , SO <sup>2</sup> , WD <sup>4</sup> , WN <sup>1,4,9,61</sup> , YO <sup>c</sup>
<i>Megachile</i> ( <i>Xanthosarus</i> ) <i>f. frigida</i> Smith, 1853	HA <sup>25,a</sup> , LI <sup>a</sup> , OX <sup>f</sup> , PE <sup>1</sup> , PI <sup>a</sup> , WN <sup>9</sup>
<i>Megachile</i> ( <i>Xanthosarus</i> ) <i>gemula</i> Cresson, 1878	CU <sup>c</sup> , FR <sup>a</sup> , HA <sup>1,2,8,a,o</sup> , LI <sup>59</sup> , PE <sup>1,14,n</sup> , WN <sup>1,8</sup> , YO <sup>a,c</sup>
<i>Megachile</i> ( <i>Xanthosarus</i> ) <i>latimanus</i> Say, 1823	HA <sup>1,25</sup> , KE <sup>2,n</sup> , LI <sup>59</sup> , OX <sup>q</sup> , PE <sup>1</sup> , WN <sup>1</sup> , YO <sup>c</sup>
<i>Megachile</i> ( <i>Xanthosarus</i> ) <i>m. melanophaea</i> Smith, 1853	FR <sup>a,57</sup> , HA <sup>1,25</sup> , LI <sup>a</sup> , PE <sup>1,2,12</sup> , SO, WN <sup>1,9</sup> , YO <sup>c</sup>
<i>Megachile</i> ( <i>Xanthosarus</i> ) <i>mucida</i> Cresson, 1878	WA <sup>61</sup> , det. Terry Griswold
<i>Heriades</i> ( <i>Neotrypetes</i> ) <i>carinata</i> Cresson, 1864	HA <sup>1,25</sup> , PE <sup>1,2</sup>
<i>Heriades</i> ( <i>Neotrypetes</i> ) <i>leavitti</i> Crawford, 1913	SO <sup>2, 29</sup>
<i>Heriades</i> ( <i>Neotrypetes</i> ) <i>v. variolosa</i> (Cresson, 1872)	HA <sup>1</sup> , Unknown county <sup>29</sup>
<i>Hoplitis</i> ( <i>Alcidamea</i> ) <i>albifrons albifrons</i> (Kirby, 1837)	HA <sup>9</sup> , WN <sup>9</sup>
<i>Hoplitis</i> ( <i>Alcidamea</i> ) <i>pilosifrons</i> (Cresson, 1864)	HA <sup>8</sup> , WN <sup>8</sup>
<i>Hoplitis</i> ( <i>Alcidamea</i> ) <i>producta producta</i> (Cresson, 1864)	HA <sup>1,8,25</sup> , PE <sup>1,12,14</sup> , WN <sup>1,8,9,10</sup> , YO <sup>c,n</sup>
<i>Hoplitis</i> ( <i>Alcidamea</i> ) <i>spoliata</i> (Provancher, 1888) [= <i>H. cylindrica</i> ]	CU <sup>o</sup> , HA <sup>25</sup> , LI <sup>m</sup> , PE <sup>1,12</sup> , PI, WN <sup>9,10,12,61</sup> , YO <sup>a,c</sup>
<i>Hoplitis</i> ( <i>Alcidamea</i> ) <i>truncata truncata</i> (Cresson, 1878)	HA <sup>25</sup> , PE <sup>1</sup> , YO <sup>2</sup>



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Scientific name	Counties (selected sources)
* <i>Osmia (Helicosmia) caerulescens</i> (L., 1758)	HA <sup>1</sup> , PE <sup>4,16,19</sup>
<i>Osmia (Melanosmia) albiventris</i> Cresson, 1864	HA <sup>25</sup> , LI <sup>60</sup> , PE <sup>2,14,n</sup> , WN <sup>9</sup>
<i>Osmia (Melanosmia) atriventris</i> Cresson, 1864	HA <sup>1,25</sup> , LI <sup>60</sup> , PE <sup>1,2,12,14</sup> , WD <sup>2,4</sup> , WN <sup>4,5,8,9,10,12,61</sup> , YO <sup>k</sup>
<i>Osmia (Melanosmia) bucephala</i> Cresson, 1864	HA <sup>8,25,a</sup> , KE <sup>4</sup> , LI <sup>60</sup> , PE <sup>1,10,n</sup> , WD <sup>2</sup> , WN <sup>4,9,12,61</sup> , YO <sup>2</sup>
<i>Osmia (Melanosmia) collinsiae</i> Robertson, 1905	PE <sup>1,29</sup>
<i>Osmia (Melanosmia) distincta</i> Cresson, 1864	HA <sup>1,25</sup> , PE <sup>1,14</sup> , YO <sup>o</sup>
<i>Osmia (Melanosmia) inspergens</i> Lovell & Cockerell, 1907	HA <sup>1,8,25</sup> , LI <sup>60,p</sup> , WN <sup>9</sup>
<i>Osmia (Melanosmia) laticeps</i> Thomson, 1872	KN <sup>36</sup>
<i>Osmia (Melanosmia) nigriventris</i> (Zetterstedt, 1838)	WN <sup>61</sup>
<i>Osmia (Melanosmia) proxima</i> Cresson, 1864	HA <sup>25,o</sup> , LI <sup>60,o</sup> , PE <sup>1,4,14</sup> , WN <sup>9,12,61</sup> , YO
<i>Osmia (Melanosmia) pumila</i> Cresson, 1864	HA <sup>8,25</sup> , PE <sup>1,n</sup> , WD <sup>2</sup> , WN <sup>8,61</sup> , YO <sup>k</sup>
<i>Osmia (Melanosmia) simillima</i> Smith, 1853	CU <sup>8</sup> , HA <sup>8,25</sup> , YO <sup>c</sup>
<i>Osmia (Melanosmia) tarsata</i> Provancher, 1888 [= <i>O. kenoyeri</i> ]	WN <sup>10,61,66</sup> , Unknown county <sup>43</sup>
<i>Osmia (Melanosmia) tersula</i> Cockerell, 1912	HA <sup>1,8,9</sup> , PE <sup>1,14</sup> , WN <sup>9,10,o</sup>
<i>Osmia (Melanosmia) virga</i> Sandhouse, 1939	HA <sup>8</sup> , PE <sup>12</sup> , WN <sup>8</sup> , YO <sup>2</sup>
<i>Osmia (Osmia) lignaria lignaria</i> Say, 1837	HA <sup>8,25</sup> , KE <sup>4</sup> , PE <sup>1,2,4,12,16,n</sup> , WN <sup>8,61</sup> , YO
<i>Macropis (Macropis) ciliata</i> Patton, 1880	LI <sup>29,55</sup>
<i>Macropis (Macropis) nuda</i> (Provancher, 1882)	CU <sup>13</sup> , HA <sup>25,a</sup> , LI <sup>a</sup> , PE <sup>1,n</sup> , WN <sup>8</sup> , YO <sup>2</sup>
<i>Melitta (Cilissa) americana</i> (Smith, 1853)	LI <sup>55</sup> , WN <sup>37</sup>
<i>Melitta (Cilissa) melittoides</i> (Viereck, 1909)	YO <sup>2</sup>

## Source Legend

Code	Item
1	Dibble specimens, or for <i>Colletes compactus</i> , photo determined by J.S. Ascher. See Dibble et al. 1997, Dibble and Drummond 1997; Roque Island 2014; Dibble and Drummond field course at Eagle Hill (2012–2016); Bee Module experiment 2012–2015, unpubl. data.
2	Veit specimens.
3	Stubbs specimens, or see Stubbs et al., 1992; Stubbs et al. 2007.
4	Drummond specimens.
5	Droege bioblitz at Acadia National Park, see Droege 2010.
6	AMNH database, includes J.S. Ascher specimens.
7	Ascher specimens and Maine Bee Type Compilation.
8	Bushmann specimens, 2010–2012 data from her Ph.D. Dissertation, and collections into 2016.
9	R. Hansen 1981, T30 MD, 1982, T4 ND, both in Washington County, and from Hancock County, see Hansen and Osgood 1983.
10	L. Guimond 1989, T32 MD, Hancock County; T31, Washington County; Deblois, Washington County; and Orono, Penobscot County.
11	Droege determinations, <i>Nomada</i> .
12	E.A. Osgood, including Orono, Penobscot County; Deblois, Washington County, 1961–1984; Vienna, Kennebec County, 1961–1990; Kennebunk, York County, 1961–66 (Boulanger et al. 1967), Katahdin, Piscataquis County.
13	“Me. Agr. Exp. Sta” N. Gray, Cumberland County. 1929 and 1930 (possibly C.R. Phipps).
14	Miliczky and Osgood 1979a, 1979b, Passadumkeag, Penobscot County.
15	Frederick Allen Eddy, ca. 1882 (red ink).
16	s.n., Orono, Penobscot Co., 1929 (C.R. Phipps?), 1941, 1961–1963.
17	Specimens housed in MCZ Harvard University collections .

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- 18 Includes specimens collected by A.E. Brower, some mention “Me. Agr. Exp. Sta.”, various sites, including Orono (1930, 1936, 1938); Bar Harbor, Hancock County (1937); T19, Washington County (1962); Patten, Penobscot County (1974).
- 19 s.n. Orono 1936-1938 (C.O. Dirk?).
- 20 s.n. 17 May 1929, S. Sedgwick, Hancock County.
- 21 s.n. 1930, Orono, Penobscot County, Maine Agricultural Experiment Station.
- 22 s.n. 7 June 1961, Twp 19, Washington Co., determined as *Andrena durangoensis*, J.S. Ascher annotated as *A. carolina*.
- 23 s.n. Machias, Washington County 1929.
- 24 s.n. Maine Agricultural Experiment Station, 1961.
- 25 Procter 1938 (amplified and revised in 1946).
- 26 s.n. Maine Agricultural Experiment Station, 1930.
- 27 Bernd Heinrich, Wilton, Franklin County, n.d., assumed by Leif Richardson from Bumblebee Economics.
- 28 “Coll. E. Norton”, presumably as “Maine” and no date, locale or county given.
- 29 Mitchell 1960, 1962, no county given; a few further details by taxon where available:
- 29a For *Agapostemon sericeus*, mapped as occurring in Maine as *A. radiatus* by Roberts (1972) [revision]
- 29b For *Anthophora bomboides*, cited by Mitchell 1960, 1962 but not by Brooks 1983.
- 29c For *Osmia collinsiae*, in Mitchell, but no record information indicated.
- 30 For *Stelis lousiae*, Parker and Bohart; recorded as extending ... north to Maine on p. 147 of Parker and Bohart, JKES 52(1) 1979, but not shown on their map.
- 31 For *Coelioxys funeraria*, Baker, mapped in Figure 20 of Baker 1975 with no details but shown about half way up Maine coast.
- 32 For *Bombus pennsylvanicus*, cited in Milliron 1973 Vol. II of Monograph. Worker from Saco, York Coounty, 13 Jun 1951, collected by T.B. Mitchell.
- 33 For *Hylaeus floridanus*, cited by Mitchell but as *H. packardi*. One of the 2 specimens in type series was from Maine (described by Mitchell, 1951). Snelling (1970) proposed the synonymy and cited the Maine occurrence.
- 34a Gibbs 2011, and Jason Gibbs’ determinations of Maine specimens.
- 34b Gibbs 2010, and Jason Gibbs’ determinations of Maine specimens.
- 34c Gibbs et al. 2013 *Evylaeus* revision.
- 35 Sheffield et al. 2011, *Megachile nivalis*, now known as *Megachile* (*Megachile*) *lapponica* Thomson, 1872. Synonymy of N. American *M. nivalis* with European *M. lapponica* at [http://cjai.biologicalsurvey.ca/srpg\\_18/srpg\\_18.pdf](http://cjai.biologicalsurvey.ca/srpg_18/srpg_18.pdf).
- 36 For *Osmia laticeps*, cited in Rightmyer et al. 2010, i.e., the ZooKeys paper on non-metallic Osmia. Record is from “USA: MAINE, 15 June 1982 (1♀, St. Charles)” (<http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3088345/>).
- 37 For *Melitta americana*, collected by Brianne DuClos, 9 July 2013, powerline corridor, DeBlois, Washington County, ME, determined by Sam Droege, GPS 44.702139, -67.989309.
- 38 Lovell, 1910.
- 39 Stephen (1954), revision of Colletes.
- 40 For *Epeolus americanus*, cited by Brumley 1965 [as *E. americanus*]; Mitchell, 1962:450; paratype of *E. lanhami* from “Oreno, Me.”[sic]. Table 2 refers to a specimen collected by R.A. Morse and C. Zmarlicki, July 19, 1961, “Washington County”, no town given.
- 41 For *Holcopasites illinosensis*, cited in Hurd and Linsley 1972.
- 42 For *Dufourea novaeangliae*, collected in Machias (Washington County) by Samantha Gallagher July 2015.
- 43a For *Pseudopanurgus aestivalis*, listed by Mitchell (1960) as *P. nebrascensis*, see Sheffield and Perron 2014.
- 43b For *Osmia tarsata*, see discussion on synonymy with *O. kenoyeri* Cockerell, 1915, see Sheffield and Perron 2014.
- 44 Roque Island 2014, Dibble and Drummond Native Bees field course at Eagle Hill, Steuben, ME.

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- 45 Ribble, D.W. 1967. Revisions of 2 subgenera of *Andrena*: *Micrandrena* Ashmead and *Derandrena*, new subgenus (Hymenoptera: Apoidea). Ph.D. Thesis, published in 1968 as Bulletin of the University of Nebraska State Museum 8(5):237–394 .
- 46 For *Andrena spiraeana*, recorded from Orono (Penobscot County) by LaBerge 1973:342
- 47 LaBerge 1961 (*Melissodes druriellus* is former *M. rustica*)
- 48 LaBerge 1956
- 49 For *Nomada armatella*, see Mitchell (1960, 1962); J.S. Ascher notes the only record with details at <http://www.discoverlife.org/mp/201?id=BBSL521175>; specimen collected 20 May 1967, Deblois (Washington County), sin nom.
- 50 Mitchell, 1956, descriptions of *Sphecodes*, as “*carolinus*”; collected on Katahdin as “*carolinus*”.
- 51 For *Stelis lateralis*, collected by D.J. Borror on 6 July 1939, no town given, Lincoln County, Ohio State U. record at <http://www.discoverlife.org/mp/201?id=GBIF311451792>.
- 52 Bug Guide photo.
- 55 Lovell 1922b (Bees of Maine, Part II).
- 56 Lovell 1925a (Bees of Maine, Part III).
- 57 Schwarz 1926.
- 58 Stubbs et al. 1992.
- 59 Lovell 1925b (Bees of Maine, Part IV).
- 60 Lovell 1925c (Bees of Maine, Part V).
- 61 Jennifer (Loose) Ryan, blueberry barrens collections, 1998.
- 62 Dearborn et al. 1983.
- 63 Kalyn Bickerman-Martens, Maine collections 2015.
- 64 Megan Leach, Maine collections 2014.
- 65 University of Maine Entomological Museum collection, housed in Augusta, ME.
- 66 Discover Life: within a species, click on global map to see details of voucher specimens.
- 67 s.n. Kennebunk, York County, 1960s (Boulanger et al. 1967?).
- 68 For *Andrena cornelli*, cited by LaBerge (1980) as *A. longifacies* LaBerge.
- 69 University of Maine, Orono collections 1905, 1915, collectors unknown.
- 70 Brianne DuClos, Maine collections 2014 –2015.
- 71 Discover Life, [http://www.discoverlife.org/mp/201?id=AMNH\\_BEES24420](http://www.discoverlife.org/mp/201?id=AMNH_BEES24420)
- 72 Discover Life, [http://www.discoverlife.org/mp/201?id=AMNH\\_BEES668](http://www.discoverlife.org/mp/201?id=AMNH_BEES668)

Symbol Abbreviation Institution or Collector

a	AMNH	American Museum of Natural History, New York, NY
b	CAES	Connecticut Agriculture Experiment Station, Storrs, CT
c	CUIC	Cornell University, Ithaca, NY
d	JML	Unknown (cited for <i>Andrena wheeleri</i> from Waldo County)
e	JSA	John Ascher
f	NYSM	New York State Museum, Albany, NY
g	RUAC	Rutgers University, Rutgers, NJ
h	UCD	University of California, R.M. Bohart Museum of Entomology, Davis, CA
i	UCMS	University of Connecticut, Storrs, CT
j	UMA	University of Massachusetts, Amherst, MA
k	UNHP	University of New Hampshire, Durham, NH
l	-	(left blank, could be confused with “l” [one])
m	OSUC	Ohio State University Insect Collection, columbus, OH
n	INHS	Illinois Natural History Survey Insect Collection, Champaign, IL
o	KU	University of Kansas, Lawrence, KS
p	USNM	Smithsonian Institution, Washington, DC
q	YPM	Yale Peabody Museum, New Haven, CT
r	FMNH	Field Museum of Natural History, Chicago, IL
s	BISON	USGS Biodiversity Information Serving Our Nation ( <a href="https://bison.usgs.gov">https://bison.usgs.gov</a> )

## Results

Sampling effort was highly uneven, and of Maine's 16 counties, only 8 have more than 50 available county records (see Fig. 1). Of these, only 5 have more than 100 bee species: Hancock County (197 confirmed species), Penobscot County (181), Washington County (162), York County (104), and Lincoln County (102). Androscoggin and Sagadahoc counties have only 11 and 8 species documented, respectively.

Despite these gaps, we list 278 described species of bees in 37 genera and 6 families for Maine (Table 2). For most of these, at least 1 voucher specimen was found or records in the literature are considered reliable. For some species (Table 2), information derived from Mitchell (1960, 1962; for 7 species) or other literature did not specify any county. A few species in Table 2 (i.e., *Colletes latitarsis*, *Epeolus pusillus*, *Melissodes bimaculatus*, *Nomada louisianae*) are mapped for Maine in Discover Life, but details about the record, including county, are pending (J.S. Ascher, unpubl. data).



Figure 2. Non-native bee, *Anthidium manicatum* (European Wool-carder Bee); the males are territorial at flowers of *Merostachys lanata* Send (Lamb's Ears), shown here, and other plants in Old Town, Penobscot County. The male chases other bees away while he awaits a visit from a conspecific female. Photograph © A.C. Dibble.

The largest genus is *Andrena* (53 spp.), followed by *Lasioglossum* (50), *Nomada* (28), *Bombus* (includes *Psithyrus*) (17), and *Osmia* (16). The total count includes at least 8 non-native species of Old World origin: *Apis mellifera*, *Lasioglossum leucozonium*, *L. zonulum*, *Andrena wilkella*, *Anthidium manicatum* (Fig. 2), *Osmia caerulea*, *Megachile rotundata*, and *M. sculpturalis*. *Megachile centuncularis* could be non-native (questionable status due in part to lack of confirmed records for Alaska; see Giles and Ascher 2006).

## Discussion

We consider the Maine bee checklist (Table 2) to be preliminary because none of the state's 16 counties have been exhaustively sampled, despite much effort in recent studies or by some collectors. Counties with few available records may be considered to have less relative documentation, in terms of numbers of bee species (indicated by shading of counties in Fig. 1), so it is not yet possible to say with any confidence that bee diversity in one county is higher than in another. Counties in southern Maine with the warmest climate and expanses of sandy habitat are expected to have the most species, but this is not yet borne out. Penobscot County is particularly well represented because the University of Maine in Orono has been an agricultural research center since the 1860s, with entomologists active on or near campus. Early and continuing research in major Lowbush Blueberry crop areas such as Hancock and Washington counties (Yarborough 2009) have led to better exploration of the bee fauna in those regions (Bushman and Drummond 2015).

### Species richness

Bee species richness in Maine is relatively low (<300 species), but not unusually so given its latitude and climate (Sheffield et al. 2003, Stubbs et al. 1996). Greater species richness was reported for bees of Wisconsin (Wolf and Ascher 2009), perhaps reflecting in part higher summer temperatures across most of that state, and much greater richness was recorded for western states such as Colorado (Scott et al. 2011). Gibbs et al. (in press) developed a checklist of 465 species in Michigan, with 38 new records. Low species richness in Maine could be due in part to the extent of forest. Maine is the most forested state in the continental US when measured as the proportion of total landscape comprised of forest vegetation landscapes (93% of land area; Wilson and Sader 2002). Much of the Maine landscape is categorized as mixed northern hardwood, coniferous forests, and boreal spruce–fir forests (Davis 1993). Dense, shady forests are not optimal habitats for generalist bees in the region (Dibble et al., in press; Romey et al. 2007) because of insufficient floral resources and lack of open sky for insolation and navigation. Powerline rights-of-way may provide suitable open habitat for many species including regional rarities (Wagner et al. 2014). In Maine, the extent of coniferous forest with a permanently shaded understory may limit the spatial distribution and abundances of native bee communities (Groff et al. 2016), whereas in hardwood forests of southern Maine many specialist bees visit spring ephemerals in the forest understory prior to leafout.

Timber harvest throughout much of Maine creates a changing light environment to which bees are likely to respond.

Native bee species richness in Maine is greatest for genera that are common across the Holarctic region and well adapted to the boreal forest and other habitats characteristic of northern latitudes (Michener 2007). Genera richest in species (*Andrena*, *Lasioglossum*, *Nomada*, *Bombus*, and *Osmia*) all include early emerging species that overwinter as adults. Their ecology has been a subject of the past 45 years in Maine bee research (Bushman and Drummond 2015; Bushmann et al. 2012; Dibble and Drummond 1997; Dibble et al. 1997; Drummond et al. 2017b; Jones et al. 2014; Osgood 1972, 1989; Stubbs et al. 1992). Of the 30–35 species of *Andrena* that occur regularly in Maine blueberry fields (Bushman 2013, Bushmann and Drummond 2015), the 5 most common are *Andrena (Andrena) carolina* and *Andrena (A.) rufosignata*, both of which have long malar spaces that facilitate their collection of nectar from blueberry flowers, and the generalists *A. (Melandrena) regularis*, *A. (M.) carlini*, and *A. (M.) nivalis*. These *Andrena* tend to be found in sandy loam soils (Osgood 1972), typified by the vast glacial plains of Washington County (Davis 1993).

Some species in the list (Table 2) are of particular interest because they are seldom collected, have a narrow distribution, were not expected to occur in the area, have been in decline, or have specific habitat requirements. There is a possibility that a taxon is under-recorded due to identification difficulties, so scarcity of records might not reflect rarity in nature. Nonetheless, one might assume that a species represented by a single recent record and 1 historic citation (Lovell 1922b) such as *Melitta (Cilissa) americana*, found in 2013 by Brianne DuClos, is genuinely less abundant than the many *Andrena* and *Osmia* species each represented by multiple specimens recorded from several counties.

We identified 21 species that could be considered unusual. Among recent state records, *Epeoloides pilosulus* (Macropis Cuckoo Bee) was found in the Kennebunk Plains in York County, June 2016 on *Apocynum* sp., by M. Veit along with its host *Macropis nuda* (known from 6 counties). *Epeoloides pilosulus* is the only member of its tribe in America North of Mexico, was recently rediscovered in New England (Wagner and Ascher 2008), and is now classified as endangered in Canada (COSEWIC 2011). M. Veit also found at this same site a new state record for *Melitta melittoides*, a rarely collected species associated with *Lyonia ligustrina* (L.) DC. (Maleberry; Wagner et al. 2014). In another recent example, Fenja Brodo, entomologist from Ottawa, ON, Canada, collected *Holcoposites calliopsidis* on *Rhus typhina* L. (Staghorn Sumac) on 14 July 2016 along a roadside in Steuben (Washington County).

In addition to the 4 species mentioned above, we consider others notable due to their limited representation in regional bee collections. These include *Colletes consors* (subspecies *mesocopus*), *Colletes hyalinus*, *Colletes impunctatus*, *Macropis (Macropis) ciliata*, *Hylaeus (Hylaeus) saniculae*, *Hylaeus (Paraprosopis) floridanus*, *Hylaeus (Metziella) sparsus*, *Andrena (Scrapteropsis) kalmiae* (newly documented for York County by M. Veit in June 2016), *Melitta (Cilissa)*

*americana*, *Heriades (Neotrypetes) leavitti*, *Hoplitis (Alcidamea) albifrons*, *Osmia (Melanosmia) inermis*, *Osmia (Melanosmia) laticeps*, *Osmia (Melanosmia) tarsata*, *Coelioxys (Boreocoelioxys) funeraria*, *Megachile (Megachile) lapponica*, *Bombus (Psithyrus) ashtoni* (collections since 2000 are few and noteworthy), and *Bombus (Bombus) affinis*, which was listed as Federally Endangered in 2017 and requires careful identification.

No well-known bee species is unique to Maine, but 2 species of *Nomada* of uncertain status are known reliably only from holotypes from the state. *Nomada proxima* has uncertain taxonomic placement and status (Mitchell 1962). *Nomada subbrutula*, described from Waldoboro in Lincoln County, has been recorded from 3 other states (Mitchell 1962), but some or all of these records may result from confusion with the widely distributed species *Nomada imbricata* and/or *N. luteoloides*. The taxonomic status of these species was only recently clarified by Schwarz and Gusenleitner (2004). Maine shares most (95%+) of its known bee fauna with New York, Michigan, Massachusetts, and Connecticut. New Brunswick, Canada, has similar climate, soils, and vegetational communities to Maine (Griffin et al. 2009, Smit et al. 2007), and studies of Lowbush Blueberry there (Javorek et al. 2002) record a bee fauna similar to that of comparable sites in Maine (Boulanger et al. 1967, Javorek et al. 2002, Stubbs et al. 1992). Certain species differ, notably *Triepeolus brittaini* Cockerell, which is now well known from all 3 Maritime Provinces of Canada, with numerous recent records (J.S. Ascher, S.K. Javorek [Agriculture and Agri-Food Canada, Kentville, NS, Canada], and J. Klymko, [Nature Serve, Atlantic Canada Conservation Data Centre, Sackville, NB, Canada], unpubl. data), but has not yet been recorded elsewhere. The bee fauna of Nova Scotia is also similar to that of Maine (Sheffield et al. 2003), but includes remarkable disjunct occurrences of “southern” species such as *Colletes willistoni* Robertson, that have not been recorded from Maine (though M. Veit has collected *C. willistoni* in Massachusetts and New Hampshire, and it could be in Maine). The influence of warming by the Gulf Stream and other ocean currents may be more extensive on Nova Scotia (Boughner 1937) than on Maine, and may explain these remarkable distributions.

Bee species other than those included in our checklist have been proposed by various sources to occur in Maine. We excluded the following because of insufficient documentation or problematic identification: *Andrena (Andrena) cornelli* Viereck, *A. (Gonandrena) fragilis* Smith, *A. (Trachandrena) heraclei* Robertson, *A. (Tylandrena) perplexa* Smith, *A. (Gonandrena) platyparia* Robertson, *A. (Micandrena) ziziae* Robertson, *Lasioglossum (Dialictus) tegulare* Robertson (most if not all records pertain to *L. ellisiae*), *Nomada lehighensis* Cockerell (see Droege 2010), and *N. subnigrocincta* Swenk. All of these species could plausibly occur in the state, but we have not been able to definitively confirm their presence. The taxonomic status of several additional cleptoparasitic *Nomada* “cuckoo bee” species and morphospecies remains uncertain pending completion of ongoing taxonomic revision of the genus (Droege et al. 2010). We have excluded a number of other records of species that cannot plausibly occur as far northeast as Maine, such as *Augochloropsis sumptuosa* (Smith), a species reported for Maine by Mitchell (1960)

but recorded reliably no nearer than New Jersey, and *Ceratina metallica* H.S. Smith (syn. *C. strenua*), reported by Procter (1946) but likely to have been misidentified.

### Life history and ecology

Life histories for most of the bees found in Maine are derived from studies conducted elsewhere and assumed to apply in Maine, but some bee species have been studied using Maine populations: *Osmia atriventris* (Drummond and Stubbs 1997a), *Andrena crataegi* (Osgood 1989), and *Bombus impatiens* (Drummond 2012a, Stubbs and Drummond 2001).

Regarding sociality and cleptoparasitism (one bee species lays its eggs in the nest of another bee species), 135 species in the Maine checklist (Table 2) are solitary bees, 39 are eusocial, 55 species are cleptoparasitic (e.g., *Nomada* and other *Nomadinae*, and *Coelioxys*) or socially parasitic in the case of some halictines (e.g., *Sphecodes*). Four species of *Bombus* (*Psithyrus*) are social parasites of other bumble bees.

Our checklist suggests that 22.7% of the total known bee species in Maine are cleptoparasites or social parasites of pollen-collecting bees. Bushmann and Drummond (2015) reported a similar percentage in a more recent survey of the bee community associated with Lowbush Blueberry in Maine. Their 4-year study involved 44 sites in Hancock, Waldo, and Washington counties. They found that 17.7% of bee species richness and 4.8% of the total bee abundance associated with Lowbush Blueberry in Maine are cleptoparasites. The number of bee cleptoparasites found in Maine is similar in species richness but is about one-fourth the relative abundance compared to that found by Sheffield et al. (2013) in Canada (varied from 1 to 10% cleptoparasite species relative to bee species richness and up to 22% in terms of individual cleptoparasite bee numbers relative to total bee abundance). Actual parasitism rates are not known for the Maine bee fauna. Over North American bee fauna, with respect to species richness, rate of cleptoparasitism might vary between 0 and 91% in individual bee species, and could be as high as 29% at the community level, based on a review of the literature (Wcislo 1996).

About half of the 278 bee species (Table 2) are known or suspected to be soil-nesting bees, including all species of *Andrena* and *Colletes* and most *Lasioglossum*. One *Andrena* species found in Maine, *A. crataegi*, is known to interconnect tunnels between individuals and may form a large communal ground nest in which each solitary sister bee is a queen (Osgood 1989). Of bees listed in Table 2, forty-three species nest in cavities and or stems, including several species of *Lasioglossum* in subgenus *Dialictus* that excavate nests in soft wood (Michener 2007), as do *Auglochloa pura* and *Anthophora terminalis*. Tiny bees in the genus *Ceratina* (small carpenter bee) may exploit an existing hole in a stem to access the hollow or pithy interior in which they lay their eggs. Examples of Maine plant species associated with stem-nesting bees are *Rubus* spp. (blackberry and raspberry), *Sambucus* spp. (elderberry), and *Rhus typhina* L. (Staghorn Sumac). Bees that nest in wood include *Xylocopa virginiana* (Eastern Carpenter Bee), which can excavate galleries in wooden structures and may cause some damage. *Megachile*



and *Osmia* can nest in holes in stumps, logs, or standing dead trees, and might use holes made by boring beetles.

Bee species differ in their overwintering condition and time of emergence, with important consequences for pollination of Maine crops (Bushmann 2013). Queen bumble bees overwinter as adults that emerged and mated during the previous autumn, while most other native bees emerge as fully developed adults for their maiden flight in spring or summer, from nests established and provisioned by their mothers during the previous season (or earlier that same season). In most native Maine bee species other than *Bombus*, males typically emerge first, a condition called protandry, and they are ready to mate when the females appear. Emergence is staggered depending on the bee species, with early bees appearing with first flowers of *Salix* spp. (willow) and *Acer rubrum* L. (Red Maple) in spring (Bushmann 2013). The importance of willow to bees active in early spring was studied by Ostaff et al. (2015) and was documented in a common garden study in Maine by A.C. Dibble, F.A. Drummond, and L. Berg Stack (unpubl. data).

Some *Bombus*, especially the currently common species *B. ternarius* (Tricolored Bumble Bee; Fig. 3) and *B. vagans* (Half-black Bumble Bee), are in evidence from early spring (the beginning of April or, recently, in warm years, as early as late March) until late October. The large queens can be seen foraging on flowers



Figure 3. Queen *Bombus ternarius* (Tricolored Bumble Bee) on flowers of *Erica tetralix* L. (Crossleaf Heath) in a garden, on 24 April 2014, Brooklin, Hancock County. Photograph © A.C. Dibble.

into June; new queens are observed as early as late July (Bushmann 2013). Bumble bee workers of various sizes can be found starting in June and then throughout the growing season, with average size of individuals increasing gradually over the summer and fall (Bushmann et al. 2012).

An especially early bee is *Colletes inaequalis*, which often emerges before the snow has fully melted from its nest aggregations. Other bees active early in spring include many species in the genera *Andrena*, *Lasioglossum*, *Nomada*, and *Osmia* (Fig. 4). Adult emergence can begin as early as late March, i.e., in southern Maine in a particularly early spring, but more typically in April (A.C. Dibble, pers. observ.; Bushmann and Drummond 2015; Stubbs et al. 1992).

Bees with long flight seasons (both univoltine and multivoltine) extending from spring until fall include primitively eusocial halictine species, e.g., in the genera *Halictus*, *Lasioglossum* (Fig. 5), and *Augochlorella*, and the subsocial carpenter bees, e.g., genera *Ceratina* and *Xylocopa*. Most *Colletes* (Fig. 6) and their *Epeolus* cleptoparasites, and *Melissodes* and their *Triepeolus* cleptoparasites, fly from summer to fall in association with peak bloom of plants in the family Asteraceae such as asters and goldenrods. Early emerging and late-flying species and most specialists have restricted flight seasons. Data for Maine on flight activity of most species is in the process of being summarized (E. Venturini and F.A.



Figure 4. Female *Osmia* (mason bee) rests briefly on a leaf while foraging on *Vaccinium vitis-idaea* L. (Northern Mountain Cranberry), in Brooklin, Hancock County, 13 June 2015. Photograph © A.C. Dibble.

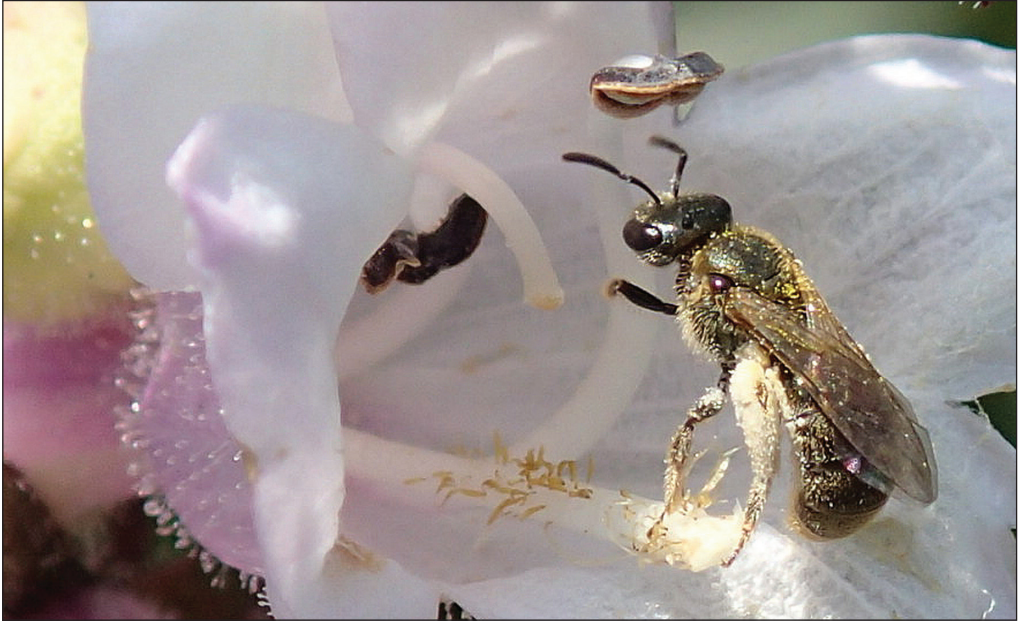


Figure 5. *Lasioglossum (Dialictus)* sp. (a metallic sweat bee) female on flowers of *Penstemon digitalis* "Mystica" (Foxglove Beardtongue), 8 July 2014, Blue Hill, Hancock County. Photograph © A.C. Dibble.



Figure 6. *Colletes compactus compactus* (Cellophane Bee) female, late-flying solitary bee species seldom collected in Maine, at her nest entrance, 16 September 2011, Brooklin, Hancock County. Photograph © A.C. Dibble.

Drummond, University of Maine, Orono, ME, unpubl. data). Many species were included in phenological diagrams for offshore islands of New York State (Ascher et al. 2014) and Massachusetts (Goldstein and Ascher 2016). Flight activity varies across sites and years. Likewise, flight activity of most *Osmia* species peaks in May–June, but collections of *O. atriventris* and *O. simillima* have been made in Maine as late as August in Hancock and Washington counties (Droege 2012). Some bee species, including several *Megachile* and their *Coelioxys* cleptoparasites, are aestival, i.e., most active in summer (A.C. Dibble and F.A. Drummond, pers. observ.; Droege 2012). *Colletes* and its *Epeolus* cleptoparasites can be active in mid-September in Hancock and Washington counties (A.C. Dibble, unpubl. data).

Information on host-plant usage includes Stubbs et al.'s (1992) reports of pollen and nectar records for native bee species associated with Lowbush Blueberry. *Osmia atriventris* is considered polylectic, but in a study in Winterport, ME, where 54 species of flowering plants came into bloom during its nesting period, individuals collected pollen from only a few species—90% was ericaceous pollen, most likely of Lowbush Blueberry (Drummond and Stubbs 1997b). Subsequently Bushmann and Drummond (2015) studied flower use and pollen collection by native bees during Lowbush Blueberry bloom, and found that in addition to ericaceous plants, the 3 most common native forage plant species or genera were *Cornus canadensis* L. (Bunchberry), *Rubus* spp. (raspberry and blackberry), and *Houstonia caerulea* L. (Azure Bluet). Fowler (2016) reviewed regional patterns of bee specialization on plants of the northeastern US.

Lowbush Blueberry is one of the native plants on which floral visitors have been studied intensively (Bushmann and Drummond 2015, Drummond et al. 2017b, Stubbs et al. 1992, and numerous other papers). Others include *Amelanchier* (shadbush; Dibble and Drummond 1997, Dibble et al. 1997), *Viburnum nudum* spp. *cassinoides* (L.) Torr. & A. Gray (Withe-rod; Miliczky and Osgood 1979b, Stubbs et al. 2007), and *Spiraea alba* var. *latifolia* (Aiton) H.E. Ahles (White Meadow-sweet; Stubbs et al. 2007).

Other than in such pollinator studies, forage-plant information from museum collections of bees is often lacking or may be unreliable. Emphasis on data regarding flowering-plant associations will enhance our ability to protect or manipulate habitat for native bees and can lead to Maine-specific recommendations with potential usefulness in other parts of northeastern North America. The most up-to-date information on Maine forage plants and larger-scale vegetational landscapes can be found in Bushmann and Drummond (2015); Dibble and Drummond (1997); Dibble et al., in press; Droege (2012); Drummond et al. (2017a); Groff et al. (2016); Stubbs et al. (1992); and Venturini et al. (2015). More Maine studies are in the pipeline (A.C. Dibble, F.A. Drummond, and L. Berg Stack, unpubl.data). These kinds of data, when considered with reference to regional reviews of specialist bees (Fowler 2016), will increase the effectiveness of pollinator plant lists (e.g., A.C. Dibble, unpubl. data; Ley et al. 2011; Venturini et al. 2015) so that bee gardens and pollinator strips are more likely to accomplish their intended goals in Maine.

### Changes in abundance

Long-term population dynamics of bee communities have not been well studied in Maine, other than climate-change data reported by Drummond et al. (2017b). In that study, continuous sampling over a 29-year period in a Lowbush Blueberry field in Winterport, Waldo County, resulted in total bee abundance varying 2–3 fold from one year to the next. Bee categories (*Bombus*, *Andrena*, *Osmia*, and “Halictids and Other”) were not highly correlated with one another and showed independence. *Osmia* declined since 2007, but the total bee community abundance was stable during the 29-year time period. Predictability from models developed by Drummond et al. (2017b) was low to moderate and suggested that abundance fluctuations depend on both density-dependent factors and stochastic density-independent factors such as weather.

The relative abundance of wild native *Bombus* species in Maine has changed dramatically since the early 1960s (Bushmann et al. 2012). Whereas the most common native bees in Maine continue to include bumble bee species such as *Bombus ternarius* (Fig. 3) and *B. vagans*, both in the subgenus *Pyrobombus*, another once-common species, *B. terricola* (Yellow-banded Bumblebee) in subgenus *Bombus*, and its social parasite *B. ashtoni* (treated by Williams et al. 2014, as conspecific with the Old World *Bombus bohemicus*) have declined in Maine (Bushmann et al. 2012; Heinrich and Heinrich 1983a, b) and across the region (Bartomeus et al. 2013, Cameron et al. 2011, Kerr et al. 2015). *Bombus affinis* (Rusty-patched Bumble Bee), also parasitized by *B. ashtoni*, appears to have been relatively common at one time in Maine and is recorded for 10 counties, but today it is seldom found. It was noted by Procter (1946) as scarce for Mount Desert Island. Boulanger et al. (1967) listed *B. affinis* from New Brunswick but did not specify any Maine counties. On the other hand, several species of subgenus *Pyrobombus* such as *B. ternarius* and especially *B. impatiens* (Eastern Bumble Bee) have increased (Bushmann and Drummond 2015). Surveys of *B. terricola* distribution in Maine in 2014–2015 indicate a resurgence of that species at many sites (Drummond 2015), but not of its social parasite *B. ashtoni*.

### Habitat and landscapes

Using literature and specimen-label data to assess relative sampling effort by habitat, we found studies in blueberry fields to be well represented, and edge habitats associated with mixed conifers were also relatively well studied. Many habitats in Maine require more attention, including coastal islands, well-drained sandy soils on islands and elsewhere, hardwood forests, swamps, bogs, open mountain summits, roadsides, and urban and suburban plantings. Bees on coastal islands in New England are of particular interest because they potentially include relictual or disjunct species (see Goldstein and Ascher 2016) or those that have potentially declined on the mainland due to infection by a microsporidian pathogen, *Nosema bombii* Fantham and Porter (Bushmann et al. 2012). On a 1-day visit in late July 2014 to Roque Island, ME, 6 *Bombus* species were documented including *B. fervidus* (Yellow Bumblebee), which is relatively scarce in Washington County, but not *B. impatiens* (A.C. Dibble, unpubl. data). In visits to Monhegan Island, ME, and when studying samples in the Cornell University Insect Collections from Appledore

Island, ME, we found no strikingly unusual species. Counties in southern Maine with sandy soils, such as York and Cumberland, could be under-represented in the checklist, and harbor bees such as *Nomada tiftonensis* that have a restricted distribution in the state. Additional bee species characteristic of northern climates have been found on Mount Washington in New Hampshire and may also extend their ranges southward into mountainous habitats in Maine, but surveys of the most promising high-elevation sites in Maine, such as Katahdin, are lacking. Bees may be genuinely scarce there. No bees other than a single *Bombus terricola* were seen on a 4-day hiking trip to a lowland forest area near Katahdin in August 2014 (A.C. Dibble, pers. observ.). In a scenario of upward-shifting treeline with climate change, open habitats that support unusual montane bee faunas in the state could change greatly in coming decades due to upslope advance of coniferous trees (Dibble et al. 2009), putting some as yet unstudied cold-adapted bee species at risk (Kerr et al. 2015) before they have been inventoried.

### Conservation concerns

Native bees of Maine could encounter competition with non-native bees for floral resources or nest sites. They could be impacted by pesticides, natural enemies, diseases, habitat degradation (through invasive plant encroachment), habitat fragmentation, and climate change (Brown and Paxton 2009, Goulson et al. 2015, Kerr et al. 2015).

Non-native bee species can be adventive, or they could arrive in Maine as purposeful introductions. Non-native bees can alter ecosystems in subtle but significant ways (Goulson 2003, Goulson et al. 2015). They may compete for floral resources and nest sites, spread pests and pathogens to native bee populations, and effect diminishing plant reproduction in native plant species that depend on native bee pollinators but are not visited much by introduced bees.

The best-known and most economically important managed non-native bee in Maine is *Apis mellifera* (European Honey Bee), which has been in North America since 1622 (Kingsbury 1906). Since 1630, when Maine was a part of Massachusetts, *Apis mellifera* has been established in the state (Martin et al. 1980). It has been used in Lowbush Blueberry pollination since the 1950s (Lee 1958), with managed colonies supplemented by feral honey bees, but since the 1990s persistent overwintering feral hives are seldom found in Maine (F.A. Drummond, unpubl. data). The disappearance of feral colonies is a phenomenon that has been observed across the entire US and is attributed to the accidental introduction of the parasitic mite *Varroa destructor* (Delaplane 2001). Colony Collapse Disorder in managed *Apis mellifera* demonstrates the collective impact of multiple simultaneous threats (Drummond 2012c, Ellis et al. 2010, Neumann and Carreck 2010, Ratnieks and Carreck 2010). This syndrome, which became evident in 2006, prompted new research on pollinator habitat quality as a means of enhancing existing native bee populations in Maine, with the idea that native bees might be required to play an increasing role as pollinators of Lowbush Blueberry and other Maine crops (Asare 2013, Venturini et al. 2015). High rates of honey bee colony losses (averaging greater than 30%; Lee et al. 2015, vanEngelsdorp and Meixner 2010) across the US since 2006 have

resulted in severe economic hardship for commercial beekeepers. Honey bee colonies continue to be reared in Maine and brought from out of state (more than 75,000 commercial colonies per year; Drummond 2012c). Many of these colonies swarm and produce initial feral colonies that last only 2–3 years in the absence of management (Drummond et al. 2012). *Apis mellifera* is present in all Maine counties, though voucher specimens could not be found for some counties. A recent survey among Maine beekeepers (most are assumed to be hobbyists) to obtain pollen for analysis of pesticide residue from honey bee colonies will be reported separately. Any counties not vouchered were filled into Table 2 based on beekeeper responses to that survey (E. Ballmann, University of Maine, Orono, ME, unpubl.data).

*Bombus impatiens* is both a native bumble bee (categorized as such in Table 2) and the species that is purchased from commercial suppliers and brought into Maine in colonies (quads) annually for blueberry, *Malus pumila* Miller (Apple), *Solanum lycopersicum* L. (Tomato), and Curcubitaceae (curcurbits) pollination in both the greenhouse and in the field (Drummond 2012a). Several thousand colonies are set out each year in Maine Lowbush Blueberry fields (Drummond 2012a, Stubbs et al. 2001). *Bombus impatiens* abundance and collecting frequency was lower in Maine prior to the 1990s compared to more recent times (Bushmann et al. 2012). Current populations of *B. impatiens* found in Maine could have multiple sources including both managed commercial colonies brought from Michigan (Drummond 2012a, Stubbs and Drummond 2001, Stubbs et al. 2001), and wild native genotypes with populations that appear to be expanding their range northward in possible association with climate change (Bushmann et al. 2012). Recent collections in more than 200 locations from 2011–2015 have shown that *B. impatiens* individuals make up ~10–20% of bumble bee individuals in Maine (F.A. Drummond, unpubl. data). Bushmann et al. (2012) showed that relative abundance of *B. impatiens* in the 1960s was much lower than current estimates in Maine (1961–1963: not detected, 1997–1998: 1–4%, 2010–2015: 10–20%). Procter (1946) did not record *B. impatiens* in coastal Hancock County.

*Megachile rotundata* (Alfalfa Leaf-cutter Bee) was used commercially as a managed pollinator for Lowbush Blueberry in Maine for more than a decade in the 1990s through to the early 2000s (Stubbs et al. 1997b) but not subsequently (F.A. Drummond, pers. observ.). Many hundreds of thousands of prepupae in individual leaf cells were imported from the western US and Canada and released by Maine growers for pollination of the Lowbush Blueberry crop (Stubbs and Drummond 1997a, b, c; Stubbs et al. 1997a, b). The bee was commonly trap nested and observed in blueberry fields in the 1990s when releases were made in Maine. Intensive bee surveys conducted from 2010 to 2012 using diverse sampling methods (Bushmann and Drummond 2015) in the same regions as these earlier releases have not recorded a single individual of *M. rotundata*, suggesting that it may be poorly adapted to long-term establishment at these sites (Stubbs and Drummond 1997a, b, c).

Several other non-native megachilids are adventive in the New World and may be a detriment to native species (Roulston and Malfi 2012, Strange et al. 2011). *Megachile sculpturalis* (Giant Asian Resin Bee) was detected in the southeastern

US in 1994 and has been dispersing rapidly across the US (Hinojosa-Díaz 2008, Mazurkiewicz 2010). It was collected in Portland, ME, by M. Mazurkiewicz in 2008, and by A.C. Dibble and S. Bushmann in Aroostook County in 2013, with additional documentation since. *Anthidium manicatum* (European Wool-carder Bee) males defend flowers of *Merostachys lanata* Send (Lamb's Ears; Fig. 2), *Agastache foeniculum* (Anise Hyssop), and horticultural bedding plants in the genus *Salvia* (Mealy Sage) against other floral visitors in Maine, and they attack bumble bees that attempt to visit such flowers (Gibbs and Sheffield 2009). *Anthidium manicatum* appears to be increasing in numbers and locales in Maine (A.C. Dibble, pers. observ.). *Osmia caerulea* (Blue Mason Bee) may be associated with urban habitats, and has been found in Maine as early as the 1930s (see sources cited in Table 2). *Osmia lignaria* (Blue Orchard Bee), indicated in Table 2 as non-native, has been recommended as a managed bee for orchards (Torchio 1976); in Maine it is relatively scarce. *Osmia (Osmia) cornifrons* (Radoszkowski) (The Horned faced Bee) was deliberately introduced from East Asia by USDA scientists (Yamada et al. 1971) and is abundant farther south in eastern North America, but has not yet been documented in Maine. Changes in abundance over time for some species of Megachilids were studied by Drummond et al. (2017b).

Additional small-bodied non-native bees could have negligible influence on native bees, but this relationship has not been measured. A mining bee, *Andrena wilkella*, and 2 sweat bees, *Lasioglossum leucozonium* and *L. zonulum*, are examples of ground-nesting bees native to Europe that are found in the Northeast and are documented for Maine. In general, with the exception of *Apis mellifera*, non-native bees appear to be increasing in richness and abundance in Maine, but they still comprise a far lower proportion than in states to the south, such as New York (see Matteson et al. 2008). Some possible explanations for this difference include Maine's colder climate, more limited international trade, and limited extent of cities and suburbs (Simberloff 2013).

Pesticide exposure may not be as important a threat to native bee health in Maine as in other states where crops are routinely treated, e.g., with imidacloprid, a widely used, systemic neonicotinoid (one class of persistent insecticides thought to harm beneficial insects even at sublethal doses; Blacquiere et al. 2012). Coating of crop seed with neonicotinoids is not much in use in the state compared to levels applied to *Brassica napus* L. (Oilseed Rape) crops in the United Kingdom, Hungary, and Germany (Woodcock et al. 2017) and *Zea mays* subsp. *mays* L. (Corn) in Ontario and Quebec, Canada (Tsvetkov et al. 2017). Even so, exposure in Maine crops can be at levels that impact local bee populations as demonstrated in a study on honey bees by Drummond (2012c). Exposure of native bees to pesticides and the resulting effects are complicated and not well studied. As an example, a recent study by Ciarlo et al. (2012) showed that the "inert ingredients" in pesticide formulations have negative effects on honey bee learning. Studies of managed pollinators such as *Apis mellifera*, *Bombus*, *Osmia*, and *Megachile* suggest either significant negative effects (Drummond 2012b, Ladurner et al. 2008, Laycock et al. 2012) or no measurable impact (Drummond



2012b, c). No true consensus has emerged with all of the conflicting data that currently exist, especially for the neonicotinoids, though recent studies suggest that site differences affect exposure rates to bees and subsequent impacts (Tsvetkov et al. 2017, Woodcock et al. 2017). In Maine, the effects of pesticides on native bees have not been extensively researched. Drummond and Stubbs (1997a) showed a negative relationship between the amount of insecticide active ingredient applied during the Lowbush Blueberry growing season and the relative abundance of *Osmia* spp. in blueberry fields. Ten percent of the variation in *Osmia* density was attributed to pesticide exposure. Bushmann (2013) in a 3-year study of native bee communities in more than 40 blueberry fields did not find evidence to suggest increased pesticide use affected native bee abundance or richness. Natural population fluctuations of bee communities between years and locations make it difficult to assess the impacts of pesticide exposure, and pesticides continue to be a serious potential concern.

Natural enemies of native bee pollinators in Maine include cleptoparasitic bees such as *Nomada* cuckoos of *Andrena* species (Bushmann and Drummond 2015), parasitoid wasps in the genus *Monodontomerus* (Torymidae), and the bee flies (Bombyliidae). *Myopa* spp. (white-faced flies) (Conopidae) attack *Bombus* in flight and lay their eggs in the abdomen of the living host. Velvet ants (Hymenoptera: Mutillidae) are found in Maine blueberry fields (Jones et al. 2014) where they parasitize soil-nesting bees and wasps. Crab spiders in the genus *Thomisus* (Thomisidae) camouflage on flowers and attack bees when they arrive to forage. Although such pests can thwart efforts to enhance populations of native species as pollinators (Cane et al. 1996), these species and their interactions might also be considered indicators of a healthy or naturally functioning ecosystem and bee community (Sheffield et al. 2013). Perspective might shift according to management goals. Drummond and Stubbs (1997a) found that *Osmia* spp. (mostly *O. atriventris*) populations nesting in artificial nest blocks had ~20% parasitization by aculeate wasps after 4 years of nest block utilization in a blueberry field in Winterport. Presence of these pest wasps might not be considered an index of a commercially healthy bee community, at least from a blueberry farmer's perspective. On the other hand, lack of *Stelis* bee cleptoparasites may indicate a disturbed system or unhealthy host-bee populations (see Sheffield et al. 2013).

A question remains regarding whether some exotic or cosmopolitan pathogens might be contracted by native bees from managed bees brought in to pollinate Lowbush Blueberry or other crops. Bushmann et al. (2012) found that *Nosema bombi*, a microsporidian pathogen of *Bombus* associated with blueberry fields, varied in its infection rate according to the bumble bee species, with a much higher rate in *B. terricola*—a species that had been in documented decline throughout its range—than in other common bumble bees. There was no correlation between farms employing the use of commercial bumble bees (*B. impatiens*) for pollination of Lowbush Blueberry and localized infection rates. Nonetheless, this is an example in which a threat can be more lethal to some species of native bees than to their congeners.

Another potential threat to native bees is encroachment into native habitats by non-native invasive plants (Pimentel et al. 2005, Stubbs et al. 2007, Weber 2017). Although many invasive plants in Maine do attract native bees (A.C. Dibble, unpubl. data; Stubbs et al. 2007), their presence can be considered a detriment because they displace native plants with which native bees evolved. We think it is possible that habitats dominated by invasive plants have lower diversity of pollen and nectar resources and subsequently a narrower range of overlapping flowering phenologies that support native bees. Stubbs et al. (2007) tested the supposition that invasive plants can become sinks for pollinators that would otherwise pollinate flowers of native plant species, leading to lower fruit set in the native flora. They found that pollination and bee abundance were not much affected by presence of 2 invasive plants, *Lythrum salicaria* L. (Purple Loosestrife) and *Rhamnus frangula* L. (Glossy Buckthorn), in Acadia National Park, but flowering period for *Berberis thunbergii* DC. (Japanese Barberry) overlapped that of Lowbush Blueberry and attracted floral visitors, mostly native bees, to such an extent that significantly lower floral visitation rates were observed on Lowbush Blueberry in the vicinity of barberry patches. In another example, Purple Loosestrife, a perennial of wet soils, attracts generalist bees (in Eurasia, where native, it also attracts specialists) but displaces native vegetation (Stubbs et al. 2007). Among the numerous bee-visited native plants that could be affected by Purple Loosestrife is *Lysimachia*, the oil and pollen source for *Macropis* (in turn, the only host of the associated cleptoparasitic genus *Epeoloides*). When meadows and roadsides become dominated by invasive *Lupinus polyphyllus* Lindl. (Bigleaf Lupine), then *Asclepias syriaca* L. (Common Milkweed) has less habitat. The latter is much more attractive to diverse native bees, including numerous *Bombus* species, and other insects such as *Danaus plexippus* (L.) (Monarch Butterfly), for which milkweed is a host for the larval stage. Bigleaf Lupine emerges earlier in spring than does Common Milkweed, and quickly shades and outcompetes any Common Milkweed that is already present.

Other examples of invasive plants that could impact Maine bees by reducing floral resources are: (1) herbs such as *Impatiens glandulifera* Royle (Ornamental Jewelweed or Himalayan Balsam), *Hypericum perforatum* L. (St. John's-wort), and *Fallopia japonica* (Houtt.) Ronse Decr. (Japanese Knotweed); (2) grasses such as *Phragmites australis* (Cav.) Trin. ex Steud. (Common Reed) and *Phalaris arundinacea* L. (Reed Canary Grass) (but pollen of nonnative *Phleum pratense* L. [Common Timothy] is gathered by bees; Rivernider et al., in press); (3) tender and woody vines such as *Solanum dulcamara* L. (Bittersweet Nightshade) and *Celastrus orbiculatus* Thunb. (Oriental Bittersweet); (4) shrubs including Japanese Barberry, *Elaeagnus umbellata* Thunb. (Autumn Olive), and *Lonicera morrowii* A. Gray (Morrow's Honeysuckle); and (5) trees including *Acer platanoides* L. (Norway Maple) and *Robinia pseudoacacia* L. (Black Locust). Most of these examples, but not all, are on the Maine Department of Agriculture, Conservation, and Forestry Invasive Plant List ([http://www.maine.gov/dacf/mnap/features/invasive\\_plants/invsheets.htm](http://www.maine.gov/dacf/mnap/features/invasive_plants/invsheets.htm)).

Habitat changes apart from invasive plant encroachment, that could impact bee populations, include agricultural practices, urbanization, and forest succession. Bee responses to most of these are not fully quantified in Maine. Venturini et al. (2017) found that pollinator plantings for native bees in association with Lowbush Blueberry agroecosystems increased abundance of native bees. This finding suggests that diverse gardens in cities and towns are also beneficial to bee diversity and abundance in Maine (Dibble et al., in press), but data are lacking. Regarding forest succession, Miliczky (1978) found 65 bee species at edges and small openings in a *Picea* (spruce)–*Abies* (fir) forest, suggesting that areas adjacent to or gaps within closed-canopy conifer stands are not necessarily devoid of bee communities. It appears likely that in addition to anthropogenic alterations to the landscape, fire, floods, and catastrophic wind-throw can be associated with early successional openings in which bees find suitable habitats. Native Americans in Maine burned small openings for centuries (Cronon 1983); presumably they altered habitats near waterways and maintained blueberry-dominated openings in conifer and mixed hardwood stands. Beginning ca. 1605, European colonists conducted what we might consider a vast deforestation (Cronon 1983), and brought in *Apis mellifera* and nonnative plants, some of which became important bee forage (e.g., *Taraxacum officinale* F.H. Wigg. [Common Dandelion]). Populations of many native bee species had potential to expand in response to increased open sky and additional forage and ground-nesting opportunities. Beginning in the the mid-1800s, large areas of agricultural fields were abandoned in Maine and many other parts of New England, and overall the trend in vegetation composition in uplands continues today toward forest-dominated ecosystems (Dibble et al. 2008, Wessels 1997). The Penobscot Experimental Forest of the University of Maine in Bradley, Penobscot County, is an example of such a forested landscape. It is dominated by *Picea rubens* Sarg. (Red Spruce) and other conifers, and some stands within this forest are periodically harvested in patches under various cutting regimes. The landscape features 343 plant species (Dibble 2013) of which about 59% offer pollen and nectar resources that might be taken by bees. Timber harvest in Maine continues, leading to large openings that favor bees in the short term; this is a landscape shift that, along with habitat fragmentation and urbanization, alters bee habitat resources, and not necessarily for the worse (Romey et al. 2007). In patches, ongoing transition through succession of edge habitats to closed-canopy forest may reduce bee diversity and abundance temporarily. Would bee communities then resemble those that were present prior to intense anthropogenic habitat alteration? This cannot be measured, and we do not know precisely what bee diversity may have been lost, but we can compare to historic collections and reasonably interpret Maine's current bee fauna as an artifact of human disturbance and its current diversity as indicative of the capacity of these animals to adapt and exploit opportunity, demonstrating resilience in a changing landscape.

Climate change and in particular hotter summer temperatures may already be resulting in changes to *Bombus* ranges in Maine and elsewhere (Kerr et al. 2015). Campbell et al. (2009) speculated that climate change will result in wetter conditions in Northeastern North America. Rainy springs, as documented by Drummond

et al. (2017b), and summers could detrimentally affect bees of Maine and other regions of northern New England in several ways: (1) upset a synchrony between bloom period for host plants and active period for native bees (but see Bartomeus et al. 2011), (2) limit good weather conditions for foraging with the result that insects are unable to provision sufficient brood for subsequent generations, and (3) lead to prolonged conditions that enhance fungal infections in soil-nesting bees (Batra et al. 1973).

Data from Drummond et al. (2017b) indicate that climate change that might affect bee activity and foraging during the spring bloom period of Lowbush Blueberry is already in effect in Maine. Their estimate of pollination days for Blue Hill in Hancock County between 1960 and 2015 showed a significant increase in the average number of pollination days as of 1990 but then a decline through to 2015. They ascribed this trend to an increase in rainy weather during bloom since 1990. There are potential impacts on crop pollination and on long-term bee population dynamics. Lack of synchrony between bees and their host plants could lead to an inadequacy of pollen and nectar sources (Miller-Rushing and Primack 2008) that might impact bee populations. A recent study (Bartomeus et al. 2011) showed that bee responses were comparable to and less extreme than the response of relevant plant species.

### Conclusions

Maine has a diversity of native bees typical for northeastern North America but with fewer species than states with warmer climates such as those to the south and west. Native bee species richness is rather high for typically Holarctic genera that overwinter as adults and are otherwise well adapted to a cold temperate climate (Michener 2007). While *Apis mellifera* feral colonies are in decline, other non-native bees could be increasing in species richness and abundance.

The preliminary county checklist focuses attention on gaps in available data, with the goal of informing future inventories. Additional sampling is needed in western, northern, and southern Maine, with particular attention to Androscoggin, Somerset, and Sagadahoc counties, along with other counties from which few species have been recorded.

Many vouchers we examined are from studies of pollinators for Lowbush Blueberry. Similarly intensive surveys of other crops (Apple, *Vaccinium macrocarpon* Aiton [American Cranberry], Highbush Blueberry, curcubits) are needed in Maine. Crops that are pollinator-independent might also be surveyed for associated bees, as for *Solanum tuberosum* L. (Potato) in Michigan (Buchanan et al. 2017). Natural habitats that could be targeted for more intensive sampling include well-drained sandy openings, coastal islands, and higher elevations with features such as tablelands and balds, among other Maine plant communities (Gawler and Cutko 2010). Our assumption that York and Cumberland County sandy areas could have high diversity compared to other counties may be confounded by the extent to which habitats are being developed in that part of the state, where changed land use, intensive lawn management, or forest succession occupy areas that were formerly openings with abundant flowers. Bee

associations with vegetation dominated by heaths (Ericaceae, e.g., *Vaccinium*) such as bogs, and other types of wetlands (Anderson and Davis 1998, Davis 1993) need further survey.

New collections should be subjected to identification by expert taxonomists. We urge that if regional bee faunas are to be fully useful assessments then they must be based on careful consideration of taxonomy and behavior (e.g., host plants and habitat associations), with attention to known biogeographic patterns (Goldstein and Scott 2015). Cane (2001) cautioned that ecological studies require correct bee identifications for their validity. Bee label data should include floral records so that host-plant associations and phenology can be summarized, and specimens should ideally include preservation of associated pollen loads for morphological and metagenomic studies. We hope that this first checklist of the bees of Maine can serve as a baseline for measuring the effects of anticipated climate and habitat changes on native and exotic bee populations in coming decades.

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