

# Cleptoparasitic Bees of the Genus *Epeolus* Latreille (Hymenoptera: Apidae) in Canada

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## Abstract

The species of the cleptoparasitic (cuckoo) bee genus *Epeolus* Latreille (Hymenoptera: Apidae) occurring in Canada are revised. A total of 12 species are confirmed, with one additional species (*E. ilicis* Mitchell) listed as possibly occurring in Canada. Morphological comparisons of primary types and continuous variation within species, in addition to DNA barcode sequence analysis of recently collected specimens from across the range of each species support the following proposed synonymies: *E. lanhami* Mitchell, syn. n., and *E. montanus* (Cresson), syn. n., under *E. americanus* (Cresson); *E. gabrielis* (Cockerell), syn. n., *E. geminatus* Cockerell and Sandhouse, syn. n., and *E. hitei* Cockerell, syn. n., under *E. compactus* Cresson; *E. arciferus* Cockerell, syn. n., *E. beulahensis* Cockerell, syn. n., *E. lutzi* Cockerell, syn. n., *E. lutzi dimissus* Cockerell, syn. n., and *E. pilatei* Cockerell, syn. n., under *E. minimus* (Robertson); and *E. humillimus* Cockerell, syn. n., *E. rubrostictus* Cockerell and Sandhouse, syn. n., *E. rufomaculatus* Cockerell and Sandhouse, syn. n., and *E. tristicolor* Viereck, syn. n., under *E. olympiellus* Cockerell. The synonyms of *E. americanus*, *E. compactus*, and *E. minimus* proposed here were first proposed by Richard L. Brumley in an M.Sc. thesis published in 1965, but have until now not been validated. A dichotomous identification key to the Canadian species is presented, and their biology and life history is discussed and contrasted with that of *Triepeolus* Robertson and other cuckoo bees.

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## Introduction

A high proportion (28%) of bees in the family Apidae (Hymenoptera: Apoidea) are cleptoparasites of nest-building bees (Cardinal *et al.* 2010). Cleptoparasitic (or cuckoo) bees appropriate the pollen food stores collected by females of their host species for their own offspring; the cleptoparasite invades the host nest and lays an egg in the brood cell. Subsequently, the host larva or egg (depending on the type of cleptoparasitic bee involved) is killed. Since female cleptoparasitic bees do not collect pollen to feed their brood, they lack the specialized pollen-carrying scopae characteristic of most nest-building bees. Most cleptoparasites are also wasp-like in appearance, exhibiting reduced hairiness, and typically have black and yellow and/or red colouration.

In the Nearctic region, the cleptoparasitic tribe Epeolini (Subfamily Nomadinae) is represented by *Epeolus* Latreille, *Odyneropsis* Schrottky (Griswold and Parker 1999), and *Triepeolus* Robertson (Robertson 1901). Of these, only *Epeolus* and *Triepeolus* occur in Canada, and they are the two most diverse genera in the entire tribe (Rightmyer 2004).

To date, no key to all the Canadian species has been published, although a key to the Epeolini of Ontario, the province with the greatest *Epeolus* diversity, exists (Romankova 2004). I have seen specimens from all provinces and territories in Canada except Newfoundland and Labrador and Nunavut (Map 14). I have verified locality records for 12 species in Canada (Table 1), but

the key provided herein includes a thirteenth (*E. ilicis* Mitchell), which may occur in southern Ontario, whose Canadian voucher specimens (Romankova 2004) cannot be traced. The purpose of the present study is thus to provide a key to all species that might occur in Canada, and to redescribe them.

## Methods

As the sexes in this genus are for the most part monomorphic (other than for typical sexually dimorphic characters), a single identification key for adult *Epeolus* species in Canada is presented. The identification key is based on external morphological differences that should be visible in dry, pinned specimens. In addition, species redescrptions of the sex opposite that of the primary type include only the key differences between females and males.

To clarify species limits and to give additional support for new synonymies reported here, the divergence levels in a 658 bp segment of the COI mitochondrial gene (DNA barcode) (Hebert *et al.* 2003a, b) were used in conjunction with morphology. Barcoding entailed the removal of a leg (the source of genetic material) from a bee for DNA extraction and gene amplification and sequencing at the Canadian Centre for DNA Barcoding (CCDB) in Guelph, Ontario, Canada. Barcode Index Numbers (BINs – automated code numbers given to unique barcode clusters) were assigned to sequences as short as >300 bp, although formal recognition of

barcode compliant sequences requires a minimum length of 500 bp (Ratnasingham and Hebert 2007, 2013). To validate species designations of specimens and to check for contamination errors, sequences with unique BINs were compared to one another and to short, non-compliant sequences that clustered with compliant ones in a neighbour-joining (NJ) tree, based on Kimura's two-parameter distance model (Kimura 1980). Cases involving change in taxonomic status always prioritized morphological evidence over DNA barcoding, and barcoding merely confirmed what was already suspected to be continuous intraspecific variation in morphology. BINs are available for all species recorded in Canada except *E. ilicis* and are provided in the taxonomic treatment for each species. Sequences for "barcoded" specimens are published in BOLD (<http://www.barcodinglife.org>) in the "Epeolus of North America" project, and will be made available on GenBank (<http://www.ncbi.nlm.nih.gov/genbank/>) following a revision of all Nearctic *Epeolus* species north of Mexico.

Anatomical and taxonomic terms used generally follow Michener (2007), except I use the terms frontal and vertexal areas instead of frons and vertex, respectively, following Prentice (1998) and Dumesh and Packer (2013), as these are not clearly delimited structural features. Puncture density is quantified as the interspace (i) relative to the puncture diameter (d). MOD is an acronym for median ocellar diameter, used as a comparative measure for indicating the dimensions of smaller features, especially hair length. F with a number corresponds to one of 10 (for female) or 11 (for male) flagellomeres of the antenna. T with a number corresponds to one of six (for female) or seven (for male) exposed metasomal terga. S with a number corresponds to one of six (for female) or eight (for male) metasomal sterna. I use the term ferruginous to distinguish black or nearly black integument from that which is any of the following colours: light brown, mahogany, reddish brown, red, and rusty orange. All measurements comparing lengths and widths are based on the longest and widest margins of an anatomical feature of a specimen at the highest magnification that would allow measurement in eyepiece micrometer units. I use the term length to describe any measurement along the longitudinal axis of a bee, and width to describe any measurement along the lateral axis, except in reference to the longitudinal extent of the transverse metasomal fasciae, for which I use the term breadth. Measurements of the scape were made excluding the radicle. Rightmyer (2008) proposed several terms specific to epeoline/nomadine bees, which I have adopted (with exceptions) and redefine here for clarity. Paramedian bands are the two longitudinal anterior lines of pale tomentum (pubescence composed of short, matted hairs) on the mesoscutum (extending posteriorly from the

anterior margin of the mesoscutum but not attaining its apex) found in most *Epeolus* species. In *E. canadensis* and *E. compactus* I do not consider as paramedian bands the anteromedial patch of pale tomentum barely separated by the admedian line. The transverse bands of Rightmyer (2008) I refer to as the basal and apical metasomal fasciae. The fasciae of T1 may be connected laterally by a longitudinal band of varying width. Discal patch refers to the dark medial region of T1 covered in brown to black tomentum that may be sparser than the off-white or yellow tomentum forming the basal and apical (when present) fasciae.

Redescriptions are based on primary type specimens, although other specimens (usually non-type sequenced) were referenced for comparison and to fill in information gaps. The description of the sex opposite that of the primary type was based on the allotype or lectoallotype specimen (if available), paratypes, or non-type specimens. Specimens for study were provided by entomological institutions, museums, and university collections across Canada and the United States of America (USA), and are indicated with the following acronyms, with full names provided in parentheses: **AMNH** (American Museum of Natural History, New York, NY), **ANSP** (Academy of Natural Sciences of Drexel University, Philadelphia, PA), **BBSL** (Utah State University USDA Bee Biology and Systematics Laboratory, Logan, UT), **BIML** (Patuxent Wildlife Research Center USGS Native Bee Inventory and Monitoring Lab, Laurel, MD), **CAS** (California Academy of Sciences, San Francisco, CA), **CNC** (Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, ON), **CTMI** (Central Texas Melittological Institute, Austin, TX), **CUIC** (Cornell University Insect Collection, Ithaca, NY), **DEBU** (University of Guelph Insect Collection, Guelph, ON), **EMEC** (University of California Essig Museum of Entomology, Berkeley, CA), **FMNH** (Field Museum of Natural History, Chicago, IL), **FSCA** (Florida State Collection of Arthropods, Gainesville, FL), **INHS** (Illinois Natural History Survey, Champaign, IL), **KUNHM** (University of Kansas Biodiversity Institute and Natural History Museum, Lawrence, KS), **NCSU** (North Carolina State University Insect Museum, Raleigh, NC), **PCYU** (Packer Collection at York University, Toronto, ON), **ROM** (Royal Ontario Museum, Toronto, ON), **RSKM** (Royal Saskatchewan Museum, Regina, SK), **UCR** (University of California Entomology Research Museum, Riverside, CA), and **USNM** (U.S. National Entomological Collection, National Museum of Natural History, Washington, D.C.).

In lists of specimens examined, the records from different localities are always separated with a semi-colon. A comma between records denotes that the collection locality is the same but at least one of the

following is different: date, collector, and entomological institution. With regard to specimen occurrence records, there were instances in which locality data were rather vague, particularly true of older records, and localities straddled county lines. In such cases, I omitted the county name and indicated the contents of the specimen labels. The same was true if I was unable to pinpoint an indicated locality on a Google map.

The key and redescriptions are accompanied by images taken with a Canon EOS 40D digital SLR camera using the Visionary Digital BK Plus imaging system, focus stacked in Helicon Focus, and edited in PaintShop Pro. In preparation for study and imaging, terminalia were excised, cleared in KOH for up to six hours, and ultimately stored in glycerine, later transferred to genitalia vials pinned under the associated specimens.

Range maps were constructed in RStudio (version 0.97.248) using the following packages installed in R (version 2.15.0): *maptools* (Bivand and Lewin-Koh 2014), *raster* (Hijmans 2014), *rgdal* (Bivand *et al.* 2014), and *rgeos* (Bivand and Rundel 2014). Maps of Canada and the USA were plotted using projected shapefiles obtained from Statistics Canada (2015) and the U.S. Census Bureau (2015). Points of occurrence for a particular species are based on GPS coordinates accurate to at least two decimal degrees. Using customized functions in R, continuous ranges were estimated by forming a splined convex hull polygon, a method also used for preparing distribution maps for the International Union for Conservation of Nature (IUCN 2012), of georeferenced occurrence records (from the literature and observed voucher specimens).

### Taxonomy

Specimens of *Epeolus* species are similar to those of *Triepeolus* in general appearance, and males can be particularly difficult to distinguish. In *Epeolus*, the male pygidial plate is generally wider basally, with the lateral margins convergent toward the apex (e.g. as in *Epeolus ainsliei* Crawford [Figure 1a] and *E. olympiellus* Cockerell [Figure 1b]). In *Triepeolus*, the pygidial plate is generally comparatively narrow (e.g. as in *Triepeolus pectoralis* (Robertson) [Figure 1c] and *T. lunatus* (Say) [Figure 1d]), and its lateral margins are typically somewhat concave or sinuate. Female *Epeolus* have a very distinct sixth sternum, which is often partly visible in pinned specimens even without dissection (Figure 2a) as two convergent spatulate lateral processes bearing setae modified into pointed denticles; the processes are joined by a large lobe-like disc, which is usually not visible unless excised (Figure 2b). By contrast, S6 in female *Triepeolus* has a pair of narrow, elongate, forceps-like processes with coarse spine-like setae, separated by a disc reduced to a narrow transverse

bar (Figure 2c, 2d). The apices of these processes and their long spine-like setae are often visible without dissection in pinned specimens. These morphological differences between females of *Epeolus* and *Triepeolus* are presumably related to host specialization (Rightmyer 2004) and the mechanism whereby the female oviposits into the cell wall of its host's nest or between the caps separating brood cells (Roig-Alsina 1991). The spinose setae of *Triepeolus* seem to be for digging holes in the soil walls of host cells (Torchio 1986) and/or may have a tactile function (Rightmyer 2004). In *Epeolus*, tooth-like setae on the lateral processes and the rigid attachment of these processes to the disc of the sternum indicate a saw-like function necessary for breaking through the tough polyester lining that separates brood cells and coats the cell walls of its host nest (Torchio and Burdick 1988). In at least one species of *Epeolus*, this process is aided by a glandular secretion that dissolves the polyester lining of the host nest on contact, and later resolidifies to close the gap (Torchio and Burdick 1988). Females of the two genera may be further distinguished by the pseudopygidial area – the medioapical region of T5 that generally changes slope (and may be elevated) from the rest of the tergum, and whose disc is flat or somewhat depressed and usually covered in shiny short hairs that are often uniform in length (Michener 2007). In *Epeolus*, the shape of this area is either campanulate (Figure 3a) or lunate (Figure 3b, 3c, 3d, 3e), whereas in *Triepeolus* it is more variable, and may be ovate or round (Figure 2c), quadrate, triangular, a shape intermediate between triangular and quadrate, or a shape more complex in outline. With one notable exception, the pseudopygidial area of *Triepeolus* is always relatively longer than in *Epeolus* (Rightmyer 2008); in the unusual Mesoamerican *T. epeolurus* Rightmyer, the transverse band of metallic setae on the pseudopygidial area (Figure 3f) is remarkably similar to that of some species of *Epeolus*, but is concave rather than arched in dorsal view. Another unusual feature of *T. epeolurus* is that the pseudopygidial setae reflect silver, whereas in most *Triepeolus* they reflect a golden colour (Rightmyer 2004).

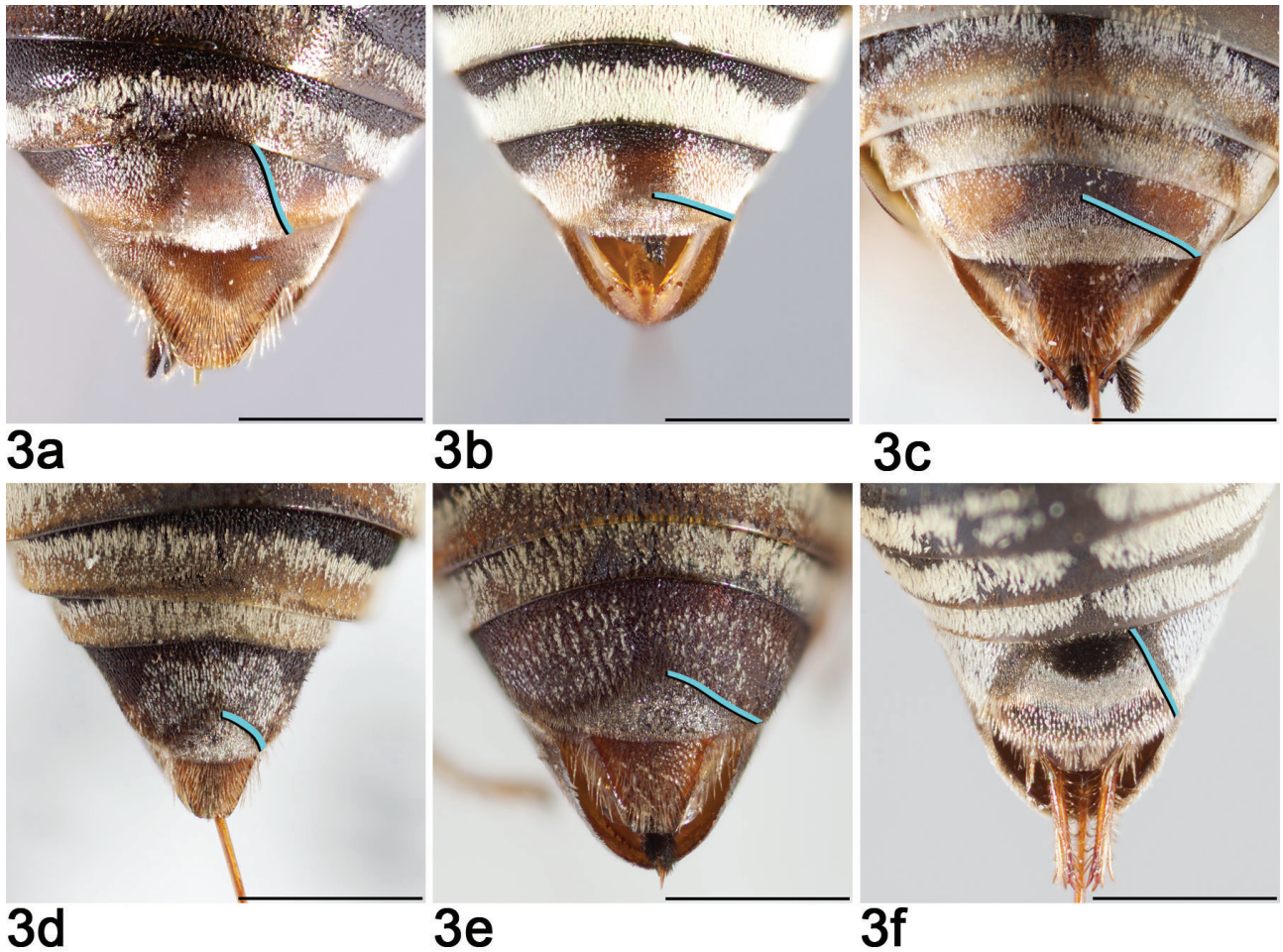
*Epeolus* is represented by 102 valid species worldwide (Integrated Taxonomic Information System on-line database, <http://www.its.gov>) [Retrieved 11.ii.2016]. Based on my own knowledge in combination with records available on Discover Life (Ascher and Pickering 2016), 45 species were until the date of this publication recognized as occurring in North America excluding Mexico and the West Indies. The first species described as being a North American *Epeolus*, *E. mercatus* Fabricius, cannot be confidently assigned to *Epeolus* or *Triepeolus*, as the original description is vague and the type material apparently has been lost (Rightmyer 2008). Therefore, the numbers above do not include *Epeolus*



**Figure 1.** Morphological differences in the T7 of male *Epeolus* (a, b) and *Triepeolus* (c, d). Pygidial plate is shown for pinned specimens of a) *E. ainsliei* and c) *T. pectoralis* (Scale bars = 0.5 mm) (dorsal view). Pygidial plate is shown entirely removed and cleared in KOH for specimens of b) *E. olympiellus* (Scale bar = 0.5 mm) and d) *T. lunatus* (Scale bar = 1 mm) (dorsal view).



**Figure 2.** Morphological differences in the terminalia of female *Epeolus* (a, b) and *Triepeolus* (c, d). S6 with exposed lateral processes is shown for pinned specimens of a) *E. ainsliei* bearing setae modified into pointed denticles and c) *T. pectoralis* bearing coarse spine-like setae (Scale bars = 0.5 mm) (dorsal view). S6 is shown entirely removed and cleared in KOH for specimens of b) *E. olympiellus* and d) *T. lunatus* (Scale bars = 1 mm) (dorsal view).



**Figure 3.** Pseudopygidial area of female Epeolini in dorsal view: a) *E. ilicis* (campanulate), b) *E. ainsliei* (lunate and wider than long), c) *E. olympiellus* (lunate and wider than long), d) *E. pusillus* (lunate and nearly as long as wide), e) *E. scutellaris* (lunate and wider than long), and f) *T. epeolurus* (unique and *Epeolus*-like in having a transverse, curved band of silvery setae). Scale bars = 1 mm. The pseudopygidial area is indicated by an area elevated from the rest of the tergum covered partially or entirely in shiny short hairs uniform in length (posteromesad the light blue lines).

*mercatus* Fabricius. Nonetheless, it would be surprising if this species did not represent another described species in one of these two genera. Brumley (1965) described an additional seven species (all from the American Southwest), but as he did not publish his work his names cannot be formally recognized. Apparently, one of these species, occurring in Arizona and Texas, USA, had already been described by Smith (1879) from Oaxaca, Mexico (Rightmyer 2008). None of the seven “new” species, however, are known to range into Canada. Despite the diversity of *Epeolus* in North America, with more known species than any other continent, the genus is poorly understood.

Several North American species of *Epeolus* were originally described as belonging to *Phileremus* Latreille and *Triepeolus*. *Phileremus* (*Ammobates* Latreille subgenus *Ammobates* Latreille s. str. in Michener 2007) included cleptoparasitic bee species in which the fore wing has two rather than three submarginal cells. This character is variable even within species (and sometimes specimens) of *Epeolus*, and *Phileremus* contained species from a large number of genera (mostly Nomadinae), including *Ammobates*, *Ammobatoides* Radoszkowski, *Biastes* Panzer, *Epeolus*, *Dioxys* Lepeletier and Serville, *Holcoposites* Ashmead, *Melanempis* Saussure, *Neolarra* Ashmead, *Neopasites* Ashmead, and *Pasites* Jurine (Ascher and Pickering 2016).

I synonymize 14 previously proposed names under those of four valid species. *Epeolus americanus* and *E. minimus* are similar to some species that are not treated here because they occur south of Canada only. They include a cryptic species revealed by DNA barcoding (BOLD:ACZ2142) within the “*americanus* group”, whose subtle morphological differences and collection date and locality record within Los Angeles County, California are shared with the holotype of *E. asperatus* Cockerell, which I have seen and examined. Also similar is the holotype of *E. melectimimus* Cockerell and Sandhouse. *Epeolus barberiellus* Cockerell is another species similar to *E. americanus*, with unique physical attributes and known to occur only in New Mexico and Texas. A species very similar to *E. minimus* is *E. banksi* (Cockerell), with unique physical attributes, and apparently restricted to parts of the mid-Atlantic and southeastern States. DNA barcode data are not yet available, but morphology suggests that specimens identified as *E. banksi* are clearly distinct from *E. minimus*. The names *E. americanus* and *E. minimus* antedate those of the abovementioned similar or cryptic species, and for the reasons stated herein I am confident that the new synonymies proposed are correct for the taxa in question, and do not apply to any other species.

## Biology

All *Epeolus* species for which host use has been assessed are cleptoparasites of *Colletes* Latreille, the type genus of the family Colletidae (Michener 2007). The reproductive biology and immature stages of *Epeolus* were first described for *E. pusillus* Cresson in association with *Colletes ciliatoides* Stephen (Torchio 1965) and *C. compactus compactus* Cresson (Rozen and Favreau 1968). Both host species construct a single cell at the end of a lateral tunnel that branches from the meandering, mostly vertical main tunnel. Rozen and Favreau (1968) noted female *E. pusillus* flying swiftly 15–20 cm above the ground, slowing down over what presumably to them seemed to be nest entrances – one female flew quickly toward a burrow from which a host *Colletes* had previously been collected, descended, and re-emerged within a minute. When Rozen and Favreau (1968) excavated the brood cell, they found that it had an *Epeolus* egg attached, positioned between the inner and outer envelopes of the cell lining.

There is some indication that female *Epeolus* repeatedly visit and inspect the nest or nests of their host species of *Colletes*, likely to confirm the suitability of the nest site and ensure that they are present at the right time for oviposition. For instance, Graenicher (1906) reported that upon discovering a *C. eulophi* Robertson nest (about midday), a female *E. minimus* (Robertson) began crawling over the ground with quivering wings. The female approached the nest from various angles without entering. The female *Epeolus* then perched motionless on a small plant, or twig at times, about 20 cm above the nest entrance while the female *Colletes* returned with provisions. The female *Epeolus* preened herself at that time, and again after the host female left before the *Epeolus* herself entered the nest for about one minute. The female then emerged and examined the surrounding area. The process of examining the nest entrance, perching, entering the nest, and examining the surrounding area was repeated within a particular day and on different days (confirmed by marking of the female *Epeolus* specimen). To be successful, the female *Epeolus* must avoid detection by the host. In Central Europe, Bogusch (2003) twice observed a female *C. similis* Schenck successfully defending a nest from a female *E. variegatus* (L.).

Like other Nomadinae, *Epeolus* females enter unsealed cells while the host is foraging during the nest provisioning stage. Whereas *Colletes* eggs were found to be attached to the inner polyester lining of the cell, the egg of *E. pusillus* was laid between the inner and outer polyester linings of the double-layered nest lining of its host (Rozen and Favreau 1968). Where the egg is laid depends on the host and type of nest constructed. Torchio and Burdick (1988) documented two strategies used

by *E. compactus* Cresson. Its host species, *C. kincaidii* Cockerell, may reuse abandoned nests. In this case, *E. compactus* inserts its eggs between the inner lining of the burrow and residual lining (assuming it is intact) from previous nest use, because there is sufficient space and presumably also to protect the egg from getting wet. Interestingly, rates of cleptoparasitism were higher for reused nests. Torchio and Burdick (1988) found overall rates of nest parasitism of *C. kincaidii* by *E. compactus* to be as high as nearly 18%. If the nest was newly founded by the female *Colletes* host (and only a single polyester layer separates the cell from bare ground), *E. compactus* instead attaches its eggs to the caps of completed cells separating the brood cells (Torchio and Burdick 1988). Although the egg is exposed within the already completed cell, the larva hatches into the cell that was incomplete when the parent *Epeolus* oviposited. In some instances, multiple eggs may be deposited through a cell cap, but it is not known if these belong to the same or multiple female *Epeolus*. Oviposition through the cellophane-like cell lining of another colletid genus (*Scrapter* Lapeletier

and Serville) has similarly been documented in the nomadine cleptoparasitic genus *Sphecodopsis* Bischoff (Rozen and Michener 1968 – as *Pseudodichroa*). Rozen (1968) suggested that *Sphecodopsis* females puncture the lining and poke a hole in the sand outside the cell (where the egg is to be embedded) using the heavily sclerotized, median process of S6.

Rozen and Favreau (1968) observed that when the larva of *E. pusillus* hatched, it immediately found and killed the host egg. Similarly, Torchio and Burdick (1988) found that the larva of *E. compactus* killed the host egg or larva using its long, sickle-shaped mandibles, and combated the other *Epeolus* larvae in superparasitized host cells until a single survivor remained. In the case of *E. pusillus*, the rate of larval development was found to be much faster than that of the host (*C. compactus compactus* in this case), and by the time the cleptoparasite larva went into diapause, neighbouring representatives of its host species had consumed less than half of their provisions (Rozen and Favreau 1968).

Table 1. *Epeolus* in Canada and associated *Colletes* host species. The nature of the evidence for all confirmed, hypothesized (based on personal assessment), or presumed (suspected and published) associations is indicated in the Discussion section of the taxonomic treatment of each species. Unless otherwise stated, confirmed associations are based on evidence of oviposition by female *Epeolus* within a *Colletes* nest, and hypothesized and presumed associations are based on spatial and temporal co-occurrence.

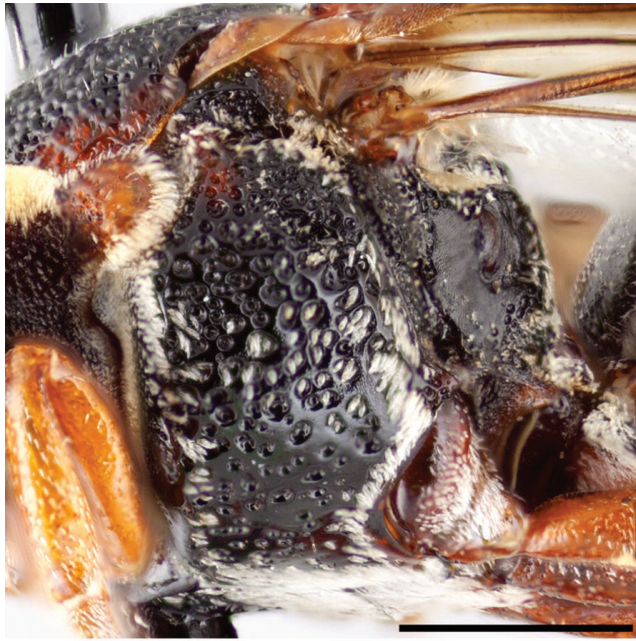
Cleptoparasite species	Associated host species	Reference(s)
<i>E. ainsliei</i>	<i>C. americanus</i> Cresson and/or <i>C. susanna</i> Swenk (presumed)	Wolf and Ascher (2009)
<i>E. americanus</i>	<i>C. consors mesocopus</i> Swenk (hypothesized based on shared habitat in Alaska and flight season, although at least three other Alaskan <i>Colletes</i> spp. are known)	Armbruster and Guinn (1989)
<i>E. autumnalis</i>	<i>C. compactus compactus</i> Cresson (presumed)	Ascher et al. (2014)
<i>E. bifasciatus</i>	<i>C. latitarsis</i> Robertson (presumed)	Mitchell (1962)
<i>E. canadensis</i>	Possibly <i>C. kincaidii</i> Cockerell (hypothesized)	MacKay and Knerer (1979)
<i>E. compactus</i>	<i>C. kincaidii</i> Cockerell (confirmed)	Torchio and Burdick (1988)
<i>E. ilicis</i>	<i>C. brimleyi</i> Mitchell (confirmed)	Rozen (1989)
<i>E. interruptus</i>	<i>C. aestivalis</i> Patton (presumed for unclear reasons)	Brumley (1965)
<i>E. lectoides</i>	<i>C. latitarsis</i> Robertson and <i>C. nudus</i> Robertson (presumed)	Shapiro and Droegge (2010) Ascher et al. (2014)
<i>E. minimus</i>	<i>C. eulophi</i> Robertson (presumed based on female <i>Epeolus</i> entering <i>Colletes</i> nest)	Graenicher (1906)
<i>E. pusillus</i>	<i>C. ciliatoides</i> Stephen and <i>C. compactus compactus</i> Cresson (confirmed)	Torchio (1965) Rozen and Favreau (1968)
<i>E. scutellaris</i>	<i>C. simulans armatus</i> Patton (presumed)	Ascher et al. (2014)
<i>E. olympiellus</i>	<i>C. hyalinus</i> Provancher (hypothesized based on co-occurrence)	pers. comm. Cory Sheffield



**Key to species of *Epeolus* in Canada**

- 1 Mesopleuron with punctures in ventrolateral half sparse ( $i > 1d$ ), the interspaces shining (Figure 4a, 4b); AND axilla with free portion at least as long as 1/3 its entire medial length (Figure 5a, 5b) ..... 2
- Mesopleuron with punctures in ventrolateral half dense ( $i \leq 1d$ ) (Figure 4c) or mesopleuron rugose with punctures ill-defined, the interspaces shining or dulled by surface sculpture; IF most punctures conspicuously sparser ventrolaterally (Figure 4d), THEN axilla with free portion clearly less than 1/3 as long as its entire medial length (Figure 5c) ..... 3
- 2(1) Head with frontal area bearing a pair of granulose protrusions, each located near upper mesal margin of compound eye (Figure 6a). Mesopleuron (excluding hypoepimeral area) with larger punctures (diameter of some nearly equal to diameter of lateral ocellus) in upper half than ventrolateral half (Figure 4a). T1 with broad, yellow basal fascia, T2 with similar but narrower apical fascia, metasoma otherwise without fasciae (Figure 7a) ..... *E. bifasciatus* Cresson
- Head with frontal area without protrusions (Figure 6b). Mesopleuron with punctures of similar size throughout (Figure 4b). T1–T4 each with conspicuous pale apical fascia (Figure 7b) ..... *E. lectoides* Robertson
- 3(1) Metanotum with blunt median process, sometimes obscured by tomentum (Figure 8a). T1 with discal patch forming rounded triangle with lateral sides concave (Figure 9a). Mesopleuron with punctures in ventrolateral half sometimes so well separated ( $i > 1d$ ) that upper half appears to be more densely punctate than ventrolateral half (Figure 4d) ..... *E. interruptus* Robertson
- Metanotum without process (Figure 8b). T1 not as above; IF discal patch triangular, THEN with convex or relatively straight sides (Figure 9b, 9c). Mesopleuron with most interspaces between punctures small ( $i \leq 1d$ ) (Figure 4c) or mesopleuron rugose, with punctures ill-defined ..... 4
- 4(3) Mandible without preapical angulation or tooth (Figure 10a). Axilla with free portion at least as long as 2/5 its entire medial length (usually somewhat longer) and distinctly hooked (medial margin of free portion concave and diverging from side of mesoscutellum) (Figure 5d, 5e) ..... 5
- Mandible with preapical tooth (Figure 10b) or obtuse angle appearing like a tooth (Figure 10c). Axilla with free portion clearly less than 2/5 its entire medial length and relatively straight along medial margin (Figure 5f) ..... 6
- 5(4) Head with preoccipital ridge joining hypostomal carina (approximately at 2/5 length of proboscoidal fossa) (Figure 11a). Metasomal terga with punctures dense ( $i < 1d$ ) (Figure 12a). T5 with pseudopygidial area of female lunate, with apex at least twice as wide as medial length (Figure 3b) ..... *E. ainsliei* Crawford
- Head with preoccipital ridge not joining hypostomal carina (Figure 11b). Metasomal terga with punctures sparser ( $i = 1-2d$ ), the terga appearing shiny due to larger interspaces (Figure 12b). T5 with pseudopygidial area of female distinctly campanulate, with apex less than twice as wide as medial length (Figure 3a) ..... *E. ilicis* Mitchell
- 6(4) Axilla with tip extending well beyond mid-length of mesoscutellum. Axilla large and robust (axillar lateral length/mesoscutellar width ratio  $> 0.40$ ), its lateral margin arcuate (except sometimes in *E. autumnalis*) (Figure 13a, 13b). T1 in dorsal view with discal patch so wide that the longitudinal band barely visible (its width less than half the breadth of apical fascia) (Figure 9d) ..... 7
- Axilla with tip at most extending to 1/2 length of mesoscutellum. Axilla small (axillar lateral length/mesoscutellar width ratio  $< 0.40$ ), its lateral margin relatively straight (Figure 13c, 13d). T1 in dorsal view with longitudinal band at least half as wide as breadth of apical fascia (Figure 9b, 9c, 9e, 9f) ..... 9

- 7(6) Axilla with tip well short of line of pale tomentum marking posterior margin of mesoscutellum; axilla and mesoscutellum entirely black (Figure 5f) ..... *E. autumnalis* Robertson
- Axilla with tip attaining or surpassing line of pale tomentum marking posterior margin of mesoscutellum (may almost attain line at medioapical extent of mesoscutellum); axilla (except sometimes in *E. pusillus*) and sometimes mesoscutellum ferruginous to some degree (Figure 13a, 13b) ..... 8
- 8(7) Mesopleuron of male entirely obscured by white tomentum (Plate 1, Figure L). Axilla of both sexes black in part; mesoscutellum entirely black (Figure 13a). T5 with pseudopygidial area of female with apex less than twice as wide as medial length (Figure 3d)..... *E. pusillus* Cresson
- Mesopleuron of male obscured by white tomentum only in upper half, with a large, sparsely hairy circle occupying much of ventrolateral half (Plate 1, Figure M). Axilla of both sexes partially to entirely ferruginous; mesoscutellum entirely black to entirely ferruginous (Figure 13b). T5 with pseudopygidial area of female with apex at least twice as wide as medial length (Figure 3e) ..... *E. scutellaris* Say
- 9(6) F2 of female not more than  $1.1 \times$  as long as wide (Figure 14a). Pronotal lobe dark brown to black (Plate 1, Figure B). Axilla with tip close to lateral margin of mesoscutellum, with free portion at most  $1/4$  as long as its medial length (Figure 13c). T1 in dorsal view with longitudinal band typically more than  $1.1 \times$  as wide as breadth of apical fascia (Figure 9e)..... *E. americanus* (Cresson)
- F2 of female at least  $1.2 \times$  as long as wide (Figure 14b). Pronotal lobe ferruginous (except sometimes in *E. minimus*) (Plate 1, Figures E, F). Axilla with tip clearly separated from lateral margin of mesoscutellum, with free portion more than  $1/4$  as long as its medial length (Figure 13d). T1 in dorsal view with longitudinal band at most  $1.1 \times$  as wide as breadth of apical fascia (Figure 9b, 9c, 9f) ..... 10
- 10(9) Mesoscutum with anteromedial patch of pale tomentum chevron-, horseshoe-, or V-shaped (convergent apically) (Figure 15a). T2 with fascia without lobe-like anterolateral extensions, although fascia may be broader laterally with hairs sparser basally (Figure 9b, 9c, 9f) ..... 11
- Mesoscutum with paramedian band or extensively obscured by tomentum (Figure 15b, 15c). T2 with fascia with lobe-like anterolateral extensions (Figure 16a, 16b) ..... 12
- 11(10) T1 with median triangular or semicircular discal patch (Figure 9b, 9c); AND metanotum with median patch of black tomentum that may be as wide as lateral patch of pale tomentum (Figure 17a) [Atlantic and Central provinces] ..... *E. canadensis* Mitchell
- T1 with median quadrangular discal patch (Figure 9f). Metanotum entirely covered in pale tomentum or with median interruption of sparser or darker tomentum narrower than width of lateral patch (Figure 17b) [Western provinces] ..... *E. compactus* Cresson
- 12(10) T3 and T4 with fasciae not broken laterally, and complete or narrowly separated medially (Figure 16a). Labrum all black or bright-to-faded orange apically to entirely; scape, pedicel, and F1 all brown or orange in part (Figure 18a). Legs, except foreleg, typically entirely orange from trochanters to tarsi (Plate 1, Figure J).....  
..... *E. minimus* (Robertson)
- T3 and T4 with fasciae broken or at least narrowed laterally, as well as medially (Figure 16b). Labrum all black or with brown apical and lateral margins; antenna all brown (Figure 18b). Legs dark in general (at least all coxae to femora mostly to entirely black) (Plate 1, Figure K)..... *E. olympiellus* Cockerell



4a



4b

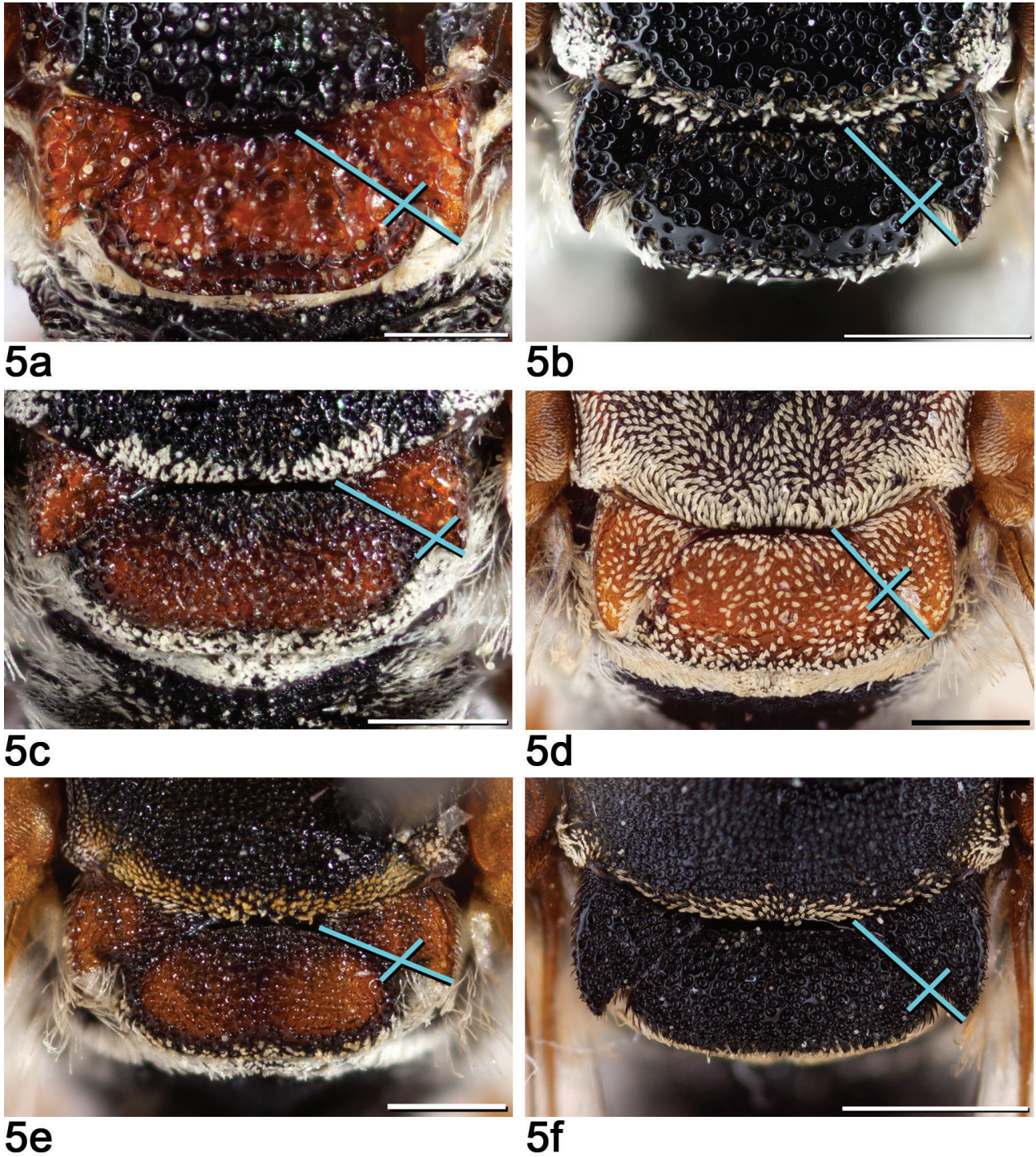


4c



4d

**Figure 4.** Mesopleuron (lateral view) of female a) *E. bifasciatus* showing sparse punctation with punctures larger in upper half than ventrolateral half, b) *E. lectoides* showing sparse punctation with punctures of similar size throughout, c) *E. autumnalis* showing dense punctation with punctures of similar size throughout, and d) *E. interruptus* showing sparse punctation with punctures of similar size throughout. Scale bars = 1 mm.



**Figure 5.** Variation in length of free portion of axilla relative to axillar medial length in dorsal view of a) female *E. bifasciatus* (Scale bar = 0.5 mm), b) female *E. lectoides* (Scale bar = 1 mm), c) female *E. interruptus* (Scale bar = 0.5 mm), d) female *E. ainsliei* (Scale bar = 0.5 mm), e) female *E. ilicis* (Scale bar = 0.5 mm), and f) female *E. autumnalis* (Scale bar = 1 mm).



6a

6b

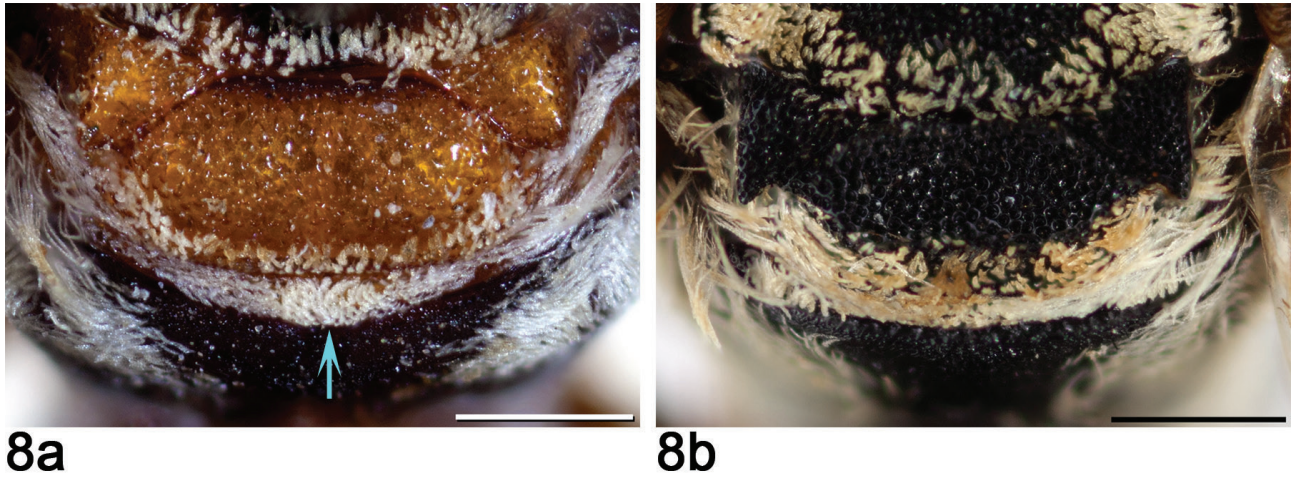
**Figure 6.** Head with frontal area of a) male *E. bifasciatus* showing pair of granulate protrusions and b) female *E. lectoides* without protrusions. Scale bars = 1 mm.



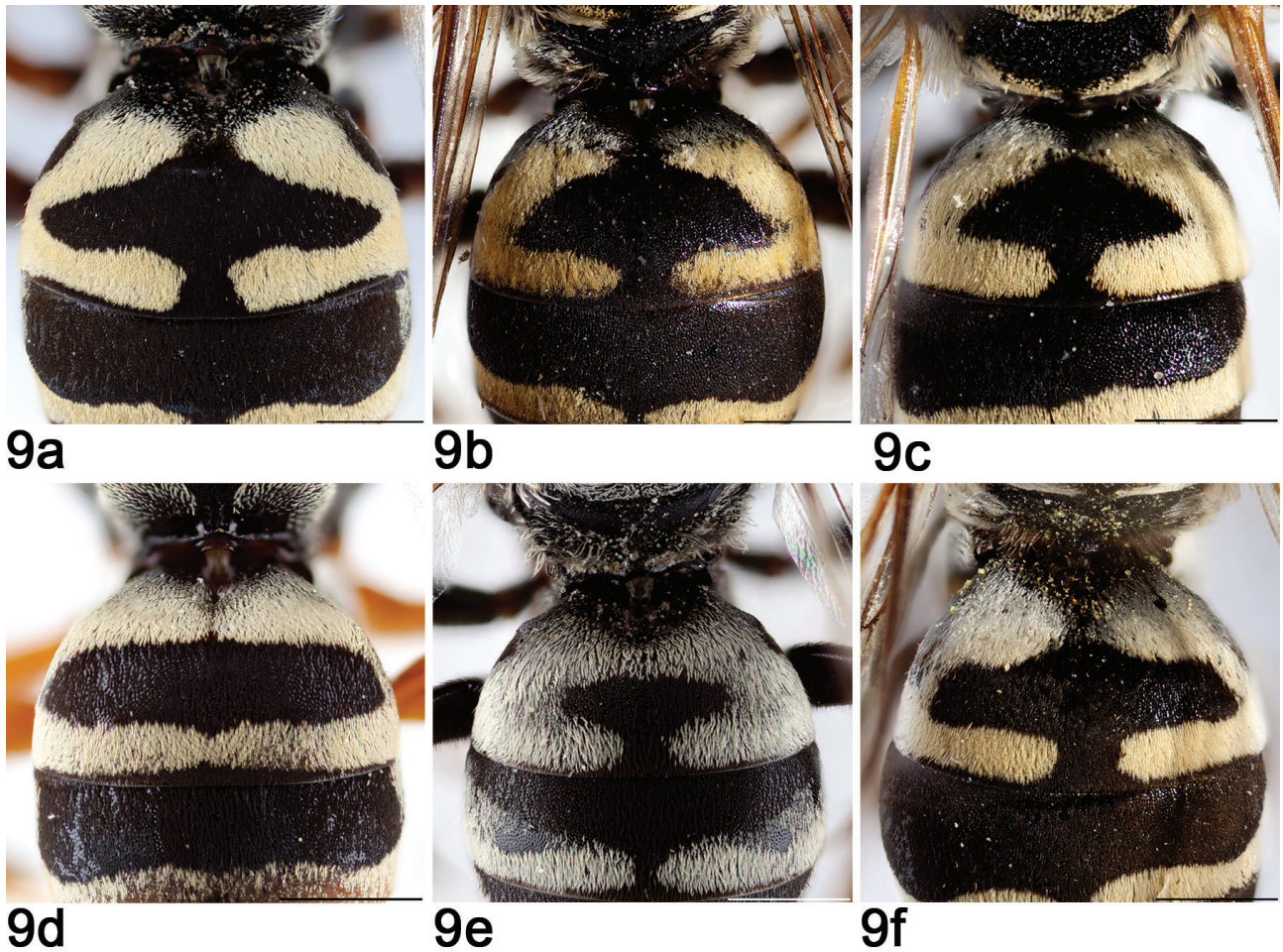
7a

7b

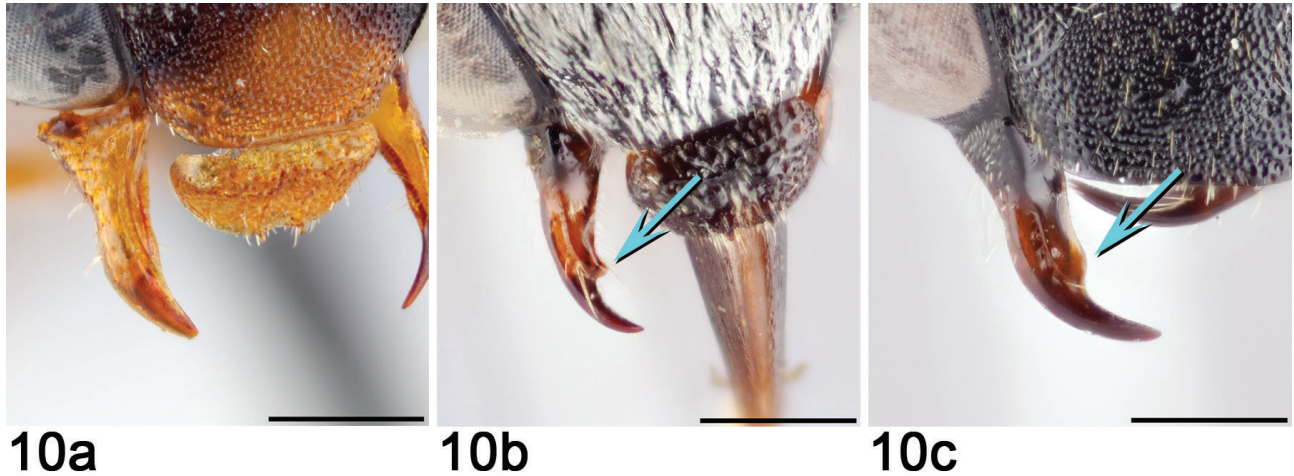
**Figure 7.** Metasoma of a) female *E. bifasciatus* (Scale bar = 1 mm) and b) female *E. lectoides* (Scale bar = 3 mm) in dorsal view.



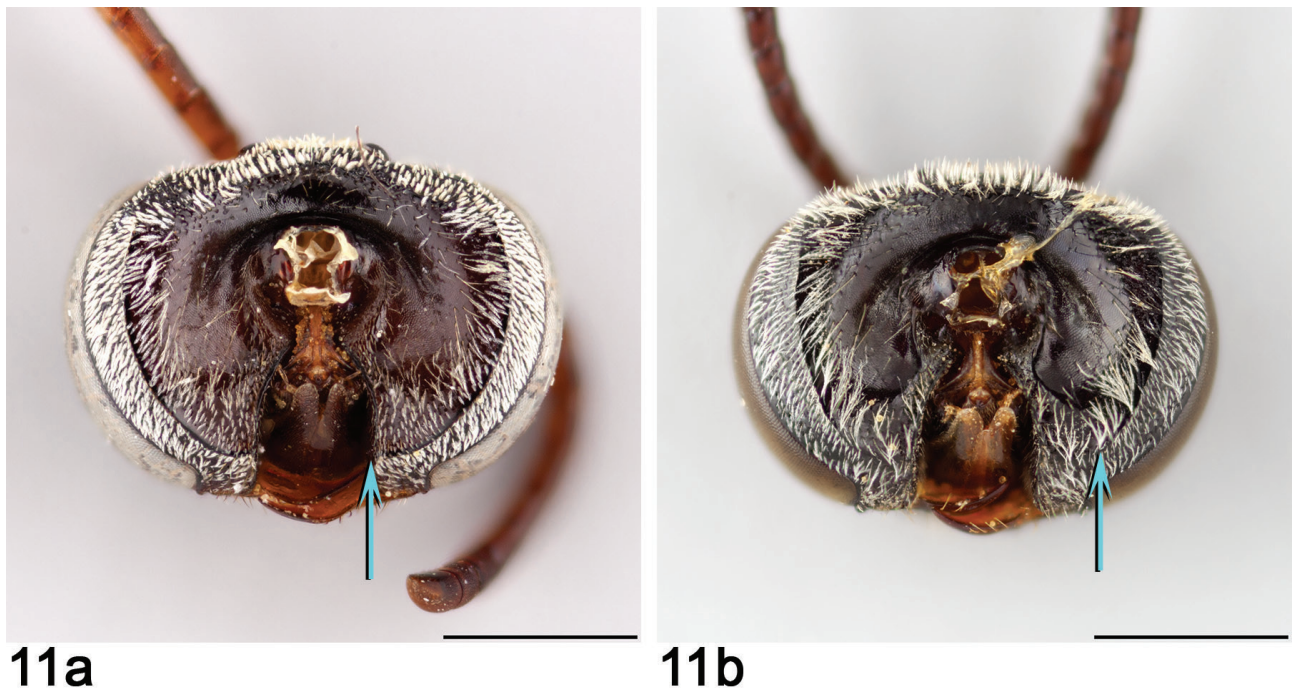
**8a** **8b**  
**Figure 8.** Mesosoma (posterior half in dorsal view) illustrating metanotum that is a) with a blunt median process in female *E. interruptus*, and b) without a process and flat in female *E. minimus*. Scale bars = 0.5 mm.



**Figure 9.** T1 at base of metasoma (dorsal view) of a) male *E. interruptus* illustrating triangular discal patch with concave lateral sides, b) female *E. canadensis* illustrating semicircular discal patch, c) male *E. canadensis* illustrating triangular discal patch, d) female *E. pusillus* illustrating wide rectangular discal patch (longitudinal band barely visible in dorsal view), e) female *E. americanus* illustrating narrow quadrangular discal patch, and f) female *E. compactus* illustrating quadrangular discal patch of intermediate width (longitudinal band clearly visible in dorsal view). Scale bars = 1 mm.

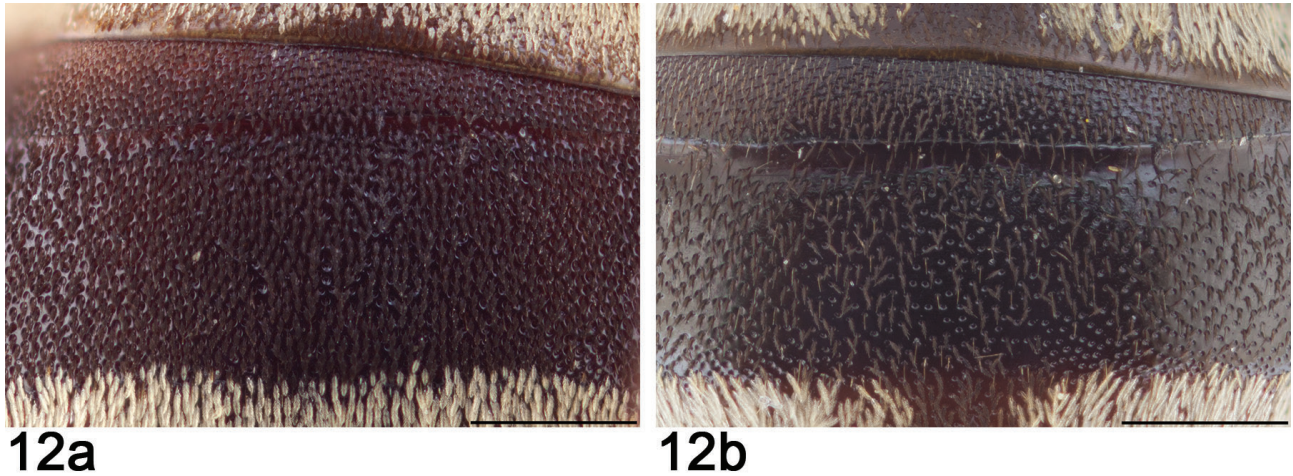


**Figure 10.** Lower faces of *Epeolus* spp. showing the mandible a) without a preapical angulation or tooth in female *E. ainsliei*, b) with a preapical tooth in male *E. compactus*, and c) with an obtuse angle appearing like a tooth in female *E. autumnalis*. Scale bars = 0.5 mm.

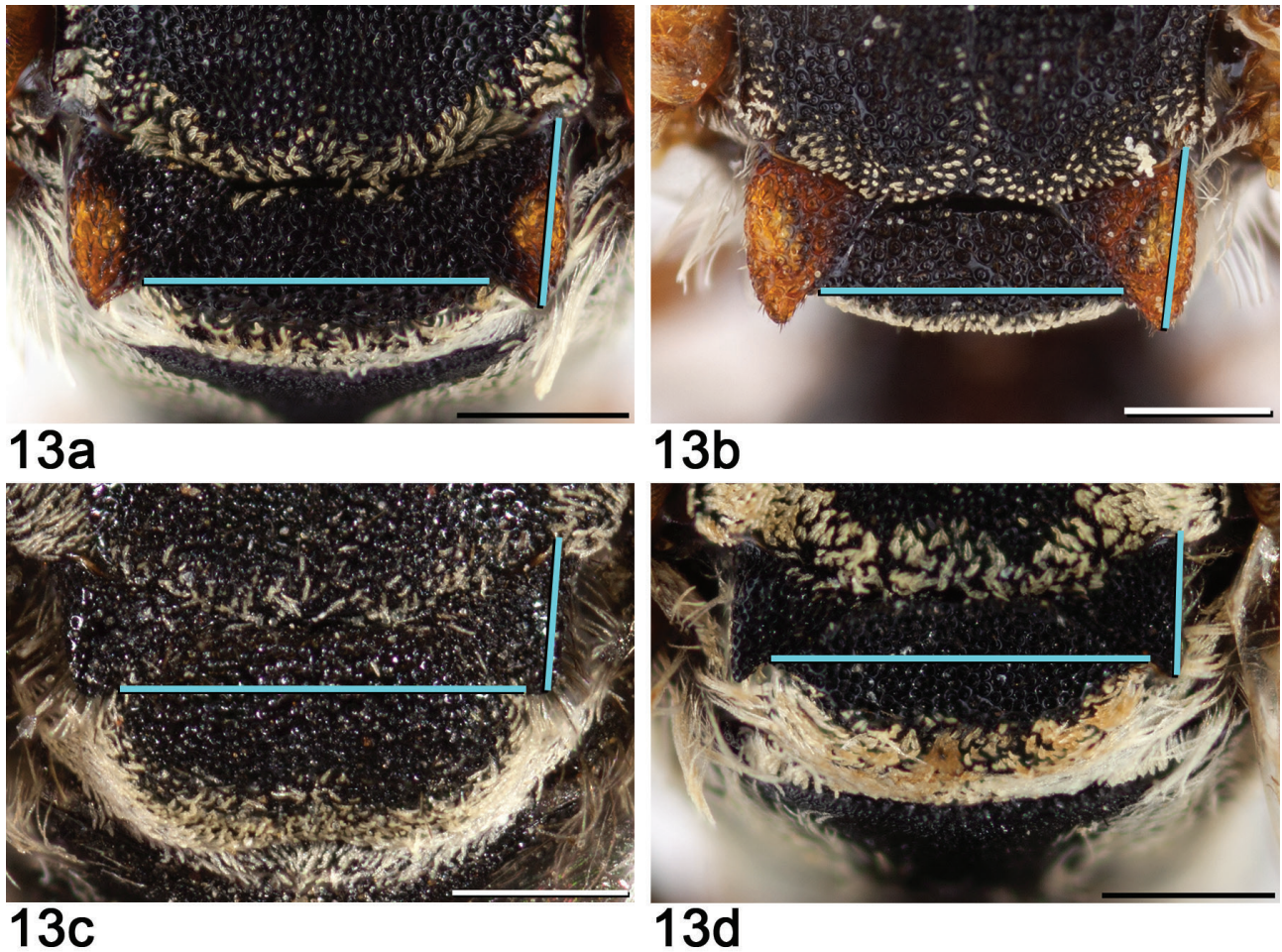


**Figure 11.** Head (posterior view) removed from a) female *E. ainsliei*, in which the preoccipital ridge joins the hypostomal carina, and b) male *E. ilicis*, in which the preoccipital ridge does not join the hypostomal carina (arrow indicates the maximum extent of the carina). Scale bars = 1 mm. Note that these features can be seen without having to detach the head.





**Figure 12.** T2 (medial portion in dorsal view) of a) female *E. ainsliei* showing dense punctation ( $i < 1d$ ) and b) male *E. ilicis* showing sparser punctation ( $i = 1-2d$ ). Scale bars = 0.5 mm.



**Figure 13.** Variation in length of lateral margin of axilla versus width of mesoscutellum between axillae posteriorly in dorsal view of a) female *E. pusillus*, b) male *E. scutellaris*, c) female *E. americanus*, and d) female *E. minimus*. Scale bars = 0.5 mm.



14a

14b

**Figure 14.** Antennae (basal portion) of female *Epeolus* spp. illustrating relative length to width of F2: a) *E. americanus*, with F2 as wide as long, or nearly so, and b) *E. olympiellus*, with F2 noticeably longer than wide. Scale bars = 0.5 mm.



15a

15b

15c

**Figure 15.** Variation in mesoscutal pubescence (dorsal view) among males of a) *E. compactus*, b) *E. minimus*, and c) *E. olympiellus*. Scale bars = 1 mm.



16a



16b

**Figure 16.** Metasoma of female (dorsal view) illustrating variation in fasciae on T3 and T4: a) *E. minimus*, in which T3 and T4 are with complete fasciae, and b) *E. olympiellus*, in which T3 and T4 are with fasciae that are separated or greatly narrowed medially and laterally. Scale bars = 1 mm.



17a



17b

**Figure 17.** Metanotum of male (posterior view) showing a) the presence of a median patch of black tomentum nearly as wide as lateral patches of pale tomentum in *E. canadensis*, and b) the presence of a median interruption of darker tomentum narrower than the width of lighter lateral patches in *E. compactus*. Scale bars = 1 mm.



18a



18b

**Figure 18.** Head of female (frontal view) a) *E. minimus* showing extensive orange colouration on the labrum and antennae, and b) *E. olympiellus*, in which the labrum and antennae are black (except for some small brown markings). Scale bars = 1 mm.

## Taxonomic treatment

### *Epeolus ainsliei* Crawford, 1932

Figures 1a, 2a, 3b, 5d, 10a, 11a, 12a;

Plate 1, Figure A; Plate 2, Figure A; Plate 3, Figure A;

Map 1

*Epeolus ainsliei* Crawford, 1932. Proc. Entomol. Soc. Wash. 34: 74 (♀).

**Primary type specimen.** Holotype ♀ (USNM, catalog number: 534035). **Collection information.** USA: Iowa: Sioux City, 15.vii.1922, C.N. Ainslie.

### Diagnosis

Both sexes of *E. ainsliei* can be readily identified by the following combination of features: preoccipital ridge joining hypostomal carina; axilla distinctly hooked, its lateral margin arcuate; and mesopleuron densely and evenly punctate. Additionally, the following characters in combination may help separate *E. ainsliei* from other Canadian species (except perhaps *E. pusillus* and *E. scutellaris*): paramedian band present, axilla and usually also mesoscutellum ferruginous, and T2–T4 with fasciae complete.

### Redescription

FEMALE: Length 7.8 mm; head length 2.0 mm; head width 2.7 mm; fore wing length 5.7 mm.

**Integument colouration.** Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, labrum, clypeus, antenna, pronotal lobe, tegula, axilla, mesoscutum, mesoscutellum, mesopleuron, metapleuron, legs, metasomal terga (including pygidial plate), and metasomal sterna. Mandible with apex darker than all but extreme base. Antenna brown except scape, pedicel, and F1 orange in part. Pronotal lobe and tegula pale ferruginous to amber. Mesoscutum with orange spot anterolaterally between pronotal lobe and tegula. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

**Pubescence.** Face with tomentum densest around antennal socket, slightly sparser on clypeus, upper paraocular and frontal areas, and vertexal area. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with paramedian band. Mesopleuron with upper half sparsely hairy, ventrolateral half sparsely covered in much shorter hairs. Metanotum with tomentum uninterrupted, uniformly off white. T1 with discal patch quadrangular and very wide, the basal and apical fasciae only narrowly joined laterally. T1 with basal and apical fasciae and T2–T4 with apical fasciae complete but somewhat narrowed medially, T2 and T3 with fascia somewhat broader laterally, and T2 with fascia with faint anterolateral extensions of sparser pale

tomentum. T5 with two large patches of pale tomentum lateral to and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, defined by silvery setae on impressed disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by more than 1/4 MOD.

**Surface sculpture.** Punctures dense. Labrum and clypeus with punctures equally dense ( $i < 1d$ ). Impunctate spot lateral to lateral ocellus absent. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally ( $i < 1d$ ), less so laterally ( $i = 1-2d$ ). Mesopleuron with ventrolateral half densely punctate ( $i \leq 1d$ ), the interspaces shining; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense ( $i \approx 1d$ ), evenly distributed on disc.

**Structure.** Mandible without preapical tooth. Labral apex with pair of small denticles preceded by carinae (difficult to see in holotype because covered in hairs; described from non-type specimens). Frontal keel present. Scape with greatest length  $2.1 \times$  greatest width. F2 noticeably longer than wide (L/W ratio = 1.5). Preoccipital ridge joining hypostomal carina. Mesoscutellum weakly bigibbous. Axilla large, its lateral margin longer than half the mesoscutellar width (L/W ratio = 0.56) and tip extending well beyond midlength of mesoscutellum but not attaining apex; axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, and free portion approximately half its medial length; axilla with lateral margin arcuate and carinate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, but still longer than wide (L/W ratio = 1.4); S4 and S5 with much longer silvery to coppery subapical hairs; pygidial plate apically rounded, with large deep, well-separated punctures, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure A.

**Male genitalia.** Plate 3, Figure A.

### Discussion

In this species, the tip of the axilla is conspicuously diverging from the side of the mesoscutellum, from which it is typically separated for half or nearly half its entire medial length. Although integument colouration is generally variable in this species, the axilla and mesoscutellum with few exceptions are entirely or almost entirely rusty orange. The discs of the metasomal terga may be entirely covered in brown to black tomentum or with tomentum of the same light colour as that comprising

the metasomal fasciae. However, if pale tomentum covers the discs then it is sparser than that comprising the metasomal fasciae.

Brumley (1965) indicated that *Epeolus ainsliei* is probably conspecific with *E. lectus* Cresson, but did not personally examine the holotype of *E. lectus*, and used sketches and descriptions of it by others for comparison. I have seen the holotypes of both species, which differ considerably. Unsurprisingly, *E. lectus* is much more similar to *E. lectoides*, but is much more coarsely punctate, and T2–T4 are with complete, broader fasciae. DNA barcoding also indicates that *E. lectus* is a valid species (BOLD:ACZ8246), distinct from both *E. ainsliei* and *E. lectoides*.

**HOST RECORDS:** According to Wolf and Ascher (2009), one specimen was collected in association with *Colletes americanus* Cresson and *C. susannae* Swenk (possible host species) over a sandy area at Spring Green Preserve in Sauk County, Wisconsin, USA.

**FLORAL RECORDS:** Labels of examined voucher specimens indicate a floral association with *Dalea villosa* (Nutt.) Spreng. (Fabaceae).

**Distribution in Canada:** Southern Manitoba west to Alberta but east of the Rocky Mountains (Map 1). Possibly restricted to the Prairie Ecozone.

**DNA barcoded material.** Available. BOLD:ACZ1957. Specimens examined and sequenced.—CANADA: **Manitoba:** Spruce Woods Provincial Park (Spirit Sands Trail), 6 km N Glenboro, vii.2007, L. Packer (1♀, PCYU).

**Non-barcoded material examined.** CANADA: **Alberta:** Medicine Hat, 17.vii.1917, Sladen (1♂, BBSL), 20.viii.1916, Sladen (10♀, CNC).

USA: **Iowa:** Sioux City, 03.ix.1927, C.N. Ainslie (1♀, AMNH); **Minnesota:** 8 mi W Hitterdal (Clay County), 03.ix.1975, J.R. Powers (1♀, EMEC); **Nebraska:** Fort Robinson (Dawes County), 11.viii.1971, J.G., B.L., and K.C. Rozen (1♀, AMNH); **North Dakota:** 1 mi SE McLeod (Ransom County), 01.viii.1961, J.R. Powers (1♀, EMEC), 20.vii.1985, J.R. Powers (1♀, EMEC); 7 mi SE Sheldon (Ransom County), 26.vii.1985, J.R. Powers (1♂, EMEC); 11 mi W Walcott (Richland County), 24.vii.1963, J.R. Powers (1♀, AMNH), 30.vi.1973, J.R. Powers (1♀, EMEC), 17.vii.1981, J.R. Powers (1♀, 1♂, EMEC), 18.vii.1984, J.R. Powers (1♂, EMEC); Denbigh, 18.viii.1935, O.A. Stevens (1♀, AMNH); Sheldon, 25.vii.1949, O.A. Stevens (1♀, AMNH); **Texas:** 6 mi E Bastrop (Bastrop County), 12-13.vi.1983, W.J. Pulawski (1♂, CAS); Camp Swift – Texas Army National Guard (Bastrop County), 02.vi.2009, J.L. Neff (1♂, CTMI); San Pedro Kenedy Ranch (Kenedy County), 20.iv.2001, J.L.

Neff (1♀, CTMI); Weser (Goliad County), 11.v.1952, M. Cazier, W. Gertsch, and R. Schrammel (2♀, AMNH); **Wyoming:** Dwyer, 15.vii.1966, R.J. Lavigne (1♀, USNM).

### *Epeolus americanus* (Cresson, 1878)

Figures 9e, 13c, 14a;

Plate 1, Figure B; Plate 2, Figure B; Plate 3, Figure B;

Map 2

*Phileremus americanus* Cresson, 1878. Trans. Am. Entomol. Soc. 7: 83 (♀, ♂); Cresson, 1916. Mem. Am. Entomol. Soc. 1: 111 (♀) [lectotype designation].

**Primary type specimen.** Lectotype ♀ (ANSP, catalog number: 2235). **Collection information.** USA: Colorado: no specific locality given, H.K. Morrison.

*Phileremus montanus* Cresson, 1878. Trans. Am. Entomol. Soc. 7: 83 (♂), **new synonymy**

**Primary type specimen.** Holotype ♂ (ANSP, catalog number: 2231). **Collection information.** USA: Nevada: no specific locality given, H. Edwards.

*Epeolus lanhami* Mitchell, 1962. N. C. Agric. Exp. Stn. Tech. Bull. 152: 450 (♀), **new synonymy**

**Primary type specimen.** Holotype ♀ (CUM, catalog number: 0000041). **Collection information.** USA: Michigan: near Saline, 26.vi.1954, U.N. Lanham.

### Diagnosis

In *Epeolus americanus*, the fore wing commonly has two submarginal cells. By contrast, in all other *Epeolus* in Canada the fore wing typically has three submarginal cells. However, in examined specimens of *E. ainsliei*, *E. minimus*, and *E. olympiellus* (including the holotype) the second or third submarginal crossvein terminates part of the way up or is missing entirely in one or both fore wings. *Epeolus americanus* can be more reliably separated from other *Epeolus* in Canada on the basis of the following features: F2 of female antenna not more than 1.1 × as long as wide, and T1 typically with narrow discal patch (longitudinal band more than 1.1 × as wide as breadth of apical fascia in dorsal view). The following features in combination help further separate this species from other *Epeolus* in Canada: pronotal lobe dark brown to black; axilla with tip inconspicuous, and axilla rather small, the tip not extending beyond midlength of mesoscutellum.

### Redescription

**FEMALE:** Length 7.9 mm; head length 1.9 mm; head width 2.5 mm; fore wing length 5.7 mm.

**Integument colouration.** Mostly black; notable exceptions as follows: at least partially ferruginous

on mandible, antenna, pronotal lobe, tegula, and legs. Mandible with apex darker than all but extreme base. Preapical tooth as dark as mandibular apex (difficult to see in the *E. americanus* lectotype because mandible retracted; described from the *E. lanhami* holotype). Flagellum brown and (except F1) faintly lighter than conspicuously dark brown scape and brown pedicel, generally due to extensive pilosity on flagellum. Pronotal lobe dark brown to black. Tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively brown or black than reddish orange.

**Pubescence.** Face with tomentum densest around antennal socket. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with paramedian band. Mesopleuron with upper half hairy, ventrolateral half nearly bare. Metanotum with tomentum sparser medially, uniformly pale yellow. T1 with median quadrangular black discal patch enclosed by pale tomentum, except for medial separation at apex. In the *E. lanhami* holotype, the patch more trapezoidal than rectangular. T2 with fascia separated medially and with anterolateral extensions of sparser tomentum. T3 and T4 with fasciae complete medially and narrowed laterally. In the *E. lanhami* holotype and the *E. montanus* holotype, same fasciae separated medially and laterally; in the *E. lanhami* allotype, fasciae separated medially and narrowed laterally. T5 with two large patches of pale tomentum lateral to and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex twice as wide as medial length, defined by silvery setae on flat disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by more than 1/4 MOD.

**Surface sculpture.** Punctures dense. Labrum with larger and sparser punctures ( $i=1-2d$ ) than clypeus ( $i<1d$ ). Small impunctate shiny spot present lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula densely punctate mesally ( $i\leq 1d$ ), less so laterally ( $i=1-2d$ ). Mesopleuron with ventrolateral half densely punctate ( $i\leq 1d$ ), the interspaces shining; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense ( $i\approx 1d$ ), evenly distributed on disc.

**Structure.** Preapical tooth with blunt edge. Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel present. Scape with greatest length  $1.9 \times$  greatest width. F2 not noticeably longer than wide ( $L/W$  ratio = 1.1). Preoccipital ridge not joining hypostomal carina, from which it is separated by 1.5 MOD at its terminal. Mesoscutellum moderately bigibbous. Axilla small to intermediate in size, its lateral margin less than half as long as mesoscutellar width ( $L/W$  ratio

= 0.35) and tip not extending beyond midlength of mesoscutellum; axilla with tip visible, but unattached to mesoscutellum for less than 1/4 its medial length; axilla with lateral margin relatively straight and without carina. Fore wing with two submarginal cells (true of the *E. lanhami* holotype and allotype as well). Pygidial plate mostly retracted in the *E. americanus* lectotype and the *E. lanhami* holotype and allotype, but apically truncate in non-type specimens.

**MALE:** Description as for female except for usual secondary sexual characters and as follows: F2 shorter, nearly as long as wide ( $L/W$  ratio = 0.8); S4 and S5 with much longer silvery to coppery subapical hairs, which individually are often darker apically; pygidial plate apically rounded, with large deep, well-separated punctures, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure B.

**Male genitalia.** Plate 3, Figure B.

### Discussion

This species was originally placed in *Phileremus* Latreille because in the type specimens the fore wing has two submarginal cells. Subsequently, specimens in which the fore wing has three submarginal cells have been discovered, and Cockerell (1904) recognized *E. americanus* as being “to all intents and purposes *Epeolus* with two submarginal cells”, even though he treated the species under the name *Phileremus americanus*. Cresson (1878) also described this species under the name *Phileremus montanus*, based on a single male specimen from Nevada. As most *Epeolus* species have been described from female type specimens, and since *E. americanus* was described from both sexes with the female having been designated as the lectotype (Cresson 1916), whereas *E. montanus* was described from only one sex, priority of the name should be given to *E. americanus*, even though both names were published simultaneously. The name *Epeolus americanus* has also become more commonly used than *E. montanus* in the literature. The types are similar except where indicated in the redescription, and the tegula of the *E. montanus* holotype is darker with sparser punctation.

*Epeolus lanhami*, with two submarginal cells, was described by Mitchell (1962), and is clearly synonymous with *E. americanus*. Except for the few abovementioned minor differences, the *E. lanhami* holotype and allotype match the present redescription of this species (based on the *E. americanus* lectotype) that includes comparisons of all three specimens. Mitchell (1962) made no mention of *E. americanus* in his taxonomic treatment of *Epeolus* of eastern USA, suggesting a lack of familiarity with the species.

Brumley (1965) identified *E. lanhami* and *E. montanus* as *E. americanus*, but also synonymized *E. asperatus* and *E. melectimimus* under this species. *Epeolus asperatus* and *E. melectimimus* appear to be the same species, native to California, USA, with distinct ornamentation on the metasomal terga and the mesopleuron and tegula more closely punctate than in *E. americanus*. Sequenced specimens most similar in morphology to the types of *E. asperatus* and *E. melectimimus* were assigned a unique BIN (BOLD:ACZ2142) separate from *E. americanus* (BOLD:AAB9110). Brumley (1965) also indicated that *E. barberiellus* is probably conspecific with *E. americanus*, but without sufficient material for comparison opted to treat the two species as distinct, a decision with which I agree based on my own morphological comparisons.

**HOST RECORDS:** As is true for most *Epeolus* species, the *Colletes* host species of *E. americanus* is/are unknown. In an intensive survey of wild bees in interior and arctic Alaska, Armbruster and Guinn (1989) collected only one species/subspecies of *Colletes* (*Colletes consors mesocopus* Swenk) and one species of *Epeolus*, which they called *Epeolus* near *americanus*, in sub-arctic steppe on south-facing bluffs along the Tanana River drainage in June (1985–1986).

**FLORAL RECORDS:** Collection records on Discover Life (Ascher and Pickering 2016) indicate the following floral associations: *Dasiphora fruticosa* (L.) Rydb. (Rosaceae) and *Lyonia ligustrina* (L.) DC. (Ericaceae). The label of one examined voucher specimen indicates an association with *Linum lewisii* Pursh (Linaceae).

**Distribution in Canada:** Known to occur in most of Canada except the high Arctic (Map 2).

**DNA barcoded material.** Available. BOLD:AAB9110. Specimens examined and sequenced.—CANADA: **Quebec:** Cap-aux-Meules (Grindstone Island, Magdalen Islands), 09.vii.2015, J. Heron and C. Sheffield (1♂, RSKM); **Yukon:** Kluane National Park and Reserve of Canada, 13.vii.2006, L. Packer (1♀, 1♂, PCYU); N. Riverdale (Whitehorse), 06.vi.2009, S.G. Cannings (3♀, PCYU); Schwatka Lake (Whitehorse), 06.vi.2009, L. Mennell (6♀, PCYU); 06.vi.2009, S.G. Cannings (2♀, 1♂, PCYU).

USA: **Colorado:** (2♀, PCYU); **Utah:** 1.46 km SE Mount Naomi, 24.vii.2008, H. Ikerd (1♀, BBSL).

**Non-barcoded material examined.** CANADA: **Alberta:** Waterton Lakes National Park, 5-14.vii.1991, H. Goulet (1♂, CNC); **British Columbia:** Atlin, 05.vii.1955, H.J. Huckel (1♂, CNC); Oliver, 04.vi.1923, C.B. Garrett (1♀, CNC); Oliver (Vaseaux Lake), 23.v.1959, R.E. Leech (1♂, CNC); **Manitoba:** Gillam, 29.vii.1950, J.F. McAlpine (1♀, CNC); **Ontario:** Black Sturgeon Lake,

10.vii.1964 (1♀, CNC); Rainy River, 24.vi.1960, S.M. Clark (4♀, 2♂, CNC); Sudbury, 07.vii.1889 (1♀, CAS); **Quebec:** Montreal Island, 24.vi.1905 (1♀, USNM); **Saskatchewan:** Athabasca Sand Dunes Provincial Park (Yakow Lake), 21-29.vi.1988, M. Polak and M. Wood (2♀, CNC); **Yukon:** Kluane National Park and Reserve of Canada, 13.vii.2006, L. Packer (1♀, PCYU); Whitehorse (Riverdale North), 06.vii.2009, S.G. Cannings (1♀, PCYU), 30.vi.2009, S.G. Cannings (2♀, PCYU); Whitehorse (Schwatka Lake), 30.vi.2009, L. Mennell (1♀, PCYU), 26.vi.2009, L. Mennell (1♂, RSKM).

USA: **Alaska:** Big Delta, 26.vi.1951, W.R.M. Mason (1♀, CNC); Nogahabara Sand Dunes (65 mi N Galena), 1-5.vii.1989, M. Polak and D.M. Wood (1♀, 3♂, CNC);

**California:** Sagehen Creek Field Station (Nevada County), 18-22.vi.1985, D.C. Darling (1♂, PCYU);

**Colorado:** Gunnison County, 26.vi.2012, R. Brennan (1♀, PCYU), 10.vii.2012, S. Turner and S. Ehlman (1♀, PCYU), 13.vi.2012, R. Brennan (1♀, PCYU); Ward (Boulder County), 14.vii.1982, L. Packer (1♀, PCYU);

**Idaho:** Buhl, 27.v.1929, C.F. Henderson (1♂, USNM);

**Michigan:** Near Saline, 26.vi.1954, U.N. Lanham (*E. lanhami* allotype ♂ [CUM, catalog number: 0000042]);

**Utah:** Pelican Canyon (Fish Lake), 26.vi.1999, L. Packer (1♀, PCYU); La Sal Mountains (Warner Lake), 29.vi.1999, L. Packer (1♀, PCYU); **Virginia:** Skyland, 26.vi.1936, R.C. Shannon (1♀, USNM).

### *Epeolus autumnalis* Robertson, 1902

Figures 4c, 5f, 10c;

Plate 1, Figure C; Plate 2, Figure C; Plate 3, Figure C;

Map 3

*Epeolus autumnalis* Robertson, 1902. Entomol. News 13: 81 (♀, ♂). Webb, 1980. Ill. Nat. Hist. Surv. Bull. 32: 108 (♀) [lectotype designation (by W.E. LaBerge)].

**Primary type specimen.** Lectotype ♀ (INHS, catalog number: 44381). **Collection information.** USA: Illinois: Carlinville, C. Robertson.

### Diagnosis

*Epeolus autumnalis* is an eastern species that can readily be identified by the following combination of features: mesopleuron closely ( $i \leq d$ ) and evenly punctate; axilla and mesoscutellum all black; and axilla large, but not conspicuously diverging from side of mesoscutellum, and tip extending well beyond midlength of mesoscutellum but not attaining apex. Specimens of *E. autumnalis* may attain a relatively large size (>10 mm). In this respect, in its overall dark colouration, and in general appearance, the species resembles *E. lectoides*. However, the integument of *E. lectoides* is much shinier, due in part to larger interspaces, and both species exhibit numerous



other structural differences. *Epeolus autumnalis* is much more akin to a dark *E. scutellaris*, but in *E. scutellaris* the axilla is larger, ferruginous to some degree, and attains or surpasses the line of pale tomentum demarcating the posterior margin of the mesoscutellum.

### Redescription

**FEMALE:** Length 8.9 mm; head length 2.4 mm; head width 3.1 mm; fore wing length 7.5 mm.

**Integument colouration.** Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, antenna, pronotal lobe, tegula, and legs. Mandible with apex darker than all but extreme base. Preapical tooth lighter than mandibular apex (difficult to see in lectotype and lectoallotype; described from non-type specimens). Flagellum brown and (except F1) faintly lighter than dark brown scape and pedicel, generally due to extensive pilosity on flagellum. Pronotal lobe dark brown to black. Tegula pale ferruginous to amber. Wing membrane subhyaline and dusky in part. Legs more extensively brown than reddish orange. **Pubescence.** Face with tomentum densest around antennal socket. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with paramedian band. Mesopleuron mostly bare (with tomentum rubbed off) in lectotype, but tomentum dense in lectoallotype, except for two almost entirely bare circular patches (one behind pronotal lobe, a larger one occupying much of ventrolateral half of mesopleuron). Metanotum with tomentum uninterrupted, uniformly pale yellow. T1 with discal patch elliptical and very wide, the basal and apical fasciae only narrowly joined laterally. T1 and T2 with apical fasciae separated medially, and T2 with fascia without anterolateral extensions of tomentum. T3 and T4 with fasciae complete medially, and T4 with fascia narrowed laterally. T5 with two large patches of pale tomentum lateral to and contacting pseudopygidial area. T5 with pseudopygidial area lunate, its apex at least twice as wide as medial length, defined by silvery setae on impressed disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by 1/3 MOD.

**Surface sculpture.** Punctures dense. Labrum with sparser punctures ( $i=1-2d$ ) than clypeus ( $i<1d$ ). Small impunctate dull/textured spot present lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally ( $i<1d$ ), less so laterally ( $i=1-2d$ ). Mesopleuron with ventrolateral half densely punctate ( $i\leq 1d$ ) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense ( $i\approx 1d$ ), evenly distributed on disc.

**Structure.** Preapical tooth blunt and obtuse. Labral apex

with pair of small denticles preceded by carinae. Frontal keel present. Scape with greatest length  $1.8 \times$  greatest width. F2 noticeably longer than wide (L/W ratio = 1.6). Preoccipital ridge not joining hypostomal carina, from which it is separated by  $\geq 2$  MOD at its terminal (difficult to see in lectotype and lectoallotype; described from non-type specimens). Mesoscutellum weakly bigibbous. Axilla large, its lateral margin nearly half as long as mesoscutellar width (L/W ratio = 0.47) and tip extending well beyond midlength of mesoscutellum but not attaining apex; axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 its medial length; axilla with lateral margin arcuate and carinate. Fore wing with three submarginal cells. Pygidial plate not visible in lectotype, but apically truncate in non-type specimens.

**MALE:** Description as for female except for usual secondary sexual characters and as follows: F2 shorter, but still longer than wide (L/W ratio = 1.3); S4 and S5 with much longer silvery to coppery subapical hairs; pygidial plate apically rounded, with large deep punctures closely clustered basally and sparser apically, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure C.

**Male genitalia.** Plate 3, Figure C.

### Discussion

The integument of this species is mostly black, and in no examined specimens are the axilla and mesoscutellum ferruginous to any degree. The pronotal lobe ranges from rusty orange to black. The axilla is large, but always well short of the posterior margin of the mesoscutellum. Although the lateral margin of the axilla is typically arcuate, it is in some specimens only very weakly curved. *Epeolus autumnalis* flies in late summer and, as its name implies, early autumn.

**HOST RECORDS:** An inferred *Colletes* host of *E. autumnalis*, based on size and flight season, is *C. compactus compactus* Cresson (Ascher *et al.* 2014). Personal observations support such an association. In King, Ontario, Canada, a single male specimen was collected at the same time (morning of September 24th, 2014) as several *C. compactus* Cresson, the only temporally co-occurring representatives of either genus sampled or observed. Also, in Toronto, Ontario, Canada, six female *E. autumnalis* were collected with many co-occurring *C. compactus* on several dates (September to October, 2015) at the same locality.

**FLORAL RECORDS:** Robertson (1929) reported *E. autumnalis* on *Bidens* L. (Asteraceae), *Helianthus* L. (Asteraceae), *Rudbeckia* L. (Asteraceae), and *Solidago* L. (Asteraceae). Mitchell (1962) indicated additional

associations with *Aster* (now *Symphyotrichum* Nees) (Asteraceae) and *Haplopappus* Cass. (Asteraceae). Collection records on Discover Life (Ascher and Pickering 2016) indicate the following floral associations: *Euthamia graminifolia* (L.) Nutt. (Asteraceae), *Leucanthemum vulgare* Lam. (Asteraceae), and *Solidago sempervirens* L. Labels of examined voucher specimens further indicate associations with *Melilotus albus* Medik. (Fabaceae), *Solidago altissima* L., *S. bicolor* L., *S. nemoralis* Aiton, and *Symphyotrichum ericoides* (L.).

**Distribution in Canada:** Atlantic and Central Canada (Map 3).

**DNA barcoded material.** Available. BOLD:AAF2361. Specimens examined and sequenced.—CANADA: **Nova Scotia:** Avonport (Kings County), 10.ix.2000, C. Sheffield (2♀, RSKM), 13.ix.2001, C. Sheffield (1♂, PCYU); **Ontario:** Black Creek Parkland (Toronto), 07.x.2015, T.M. Onuferko (1♀, PCYU). USA: **New York:** Gardiners Island (Suffolk County), 28.ix.2007, R.G. Goelet (1♀, AMNH).

**Non-barcoded material examined.** CANADA: **Nova Scotia:** Avonport (Kings County), 10.ix.2000, C. Sheffield (1♀, PCYU), 28.viii.2000, C. Sheffield (1♀, RSKM); **Ontario:** Alderville, 01.ix.2001, S. Paiero (2♂, DEBU); Caledon Village, 02.ix.2003, J. Grixti (1♀, 1♂, PCYU), 08.ix.2003, J. Grixti (3♀, PCYU); Caledon (Forks of the Credit Provincial Park), 12.ix.1969, P. MacKay (1♂, PCYU), 29.viii.1969, P. MacKay (1♂, ROM); King, 12.ix.2000, J. Grixti (1♀, 1♂ PCYU), 29.viii.2001, M. Somers (3♂, PCYU), 21.viii.2001, M. Somers (1♂, PCYU), 16.ix.2001, M. Somers (1♀, PCYU), 23.vii.2002, J. Grixti (1♂, PCYU), 28.viii.2002, J. Grixti (1♀, 2♂ PCYU), 28.viii.2002, V. Kushnir (1♂, PCYU), 14.ix.2002, J. Grixti (1♀, PCYU), 06.ix.2003, A. Gravel (1♀, 4♂, PCYU), 06.ix.2003, J. Grixti (1♀, 1♂ PCYU); Kingston, 05.ix.1987, C. Shilton (2♀, DEBU); Niagara Falls (Niagara Whirlpool, Welland County), 11.ix.2004, M. Buck (5♂, DEBU); Toronto (York University Campus), 15.ix.2006, E. Willis (1♀, PCYU); Windsor (Ojibway Prairie), 22.ix.2001, S. Marshall (1♀, DEBU).

USA: **Illinois:** Carlinville, C. Robertson (lectoallotype ♂ [INHS, catalog number: 44382]); **Maryland:** Jug Bay Wetlands Sanctuary (Anne Arundel County), 01.x.2004, B. Hollister (1♂, BIML), 15.ix.2007, S.W. Droege (1♂, BIML); **Massachusetts:** Long Point Wildlife Refuge (West Tisbury, Dukes County), 09-10.ix.2011, P.Z. Goldstein (1♂, AMNH); Middle Moors (Nantucket County), 22.ix.2010, J.M. Karberg (1♀, AMNH); Suffolk County, 14-15.ix.2010, J. Rykken (1♂, BIML); **New York:** Gardiners Island (Suffolk County), 07.x.2005,

R.G. Goelet (1♀, AMNH); Lancaster, 13.ix.1968, M.C. VanDuzee (1♂, CAS).

### *Epeolus bifasciatus* Cresson, 1864

Figures 4a, 5a, 6a, 7a;

Plate 1, Figure D; Plate 2, Figure D; Plate 3, Figure D;

Map 4

*Epeolus bifasciatus* Cresson, 1864b. Proc. Entomol. Soc. Phil. 3: 38 (♂); Cresson, 1916. Mem. Am. Entomol. Soc. 1: 113 (♂) [lectotype designation].

**Primary type specimen.** Lectotype ♂ (ANSP, catalog number: 2658). **Collection information.** USA: Illinois: no specific locality given.

### Diagnosis

*Epeolus bifasciatus* is unmistakable among Canadian species of the genus, and both sexes can be readily identified by each of the following features that is diagnostic for the species in Canada: frontal area with pair of conspicuous granulose protrusions, each located near upper mesal margin of compound eye; punctures dense, but those of head and mesosoma sparser in some areas, larger, deep, and distinct; dorsal surface of pronotum long and distinctly angulate on anterior margin; mesoscutum without pale tomentum; and bright yellow tomentum on dorsal surface of mesosoma and metasoma.

### Redescription

**MALE:** Length 7.8 mm; head length 2.3 mm; head width 2.6 mm; fore wing length 6.5 mm.

**Integument colouration.** Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, labrum, antenna, pronotal collar, pronotal lobe, tegula, axilla, mesoscutellum, metanotum, and legs. Mandible with apex darker than all but extreme base. Preapical tooth lighter than mandibular apex (difficult to see in lectotype; described from non-type specimens). Antenna brown except scape, pedicel, and F1 orange. Pronotal collar, pronotal lobe, and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black. **Pubescence.** Face with tomentum densest around antennal socket. Pronotal collar and dorsum of metasoma with bright yellow setae. Mesoscutum without pale tomentum. Mesopleuron nearly bare, except along margins. Metanotum with tomentum narrowly interrupted medially, uniformly pale yellow. T1 with broad, medially interrupted bright yellow basal fascia. T2 with narrower, complete bright yellow apical fascia. Metasoma otherwise without fasciae, although T3–T6 with few sparsely scattered pale hairs present on apical impressed areas. S4 and S5 with long silvery to coppery

subapical hairs.

**Surface sculpture.** Punctures dense, but those of head and mesosoma sparser in some areas, larger, deep, and distinct. Labrum and clypeus with similar punctation. Impunctate spot lateral to lateral ocellus absent in lectotype, but shiny spot present in non-type specimens. Mesoscutum, mesoscutellum, and axilla very coarsely and densely rugose-punctate. Tegula densely punctate mesally ( $i \leq 1d$ ), less so laterally ( $i = 1-2d$ ). Mesopleuron with larger and denser ( $i \leq 1d$ ) punctures in upper half than ventrolateral half ( $i > 1d$ ), the interspaces shining. Metasomal terga with punctures very fine, dense ( $i \approx 1d$ ), evenly distributed on disc.

**Structure.** Labral apex with three small denticles not preceded by carinae. Frontal keel present. Frontal area with pair of granulate protrusions, each located near upper mesal margin of compound eye. Scape with greatest length  $1.7 \times$  greatest width. F2 not noticeably longer than wide (L/W ratio = 1.1). Preoccipital ridge not joining hypostomal carina, from which it is separated by  $\geq 2$  MOD at its terminal (difficult to see in lectotype; described from non-type specimens). Pronotal collar dilated laterally to about  $2 \times$  medial length in dorsal view. Mesoscutellum moderately bigibbous, depressed along apical margin. Axilla intermediate in size, its lateral margin nearly half as long as mesoscutellar width (L/W ratio = 0.45) and tip extending well beyond midlength of mesoscutellum but not attaining apex; axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, and free portion  $2/5$  its medial length; axilla with lateral margin relatively straight and carinate. Fore wing with three submarginal cells. Pygidial plate apically truncate, with large deep, closely clustered punctures, with the interspaces shining.

**FEMALE:** Description as for male except for usual secondary sexual characters and as follows: F2 noticeably longer than wide (L/W ratio = 1.6); T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, defined by silvery setae on disc of medioapical region elevated from rest of tergum. S4 and S5 with much shorter hairs (S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by  $2/5$  MOD); Pygidial plate with smaller punctures.

**Male hidden sterna.** Plate 2, Figure D.

**Male genitalia.** Plate 3, Figure D.

### Discussion

Although ranging into the American Southwest, this species is more commonly known from eastern North America. *Epeolus bifasciatus* belongs to a group of Neotropical *Epeolus* so unique that they were until

recently placed in their own subgenus (*Trophocleptria* Holmberg). However, in a phylogeny based on morphological characters, the subgeneric designation of this group rendered the rest of *Epeolus* paraphyletic (Rightmyer 2004). As a result, Michener (2007) proposed that the term “*Trophocleptria* group” be used for this monophyletic taxon until a thorough revision of the genus is made. Other similar species occur in the Neotropics and possibly along the U.S. border with Mexico, but at present only one valid species is known to occur in Canada and eastern USA.

**HOST RECORDS:** According to Mitchell (1962), *Colletes latitarsis* Robertson is probably the host of *E. bifasciatus*.

**FLORAL RECORDS:** Robertson (1929) reported *E. bifasciatus* on *Aster* (now *Symphyotrichum* Nees) (Asteraceae), *Bidens* L. (Asteraceae), *Boltonia* L'Hér. (Asteraceae), *Dalea* L. (Fabaceae), *Eryngium* L. (Apiaceae), *Eupatorium* L. (Asteraceae), *Heliopsis* Pers. (Asteraceae), *Justicia* L. (Acanthaceae), *Lythrum* L. (Lythraceae), *Pycnanthemum* Michx. (Lamiaceae), *Ratibida* Raf. (Asteraceae), *Solidago* L. (Asteraceae), *Trifolium* L. (Fabaceae), *Verbena* L. (Verbenaceae), and *Verbesina* L. (Asteraceae). Mitchell (1962) indicated additional associations with *Asclepias* L. (Apocynaceae), *Cirsium* Mill. (Asteraceae), *Coreopsis* L. (Asteraceae), *Erigeron* L. (Asteraceae), *Helianthus* L. (Asteraceae), *Melilotus* Mill. (Fabaceae), *Nepeta* L. (Lamiaceae), *Rudbeckia* L. (Asteraceae), and *Vernonia* Schreb. (Asteraceae). Collection records on Discover Life (Ascher and Pickering 2016) indicate the following floral associations: *Daucus carota* L. (Apiaceae), *Rudbeckia hirta* L., and *Melilotus officinalis* (L.) Lam. The label of one examined voucher specimen indicates an association with *Sonchus arvensis* L. (Asteraceae).

**Distribution in Canada:** Central Canada (Map 4).

**DNA barcoded material.** Available. BOLD:ADD5310. Specimens examined and sequenced.—CANADA: **Ontario:** Point Pelee National Park (Essex County), 26-27.vii.2016, R. Ferrari and T.M. Onuferko (1♀, 1♂, PCYU).

USA: **Florida:** Lake Louisa State Park (12 km S Clermont, Lake County), 05.iv.2014, K.A. Williams (1♂, FSCA).

**Non-barcoded material examined.** CANADA: **Ontario:** Caledon Village, 07.viii.2003, J. Grixti (1♀, PCYU); Grimsby, 29.vii.1944 (1♀, CNC); Hillman Marsh Conservation Area (Essex County), 03.viii.2007, S.M. Paiero (2♀, DEBU); Ottawa, 15.viii.1955, P. Taschereau (1♂, CNC); Pelee Island (Essex County), 08.vii.1965, J.C.E. Riotte and P. Hebert (1♀, ROM); Point

Pelee, 29.vii.1920, N.K. Bigelow (1♂, ROM); Rondeau Park, 17.vii.1962, S.M. Clark (2♂, CNC), 18.vii.1962, S.M. Clark (2♂, CNC).

USA: **Florida:** Ormond, A.T. Solsson (1♂, AMNH); Sarasota, 20.x.1983, L. Packer (1♂, PCYU); **Illinois:** W Arthur (Moultrie County), 14.viii.1964, A.R. Moldenke (2♀, AMNH); **Maryland:** Cabin John, 18.viii.1914, J.C. Crawford (1♀, AMNH); Fulton (Howard County), 12.viii.2011, C. White (1♀, BIML); **New York:** Elba (Genesee County), 04.viii.2011, D. Green (1♂, BIML); **North Carolina:** Kill Devil Hills, 26.v.1948, K.V. Krombein (1♂, AMNH); **Pennsylvania:** Centre County, 05.viii.2016, L. Russo (1♂, BIML); **South Carolina:** Hobcaw Barony (5 km E Georgetown, Georgetown County), 11-17.ix.2007, S.M. Paiero (1♂, DEBU); **Wisconsin:** Kettle Moraine State Forest (Waukesha County), 29.viii.-28.ix.2002, C.M. Brabant (1♀, PCYU).

### *Epeolus canadensis* Mitchell, 1962

Figures 9b, 9c, 17a;

Plate 1, Figure E; Plate 2, Figure E; Plate 3, Figure E;

Map 5

*Epeolus canadensis* Mitchell, 1962. N. C. Agric. Exp. Stn. Tech. Bull. 152: 444 (♀).

**Primary type specimen.** Holotype ♀ (MCZ, catalog number: 32859). **Collection information.** CANADA: Nova Scotia: Ingonish (Cape Breton Island), 07.viii.1928, G. Fairchild.

### Diagnosis

The combination of the following features separates *Epeolus canadensis* from all other species in Canada except *E. compactus*, *E. minimus*, and *E. olympiellus*: integument mostly black; axilla (except perhaps tip) and mesoscutellum all black; legs partially ferruginous; and T1 with longitudinal band  $\sim 1 \times$  as wide as breadth of apical fascia in dorsal view. This species most closely resembles *E. compactus*, and the character that separates both species from all other *Epeolus* in Canada is the presence of a small anteromedial patch of pale tomentum in the shape of a chevron, horseshoe, or V on the mesoscutum. By contrast, in all other Canadian species (except *E. bifasciatus*, in which the mesoscutum is without distinct pale hairs) the mesoscutum is with paramedian bands if not entirely obscured by tomentum. The fascia of T2 is without anterolateral extensions of tomentum, which are present in *E. minimus* and *E. olympiellus*. In *E. canadensis*, T1 is with a median triangular to semicircular black discal patch enclosed by pale tomentum (except for medial separation at apex), unlike the quadrangular discal patch of *E. compactus*. In Canada, both species are also separated by geography,

with *E. canadensis* not known to occur in provinces or territories west of Ontario and *E. compactus* not known to occur in provinces east of Manitoba.

### Redescription

FEMALE: Length 8.7 mm; head length 2.1 mm; head width 2.9 mm; fore wing length 6.6 mm.

**Integument colouration.** Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, labrum, antenna, pronotal lobe, tegula, axilla, legs, T5, and pygidial plate. Mandible with apex and preapical tooth darker than rest of mandible. Antenna brown except scape, pedicel, and F1 extensively orange. Axilla only with tip orange. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs extensively reddish orange from tibia to tarsus. **Pubescence.** Face with tomentum densest around antennal socket. Clypeus, upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with anteromedial V-shaped patch of pale tomentum. Mesopleuron with upper half densely hairy, except patch beneath base of fore wing (hypoepimeral area); ventrolateral half nearly bare. Metanotum with tomentum uninterrupted except for median bare patch on apical half, off white laterally and black medially. T1 with median semicircular black discal patch enclosed by pale tomentum, except for medial separation at apex. T2–T4 with fasciae narrowed before becoming somewhat broader laterally, and T2 with fascia separated medially and without anterolateral extensions of tomentum. T3 and T4 with fasciae complete, but somewhat narrowed medially. T5 with large, nearly continuous patch of pale tomentum bordering and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, defined by silvery setae on flat disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by more than 1/4 MOD.

**Surface sculpture.** Punctures dense. Labrum with larger and sparser punctures ( $i=1-2d$ ) than clypeus ( $i<1d$ ). Small impunctate shiny spot present lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally ( $i<1d$ ), less so laterally ( $i=1-2d$ ). Mesopleuron with ventrolateral half densely punctate ( $i\leq 1d$ ) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense ( $i\approx 1d$ ), evenly distributed on disc.

**Structure.** Labrum with pair of small subapical denticles preceded by small discreet ridges. Frontal keel present. Scape with greatest length  $1.8 \times$  greatest width. F2 noticeably longer than wide ( $L/W$  ratio = 1.2). Preoccipital

ridge not joining hypostomal carina, from which it is separated by about 1.5 MOD at its terminal (difficult to see in holotype; described from non-type specimens). Mesoscutellum weakly bigibbous. Axilla intermediate in size, its lateral margin nearly half as long as mesoscutellar width (L/W ratio = 0.40) and tip not extending much beyond midlength of mesoscutellum; axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 its medial length; axilla with lateral margin relatively straight and without carina. Fore wing with three submarginal cells. Pygidial plate apically truncate. MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, as long as wide (L/W ratio = 1.0); S4 and S5 with much longer silvery to coppery subapical hairs, which individually are often darker apically; pygidial plate apically rounded, with large deep punctures more or less evenly spaced throughout, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure E.

**Male genitalia.** Plate 3, Figure E.

#### Discussion

This species is not particularly variable, but there are differences among specimens in the width of the patch of black tomentum on the middle of the metanotum. Also, the tip of the axilla, which is typically all black, is ferruginous in some examined specimens. Although the black discal patch forms a triangle in some specimens and a semicircle in others, it is always straight basally and longest medially.

**HOST RECORDS:** The *Colletes* host species of *E. canadensis* is/are unknown. In the Caledon Hills of Ontario, Canada, a single female specimen was collected at the same time of year (July 9<sup>th</sup>) as *C. kincaidii* Cockerell, the only temporally co-occurring *Colletes* species sampled from the same study area (MacKay and Knerer 1979). In a follow-up study of the same wild bee community 34 years later, Grixti and Packer (2006) rediscovered all *Epeolus* species except *E. canadensis*, and noted the near disappearance of *C. kincaidii* from the resampled site.

**FLORAL RECORDS:** MacKay and Knerer (1979) reported *E. canadensis* on *Melilotus albus* Medik. (Fabaceae), and Discover Life (Ascher and Pickering 2016) indicates a floral association with *Rudbeckia hirta* L. (Asteraceae). The label of one examined voucher specimen indicates an association with *Erigeron* L. (Asteraceae).

**Distribution in Canada:** Atlantic and Central Canada (Map 5).

**DNA barcoded material.** Available. BOLD:ADA0845. Specimens examined and sequenced.—CANADA: **Ontario:** 2 km N Shiloh (Wellington County), 08.viii.2004, M. Buck (1♀, DEBU); Sixteen Mile Creek near Hwy 407 (Oakville, Halton Region), 21.viii.2004, M. Buck (1♂, DEBU).

USA: **Arizona:** AZ-366 (Mount Graham), 01.ix.2015, C. Nicholson (1♂, PCYU); **New Mexico:** Emory Pass (Gila National Forest), 16.viii.2007, M. Buck (1♂, DEBU); NM-15 Scenic (Gila National Forest), 03.ix.2015, R. Ferrari (1♂, PCYU).

**Non-barcoded material examined.** CANADA: **Nova Scotia:** Kings County, 23-24.vii.1931, C.E. Atwood (3♀, 4♂, CNC); **Ontario:** Caledon (Forks of the Credit Provincial Park), 09.vii.1968, P. MacKay (1♀, ROM), 28.vi.1965, G. Knerer (1♂, ROM); Dyer's Bay, 19.vii.1953, D.H. Pengelly (1♂, CNC); Dyer's Bay, 29.vii.1952, D.H. Pengelly (1♂, CNC); King, 10.vii.2002, V. Kushnir (1♂, PCYU); Ottawa, 07.vii.1913, F.W.L. Sladen (6♀, 9♂, CNC), 11.vii.1913, F.W.L. Sladen (2♀, CNC), 15.vii.1913, F.W.L. Sladen (1♂, CNC); Rondeau Park (Kent County), 11.vii.2005, M. Buck (1♀, DEBU); Walpole Island (Lambton County), 04.viii.2006, S.M. Paiero (1♂, DEBU); **Prince Edward Island:** Dalvay by the Sea, 05.viii.1940, J. McDunnough (1♀, CNC); **Quebec:** Gatineau (Aylmer), 03-17.viii.1924, C.H. Curran (2♀, CNC), 09.viii.1924, A.R. Graham (1♀, CNC).

USA: **Arizona:** 3 km SW Nicksville (Cochise County), 03.ix.2009, S. Dumesht and C. Sheffield (2♂, PCYU); Chiricahua Mountains (Cochise County), 24.viii.1966, V.O. Roth (1♂, AMNH); Huachuca Mountains – Ash Canyon (19 mi S Sierra Vista), 30.v.1968, R.F. Sternitzky (1♀, CNC); Huachuca Mountains – Garden Canyon (Cochise County), 1966, R.F. Sternitzky (1♀, CNC); San Francisco Peaks (Flagstaff, Coconino County), 10.viii.1934, F.E. Lutz (1♀, AMNH), 15.viii.1934, E.L. Bell (1♀, AMNH), 18-24.vii.1979, S. and J. Peck (1♀, CNC); **Arkansas:** 5 mi S Fayetteville, 10.ix.1967, R. Heitzman (1♀, FSCA); **Illinois:** Roseville, 20.viii.1940, R.I. Sailer (1♀, KUNHM); **Kansas:** Breidenthal Biological Reserve (Baldwin Woods area, Douglas County), v.-vi.1987, S.G. Reyes (1♀, KUNHM); Tuttle Creek State Park (Pottawatomie County), 06.ix.1992, B. Alexander (1♀, KUNHM); **Missouri:** Lebanon, 20.viii.1953, C.D. Michener (1♀, KUNHM); **New Mexico:** 1.5 km NE McMillan Campground (Grant County), 02.ix.2010, T.L. Griswold (1♂, BBSL); 7.8 km NE Silver City (Grant County), 30.viii.2009, T.L. Griswold (1♀, BBSL); Bear Trap Campground (28 mi SW Magdalena, Socorro County), 12.vii.1965, F., P., and M. Rindge (1♂, AMNH); Cherry Creek Campground (14 mi N Silver City, Grant County), J.E. O'Hara (4♀, 2♂,

CNC), 26.v.1991, J.E. O'Hara (1♂, CNC); **New York:** 9-Mile Creek (Ithaca), 10.vii.1937, P.P. Babi (allotype ♂ [CUIC, catalog number: 00015611]).

### *Epeolus compactus* Cresson, 1878

Figures 9f, 10b, 15a, 17b;

Plate 1, Figure F; Plate 2, Figure F; Plate 3, Figure F;

Map 6

*Epeolus compactus* Cresson, 1878. Trans. Am. Entomol. Soc. 7: 89 (♀, ♂); Cresson, 1916. Mem. Am. Entomol. Soc. 1: 115 (♀) [lectotype designation].

**Primary type specimen.** Lectotype ♀ (ANSP, catalog number: 2227). **Collection information.** USA: Texas: no specific locality given, G.W. Belfrage.

*Epeolus hitei* Cockerell, 1908. Entomologist 41: 60 (♀), **new synonymy**

**Primary type specimen.** Holotype ♀ (USNM, catalog number: 534045). **Collection information.** USA: Colorado: Copeland Park (Boulder County), 06.ix.1907, G.M. Hite.

*Triepeolus gabrielis* Cockerell, 1909. Ann. Mag. Nat. Hist. 5: 26 (♂), **new synonymy**

**Primary type specimen.** Holotype ♂ (USNM, catalog number: 534044). **Collection information.** USA: California: San Gabriel Mountains (near Pasadena), 15.vii.1909, F. Grinnell, Jr.

*Epeolus geminatus* Cockerell and Sandhouse, 1924. Proc. Calif. Acad. Sci. (4) 13: 315 (♀), **new synonymy**

**Primary type specimen.** Holotype ♀ (CAS, catalog number: 01610). **Collection information.** USA: California: Mill Creek Canyon (San Bernardino County), 12.ix.1923, E.P. Van Duzee.

### Diagnosis

In integument colouration, pubescence, surface sculpture, and structure, this species most closely resembles *E. canadensis*, from which it can be separated on the basis of the shape of the discal patch of T1. In *E. compactus*, the discal patch is quadrangular, not triangular or semicircular as in *E. canadensis*. These species are otherwise nearly identical, and presumably sister species. For comments with regard to other similar species in Canada, see diagnosis for *E. canadensis*.

### Redescription

**FEMALE:** Length 8.7 mm; head length 2.2 mm; head width 3.1 mm; fore wing length 7.1 mm.

**Integument colouration.** Mostly black; notable exceptions as follows: partially to entirely ferruginous

on mandible, labrum, antenna, pronotal lobe, tegula, axilla, legs, and pygidial plate. Mandible with apex darker than rest of mandible. Preapical tooth faintly lighter than mandibular apex (difficult to see in the *E. compactus* lectotype; described from non-type specimens). Antenna brown except scape, pedicel, and F1 extensively orange. Axilla only with tip faintly orange. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black. **Pubescence.** Face with tomentum densest around antennal socket. Clypeus, upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with anteromedial horseshoe-shaped patch of pale (mostly rubbed off) tomentum. Mesopleuron with upper half densely hairy, except patch beneath base of fore wing (hypoepimeral area); ventrolateral half nearly bare. Metanotum with tomentum uninterrupted, pale yellow laterally and darker medially on basal half. T1 with median quadrangular black discal patch enclosed by pale tomentum, except for medial separation at apex. T2–T4 with fasciae narrowed before becoming somewhat broader laterally, and T2 with fascia separated medially and without anterolateral extensions of tomentum, although few sparsely scattered pale hairs present. T3 and T4 with fasciae complete, but somewhat narrowed medially. T5 with large, continuous patch of pale tomentum bordering and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, defined by silvery setae on flat disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by 2/5 MOD.

**Surface sculpture.** Punctures dense. Labrum with larger and sparser punctures ( $i=1-2d$ ) than clypeus ( $i<1d$ ). Small impunctate shiny spot present lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally ( $i<1d$ ), less so laterally ( $i=1-2d$ ). Mesopleuron with ventrolateral half densely punctate ( $i\leq 1d$ ) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense ( $i\approx 1d$ ), evenly distributed on disc.

**Structure.** Labrum with pair of small subapical denticles preceded by small discreet ridges. Frontal keel present. Scape with greatest length  $1.7 \times$  greatest width. F2 noticeably longer than wide ( $L/W$  ratio = 1.2). Preoccipital ridge not joining hypostomal carina, from which it is separated by about 1.5 MOD at its terminal (difficult to see in the *E. compactus* lectotype; described from non-type specimens). Mesoscutellum moderately bigibbous. Axilla intermediate in size, its lateral margin nearly half as long as mesoscutellar width ( $L/W$  ratio

= 0.40) and tip not extending much beyond midlength of mesoscutellum; axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 its medial length; axilla with lateral margin relatively straight and without carina. Fore wing with three submarginal cells. Pygidial plate apically truncate.

**MALE:** Description as for female except for usual secondary sexual characters and as follows: F2 shorter, as long as wide (L/W ratio = 1.0); S4 and S5 with much longer silvery to coppery subapical hairs, which individually are often darker apically; pygidial plate apically rounded, with large deep punctures more or less evenly spaced throughout, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure F.

**Male genitalia.** Plate 3, Figure F.

### Discussion

*Epeolus compactus* appears to be very closely related to *E. canadensis*. I believe the two to be heterospecific on the basis of the following consistent morphological difference: T1 of *E. canadensis* has a wide median triangular to semicircular black discal patch enclosed by pale tomentum, which in *E. compactus* is distinctly quadrangular. In Canada, both species can be separated by geography, with *E. canadensis* occurring in Atlantic and Central Canada and *E. compactus* occurring in Western Canada.

*Epeolus hitei* was described as a species similar to *E. beulahensis* that exhibits the following morphological differences: the mesosoma is hairier; the discal patch of T1 is not pure black but covered in fine golden-brown pubescence; and T2 is without lateral oval spots (presumably a reference to the anterolateral extensions of the apical fascia) (Cockerell 1908). However, no comparisons or references were made to the much more similar *E. compactus* type specimens.

Cockerell (1909) described *Triepeolus gabrielis* from a single male specimen, which was said to resemble *Triepeolus norae* Cockerell in general appearance and size, differing in the colouration of the legs and markings on T2, among other unspecified features. I have examined the holotypes of *E. hitei* and *E. gabrielis*, and the specimens both clearly exhibit the following features typical of *E. compactus*: the mesoscutum has an anteromedial patch of pale tomentum, which is chevron-shaped in the female holotype of *E. hitei* and V-shaped in the male holotype of *E. gabrielis*; T1 is with a median quadrangular black discal patch; and the fascia of T2 is without lobe-like anterolateral extensions of tomentum. Cockerell and Sandhouse (1924) described *E. geminatus* as a distinct species, recognizable by the V-shaped patch of pale tomentum on the mesoscutum, which the authors

used to separate the females from *E. rufomaculatus* (synonymized herein under *E. olympiellus*) and males from other *Epeolus* spp. in the accompanying key. I have examined the female holotype of *E. geminatus*, and the specimen with few exceptions (related to intraspecific variation in size and colour) agrees with the present redescription based on the female lectotype of *E. compactus*. Given this, and that Cockerell and Sandhouse (1924) made no comparisons of *E. geminatus* or references to *E. compactus* or *E. hitei*, it is unlikely that the three type specimens are heterospecific. Brumley (1965) first proposed that *E. gabrielis*, *E. geminatus*, and *E. hitei* are synonyms of *E. compactus*, and the present study, given molecular and morphological evidence, corroborates his discovery.

**HOST RECORDS:** A known *Colletes* host of *E. compactus* is *C. kincaidii* Cockerell, an association confirmed by Torchio and Burdick (1988).

**FLORAL RECORDS:** Collection records on Discover Life (Ascher and Pickering 2016) indicate the following floral associations: *Baileya multiradiata* Harv. and A. Gray ex A. Gray (Asteraceae), *B. pleniradiata* Harv. and A. Gray ex A. Gray, *Eriogonum umbellatum* Torr. (Polygonaceae), *Melilotus officinalis* (L.) Lam. (Fabaceae), and *Palafoxia arida* B.L. Turner and Morris (Asteraceae). Labels of examined voucher specimens further indicate associations with *Encelia farinosa* A. Gray ex Torr. (Asteraceae), *Heterotheca villosa* (Pursh) Shinnars (Asteraceae), and *Melilotus albus* Medik. I have personally collected this species on *Sphaeralcea* A. St.-Hil. (Malvaceae) in the American Southwest.

**Distribution in Canada:** Western Canada (Map 6).

**DNA barcoded material.** Available. BOLD:ACU6228. Specimens examined and sequenced.—USA: **California:** Hwy 20 (Mendocino County), 05.vii.2007, J. Gibbs and C. Sheffield (1♀, PCYU); **Oregon:** Hwy 140 (Jackson County), 02.vii.2007, J. Gibbs and C. Sheffield (3♂, PCYU); **Washington:** Pierce County, 24.vii.2009, C. Fimbel (1♀, PCYU).

**Non-barcoded material examined.** CANADA: **Alberta:** Lethbridge, 06.viii.1978, C.D. Michener (1♀, KUNHM); **British Columbia:** Robson, 25.vii.1955, H.R. Foxlee (1♀, CNC); Summit Creek (Creston), 28.vi.1958, H. and A. Howden (1♂, CNC); Vernon, 26.vi.1906 (1♀, CNC); **Saskatchewan:** Prince Albert, 23.vii.1959, A. and J. Brooks (1♂, CNC).

USA: **Arizona:** 1 mi NE Portal (Cochise County), 10.v.1962, W.J. Gertsch and J.A. Woods (1♂, AMNH); Douglas R/C Flying Field (Cochise County), 23.iv.2016, T.M. Onuferko (1♀, PCYU); Skeleton Canyon (Cochise County), 12.v.1977, J.G. Rozen (1♀, AMNH);

**California:** 1 mi S Desert Studies Center at Zzyzx Springs (San Bernardino County), 14.iv.2008, J.S. Ascher (1♂, AMNH); Monrovia (Los Angeles County), 14.vi.1921, F.E. Lutz (1♀, AMNH); Palm Springs station (Riverside County), 26.iii.1960, M. Wasbauer (1♂, AMNH); Point Molate (Richmond), 19.vii.????, F.J. Santana (1♂, FSCA); **Colorado:** (*E. compactus* paratype ♀, AMNH), (1♀, AMNH); I-70 W Silverthorne Scenic Area, 23.vii.2013, A. Payne (1♀, AMNH); Ward (Boulder County), 14.vii.1982, L. Packer (1♀, PCYU); **New Mexico:** 11 mi N Rodeo (Hidalgo County), 01.v.1969, J.G. Rozen and M.S. Favreau (5♂, AMNH); NM-146 (N Hachita, Grant County), 30.iv.2016, T.M. Onuferko (3♂, PCYU); **Oklahoma:** Garfield County, 06.vii.1962, J.F. Reinert (1♀, FSCA); **Oregon:** Hwy 140 (Jackson County), 02.vii.2007, J. Gibbs and C. Sheffield (1♂, PCYU); **Washington:** Pierce County, 24.vii.2009, C. Fimbel (1♀, PCYU); **Wyoming:** Lake Creek Camp (13 mi SE Cooke City, Montana) (Park County), 29.vii.1962, F., P., and M. Rindge (1♂, AMNH); Pacific Creek Road (Teton County), 13.viii.2013, A. Payne (1♀, AMNH); Yellowstone National Park, 09.vii.1930 (1♂, AMNH).

### *Epeolus ilicis* Mitchell, 1962

Figures 3a, 5e, 11b, 12b;

Plate 1, Figure G; Plate 2, Figure G; Plate 3, Figure G;

Map 7

*Epeolus ilicis* Mitchell, 1962. N. C. Agric. Exp. Stn. Tech. Bull. 152: 448 (♀).

**Primary type specimen.** Holotype ♀ (USNM, catalog number: 534048). **Collection information.** USA: North Carolina: Holly Shelter, 30.v.1950, T.B. Mitchell.

### Diagnosis

Among Canadian species, *E. ilicis* most closely resembles *E. lectoides* in general appearance, and especially similar are the shapes of the axilla and pseudopygidial area. Both species exhibit the following similarities: F2 of female antenna noticeably longer than wide; axilla distinctly hooked and well short of posterior margin of mesoscutellum; T1 with discal patch very wide; metasomal terga with punctures sparser ( $i=1-2d$ ); and T5 with pseudopygidial area distinctly campanulate, with apex clearly less than twice as wide as medial length. In contrast to *E. lectoides*, the axilla in *E. ilicis* is more strongly angled to the side than apically, and the mesopleuron in *E. ilicis* is densely punctate, with most interspaces equally narrow above and below.

### Redescription

**FEMALE:** Length 7.4 mm; head length 2.2 mm; head

width 3.1 mm; fore wing length 6.0 mm.

**Integument colouration.** Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, antenna, pronotal lobe, tegula, axilla, mesoscutellum, and legs. Mandible with apex darker than all but extreme base. Antenna brown except scape, pedicel, and F1 orange in part. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black. **Pubescence.** Face with tomentum densest around antennal socket. Clypeus, upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with paramedian band. Mesopleuron with upper half hairy, except patch beneath base of fore wing (hypoepimeral area); ventrolateral half nearly bare. Metanotum with tomentum uninterrupted, uniformly off white. T1 with discal patch elliptical and very wide, the basal and apical fasciae only narrowly joined laterally. T1–T3 with apical fasciae separated medially; those of T2 and T3 somewhat broader laterally; and T2 with fascia without anterolateral extensions of tomentum, although few sparsely scattered pale hairs present. T4 with fascia complete medially. T5 with two large patches of pale tomentum lateral to and separate from pseudopygidial area. T5 with pseudopygidial area campanulate, its apex less than twice as wide as medial length, defined by silvery setae on disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by  $2/5$  MOD.

**Surface sculpture.** Punctures dense. Labrum with larger punctures than clypeus, but punctures of both equally dense ( $i < 1d$ ). Small impunctate shiny spot present lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally ( $i < 1d$ ), less so laterally ( $i = 1-2d$ ). Mesopleuron with ventrolateral half densely punctate ( $i \leq 1d$ ), the interspaces shining; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense ( $i = 1-2d$ ), evenly distributed on disc; the interspaces shining somewhat.

**Structure.** Mandible without preapical tooth (difficult to see in holotype; described from non-type specimens). Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel present. Scape with greatest length  $1.8 \times$  greatest width. F2 noticeably longer than wide ( $L/W$  ratio = 1.7). Preoccipital ridge not joining hypostomal carina, from which it is separated by no less than 1 MOD at its terminal (difficult to see in holotype; described from non-type specimens). Mesoscutellum moderately bigibbous. Axilla intermediate in size, its lateral margin nearly  $2/5$  as long as mesoscutellar width



(L/W ratio = 0.38), but tip not extending beyond midlength of mesoscutellum; axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, and axilla with free portion 2/5 its medial length; axilla with lateral margin relatively straight and without carina. Fore wing with three submarginal cells. Pygidial plate not visible in holotype, but apically truncate in non-type specimens. MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, but still longer than wide (L/W ratio = 1.4); S4 and S5 with much longer silvery to coppery subapical hairs; pygidial plate apically rounded, with large deep punctures closely clustered basally and sparser apically, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure G.

**Male genitalia.** Plate 3, Figure G.

### Discussion

In *Epeolus ilicis*, the mesopleuron is always densely punctate, the axilla is always strongly angled to the side of the mesoscutellum, and (in females) the pseudopygidial area is always distinctly campanulate. Among specimens of this species, the metasomal fasciae are narrowly interrupted or (on T3 and T4) complete. The axilla is in many specimens partially ferruginous, and in some examined specimens the mesoscutellum is partially ferruginous as well.

**HOST RECORDS:** A known *Colletes* host of *E. ilicis* is *C. brimleyi* Mitchell, an association confirmed by Rozen (1989), who recovered two first instar larvae of the former species from a nest of the latter. **FLORAL RECORDS:** Mitchell (1962) indicated floral associations with *Amorpha* L. (Fabaceae), *Ilex glabra* (L.) A. Gray (Aquifoliaceae), *Rhus glabra* L. (Anacardiaceae), and *Vaccinium* L. (Ericaceae), and Discover Life (Ascher and Pickering 2016) indicates an association with *Lyonia ligustrina* (L.) DC. (Ericaceae).

**Distribution in Canada:** I have not been able to verify the occurrence of *E. ilicis* in Canada, and its record in the country (Map 7) is questionable. Romankova (2004) reported this species as a new record for Canada based on three male specimens collected in southern Ontario. I have checked the holdings at DEBU, where all three are supposed to be housed, but they are missing. There are no specimens from Canada at the CNC, PCYU, ROM, and RSKM. As *E. ilicis* ranges into New York and New England, its occurrence in eastern Canada is entirely plausible. For this reason, I have not excluded *E. ilicis* from the present key, and treat it as a possible Canadian species.

**DNA barcoded material.** Unavailable.

**Non-barcoded material examined.** CANADA: None. USA: **Georgia:** Fort Gordon (Richmond County), 25.iv.1959 (paratype ♂, NCSU); Rabun Bald (Rabun County), 14.vii.1957, J.G. Chillcott (1♀, CNC); Satolah (Rabun County), 01.vii.1957, J.R. Vockeroth (1♀, CNC), 04.vii.1957, W.R.M. Mason (1♂, CNC); St. Catherines Island (Liberty County), 10-14.iv.1991, J.G. Rozen, E. Quinter, and A. Sharkov (1♀, AMNH); **Massachusetts:** Amherst, Spring 1929, L.A. Carruth (1♂, USNM); **North Carolina:** Highlands, 27.vi.1957, W.R.M. Mason (1♀, CNC); Highlands (Horse Cove), 25.vi.1957, W.R.M. Mason (1♂, CNC), 27.vi.1957, J.R. Vockeroth (4♂, CNC); Highlands (Whiteside Mountain), 11.vii.1937, T.B. Mitchell (paratype ♂, NCSU), 29.vi.1957, W.R.M. Mason (1♀, CNC), 29.vi.1957, J.R. Vockeroth (1♀, CNC); Wayah Bald (Macon County), 06.vii.1957, W.R.M. Mason (1♀, CNC); **South Carolina:** Hunting Island State Park (Beaufort County), 08.iv.1963, J.G. and B.L. Rozen (1♂, AMNH); McClellanville, 12.v.1944, H. and K. Townes (paratype ♂, NCSU), 19.v.1944, H. and G. Townes (paratype ♂, NCSU); Mountain Rest, 14.vi.1957, W.R.M. Mason (1♂, CNC).

### *Epeolus interruptus* Robertson, 1900

Figures 4d, 5c, 8a, 9a;

Plate 1, Figure H; Plate 2, Figure H; Plate 3, Figure H;

Map 8

*Epeolus interruptus* Robertson, 1900. Trans. Acad. Sci. St. Louis 10: 55 (♀).

**Primary type specimen.** Holotype ♀ (INHS, catalog number: 44384). **Collection information.** USA: Illinois: Carlinville, C. Robertson.

### Diagnosis

The distinguishing features that separate *E. interruptus* from all other *Epeolus* in North America include the presence of a blunt median process on the metanotum, which is partially if not entirely obscured by tomentum, and the very wide discal patch of T1 uniquely forming a rounded triangle with concave lateral sides. Other defining attributes include the following in combination: F2 of female antenna noticeably longer than wide; mesoscutum with paramedian band; axilla with tip inconspicuous, and axilla rather small and tip not extending beyond midlength of mesoscutellum; and T1–T4 with basal and apical fasciae interrupted medially.

### Redescription

**FEMALE:** Length 7.6 mm; head length 2.3 mm; head width 2.8 mm; fore wing length >6.6 mm (margins of

both very worn in holotype).

**Integument colouration.** Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, labrum, antenna, pronotal lobe, tegula, axilla, mesoscutellum, legs, and pygidial plate. Mandible with apex darker than all but extreme base. Preapical tooth faintly lighter than mandibular apex (difficult to see in holotype; described from non-type specimens). Antenna brown except scape, pedicel, and F1 orange in part. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

**Pubescence.** Face with tomentum densest around antennal socket. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with paramedian band. Mesopleuron with upper half hairy, except patch beneath base of fore wing (hypoepimeral area); ventrolateral half nearly bare. Metanotum with tomentum denser medially except for bare patch on apical half, uniformly off white. T1 with discal patch very wide, the basal and apical fasciae only narrowly joined laterally and forming rounded triangle with lateral sides concave. T1 with basal fascia interrupted medially, T1–T4 with apical fasciae interrupted medially and narrowed before becoming somewhat broader laterally, and T2 with fascia with anterolateral extensions of sparser tomentum. T5 with two large patches of pale tomentum lateral to and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, defined by silvery setae on flat disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by 1/3 MOD.

**Surface sculpture.** Punctures dense. Labrum with larger punctures than clypeus, but punctures of both more or less equally dense ( $i < 1d$ ). Small impunctate shiny spot present lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally ( $i < 1d$ ), less so laterally ( $i = 1-2d$ ). Mesopleuron with denser ( $i \leq 1d$ ) punctures in upper half than ventrolateral half ( $i > 1d$ ), the interspaces shining. Metasomal terga with punctures very fine, dense ( $i \approx 1d$ ), evenly distributed on disc.

**Structure.** Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel present. Scape with greatest length  $1.8 \times$  greatest width. F2 noticeably longer than wide ( $L/W$  ratio = 1.4). Preoccipital ridge not joining hypostomal carina, from which it is separated by no less than 1 MOD at its terminal. Mesoscutellum moderately bigibbous. Axilla small to intermediate in size, its lateral margin less than half as long as mesoscutellar width ( $L/W$  ratio = 0.38) and tip not extending beyond midlength of mesoscutellum; axilla with tip visible, but unattached to mesoscutellum for less than 1/3 its medial length;

axilla with lateral margin relatively straight and without carina. Metanotum with blunt median process obscured by tomentum. Fore wing with three submarginal cells. Pygidial plate apically truncate.

**MALE:** Description as for female except for usual secondary sexual characters and as follows: F2 shorter, but still longer than wide ( $L/W$  ratio = 1.2); S4 and S5 with much longer silvery to coppery subapical hairs; pygidial plate apically rounded, with large deep, closely clustered punctures, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure H.

**Male genitalia.** Plate 3, Figure H.

### Discussion

*Epeolus interruptus* is an enigmatic species, and does not closely resemble any other in Canada. Punctuation density of the mesopleuron is generally variable ( $1 \geq i > 1$ ), showing continuous variation with no consistent geographic pattern among specimens. Although the axilla and mesoscutellum are typically all-ferruginous, in some examined specimens they are partially to entirely black. I do not know of very many records of this species in Canada, and presumably it is uncommon in the northern part of its range.

**HOST RECORDS:** According to Brumley (1965), the *Colletes* host of *E. interruptus* is *C. aestivalis* Patton, but no details were provided with regard to the basis of this apparent association. In Cache County, Utah, USA, several *E. interruptus* specimens were collected with many co-occurring *C. willistoni* Robertson (all from *Physalis longifolia* Nutt. [Solanaceae]) on several dates in July 2015 at the same locality, suggesting a different host-parasite association (T. Griswold, personal communication, 2015).

**FLORAL RECORDS:** Robertson (1929) reported *E. interruptus* on *Coreopsis* L. (Asteraceae), *Krigia* Schreb. (Asteraceae), *Psoralea* L. (Fabaceae), and *Rudbeckia* L. (Asteraceae). Mitchell (1962) indicated additional associations with *Chrysanthemum* L. (Asteraceae) and *Trifolium* L. (Fabaceae), and Discover Life (Ascher and Pickering 2016) indicates a floral association with *Baccharis* L. (Asteraceae). Labels of examined voucher specimens further indicate associations with *Kallstroemia* Scop. (Zygophyllaceae), *Melilotus albus* Medik. (Fabaceae), and *Physalis longifolia*.

**Distribution in Canada:** Central to Western Canada, east of the Rocky Mountains (Map 8).

**DNA barcoded material.** Available. BOLD:ACZ9058. Specimens examined and sequenced.—USA: **Arizona:** Geronimo Trail at Sycamore Creek (Cochise County),

28.viii.2016, L. Packer (3♀, 2♂, PCYU); **Utah:** 1 km W Hyrum Dam (Cache County), 19.vii.2015, T.L. Griswold (1♂, BBSL); **Virginia:** Lancaster (Lancaster County), 02-10.vi.2011, A.W. Hook (1♀, CTMI).

**Non-barcoded material examined.** CANADA: **Manitoba:** Aweme, 01.vii.1925, B.D. Bird (6♀, CNC); **Ontario:** Ottawa, 29.vii.1947, W.R.M. Mason (1♀, CNC).

Mexico: **Baja California:** San Vicente, 08.vii.1963, P.D. Hurd (1♂, EMEC); USA: **Arizona:** 1 mi E Douglas (Cochise County), 16.viii.1962, M. Statham (1♀, AMNH); 14 mi SW Apache (Cochise County), 04.viii.1961, J.G. Rozen (1♂, AMNH); 15 mi SW Apache (Cochise County), 23.viii.1997, B. McAdams and J.G. Rozen (1♀, AMNH); 18 mi SW Apache (Cochise County), 18.viii.1994, J.S. Ascher and J.G. Rozen (1♂, AMNH); 26 mi E Douglas, 29.viii.2013, G. Rowe (1♂, PCYU); AZ-80 (Cochise County), 03.v.2012, A. Payne and J.G. Rozen (1♂, AMNH); **Iowa:** Sioux City, 10.vii.1920, C.N. Ainslie (1♀, AMNH); **Louisiana:** C.F. Baker (1♂, USNM); **Nebraska:** Cedar Point Biological Station (Keith County), 11-18.vii.1968, J.G. Rozen and E. Quinter (1♀, AMNH); **New Mexico:** 1.8 km NW Manzano (Cañon Nuevo), 02.viii.2009, T.L. Griswold (1♂, BBSL); 4 mi N NW Las Vegas, 02.vii.1946, B.A. Maina (1♂, FMNH); **Texas:** 6 mi W Uvalde (Uvalde County), 22.iii.2001, J.L. Neff (1♀, CTMI); Chaparral Wildlife Management Area (Dimmit County), 16-18. iv.1993, A.W. Hook (1♀, CTMI); San Antonio, H.B. Parks (1♀, AMNH); **Utah:** 1 km W Hyrum Dam (Cache County), 05.vii.2015, T.L. Griswold (1♂, BBSL).

### *Epeolus lectoides* Robertson, 1901

Figures 4b, 5b, 6b, 7b;

Plate 1, Figure I; Plate 2, Figure I; Plate 3, Figure I;

Map 9

*Epeolus lectoides* Robertson, 1901. Can. Entomol. 33: 231 (♀).

**Primary type specimen.** Holotype ♀ (INHS, catalog number: 44383). **Collection information.** USA: Illinois: Carlinville, C. Robertson.

*Epeolus semilectus* Cockerell, 1907. Entomologist 40: 136 (♂).

**Primary type specimen.** Holotype ♂ (USNM, catalog number: 534053). **Collection information.** USA: Virginia: Falls Church, 04.vii.????, N. Banks.

### Diagnosis

Although separated from *E. bifasciatus* in the key, this species most closely resembles *E. ilicis* among Canadian

*Epeolus*, particularly in the campanulate shape of the pseudopygidial area of T5 in the female. *Epeolus ilicis* and *E. lectoides* exhibit several structural similarities (F2 of female antenna noticeably longer than wide, axilla distinctly hooked, and metasomal terga with sparse punctation), but in contrast to *E. ilicis* the mandible of *E. lectoides* is with a preapical tooth, the ventrolateral half of the mesopleuron of *E. lectoides* is sparsely punctate ( $i > 1d$ ), and the axilla of *E. lectoides* is angled posteriorly and its tip extends well beyond the midlength of the mesoscutellum.

### Redescription

**FEMALE:** Length 8.7 mm; head length 2.2 mm; head width 3.1 mm; fore wing length 7.2 mm.

**Integument colouration.** Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, labrum, antenna, pronotal lobe, tegula, axilla, and legs. Mandible with apex darker than all but extreme base. Preapical tooth faintly lighter than mandibular apex. Flagellum brown and (except F1) faintly lighter than partially dark brown (otherwise orange) scape and F1 and entirely dark brown pedicel, generally due to extensive pilosity on flagellum. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline and dusky in part. Legs more extensively reddish orange than brown or black. **Pubescence.** Face with tomentum tarnished in the *E. lectoides* holotype, but white and densest around antennal socket in non-type specimens. Tomentum slightly sparser on clypeus; upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white setae. Mesoscutum with paramedian band. Mesopleuron with upper half sparsely hairy, ventrolateral half nearly bare. Metanotum with tomentum uninterrupted except for median bare patch on apical half, uniformly white. T1 with discal patch quadrangular and very wide, the basal and apical fasciae only narrowly joined laterally. T1 with basal and apical fasciae and T2–T4 with apical fasciae separated medially, those of T2 and T3 somewhat broader laterally, and T2 with fascia with faint anterolateral extensions of sparser pale tomentum. T5 with two large patches of pale tomentum lateral to and separate from pseudopygidial area. T5 with pseudopygidial area campanulate, its apex less than twice as wide as medial length, defined by silvery setae on impressed disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by 2/5 MOD.

**Surface sculpture.** Punctures dense, but those of head and mesosoma sparser in some areas, larger, deep, and distinct. Labrum with larger punctures than clypeus, but punctures of both equally dense ( $i < 1d$ ). Small impunctate

shiny spot present lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla very coarsely and densely punctate; the interspaces shining. Tegula very densely punctate mesally ( $i < 1d$ ), less so laterally ( $i = 1-2d$ ). Mesopleuron with denser ( $i \leq 1d$ ) punctures in upper half than ventrolateral half ( $i > 1d$ ), the interspaces shining. Metasomal terga with punctures very fine, dense ( $i = 1-2d$ ), evenly distributed on disc; the interspaces shining somewhat.

**Structure.** Preapical tooth blunt and obtuse. Labrum with pair of small subapical denticles preceded by small discreet ridges. Frontal keel present. Scape with greatest length  $1.8 \times$  greatest width. F2 noticeably longer than wide ( $L/W$  ratio = 1.6). Preoccipital ridge not joining hypostomal carina, from which it is separated by less than 1 MOD at its terminal (difficult to see in the *E. lectoides* holotype; described from non-type specimens). Mesoscutellum moderately bigibbous. Axilla large, its lateral margin half as long as mesoscutellar width ( $L/W$  ratio = 0.51) and tip extending well beyond midlength of mesoscutellum but not attaining apex; axilla with tip conspicuously diverging from side of mesoscutellum, distinctly hooked, and axilla with free portion  $2/5$  its medial length; axilla with lateral margin arcuate (somewhat) and carinate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

**MALE:** Description as for female except for usual secondary sexual characters and as follows: F2 shorter, but still longer than wide ( $L/W$  ratio = 1.4); S4 and S5 with much longer silvery to coppery subapical hairs; pygidial plate apically rounded, with large deep punctures more or less evenly spaced throughout, with the interspaces somewhat dull.

**Male hidden sterna.** Plate 2, Figure I.

**Male genitalia.** Plate 3, Figure I.

### Discussion

Mitchell (1962) synonymized *Epeolus semilectus* under *Epeolus lectoides*. I have examined the male holotype specimen of *E. semilectus*, and agree with Mitchell's treatment. Excluding sex-specific characters, the redescription of the *E. lectoides* holotype with few exceptions (related to intraspecific variation in size and colour) applies equally well to that of *E. semilectus*. Cockerell (1907) suggested that *E. semilectus* is a "geographical race" of *E. lectoides*, but one in which only a single metasomal fascia is interrupted medially. In fact, all metasomal fasciae of the *E. semilectus* holotype are narrowly interrupted medially except for the apical fascia of T1, which is more widely interrupted than the other fasciae.

**HOST RECORDS:** Inferred *Colletes* hosts of *E. lectoides*,

based on co-occurrence, are *C. latitarsis* Robertson (Shapiro and Droege 2010) and *C. nudus* Robertson (Ascher *et al.* 2014). It should be noted, however, that the single specimen of *C. latitarsis* was collected two months earlier than the specimen of *E. lectoides*, and at a different site within the larger study area around the Cove Point Liquefied Natural Gas Site in Calvert County, Maryland, USA.

**FLORAL RECORDS:** Robertson (1929) reported *E. lectoides* on *Pycnanthemum* Michx. (Lamiaceae). Mitchell (1962) indicated additional associations with *Ceanothus* L. (Rhamnaceae), *Cephalanthus* L. (Rubiaceae), *Helenium* L. (Asteraceae), *Hypericum* L. (Hypericaceae), and *Rhus* L. (Anacardiaceae). Collection records on Discover Life (Ascher and Pickering 2016) indicate the following floral associations: *Achillea millefolium* L. (Asteraceae), *Lycopus* L. (Lamiaceae), *Mentha X piperita* L. (Lamiaceae), *Pluchea odorata* (L.) Cass. (Asteraceae), *Tanacetum vulgare* L. (Asteraceae), and *Teucrium canadense* L. (Lamiaceae). Labels of examined voucher specimens further indicate associations with *Cryptantha cinerea* (Greene) Cronquist (Boraginaceae) and *Dalea villosa* (Nutt.) Spreng. This species has been collected on *Melilotus albus* Medik. (Fabaceae) in Point Pelee National Park, Ontario, Canada (R. Ferrari, personal communication, 2016).

**Distribution in Canada:** Central Canada (Map 9).

**DNA barcoded material.** Available. BOLD:AAF2273. Specimens examined and sequenced.—**CANADA:** **Ontario:** Point Pelee National Park (Essex County), 25-30.vii.2003, Paiero and Cheung (1♂ DEBU); Rondeau Park, 01.viii.2005, M. Buck (1♂, DEBU). **USA:** **Nebraska:** Mahoney State Park (Cass County), 2-3.vii.2011, J. Droege Mueller (1♂, BIML); **South Carolina:** (1♀, 2♂, PCYU).

**Non-barcoded material examined.** **CANADA:** **Ontario:** Pinery Provincial Park, 25-28.vi.1986, L. Packer (1♂, PCYU); Point Pelee, 02.viii.1920, N.K. Bigelow (1♀, ROM), 04.viii.1920, N.K. Bigelow (1♀, 1♂, ROM), 08.viii.1920, N.K. Bigelow (1♀, ROM), 13.viii.1920, N.K. Bigelow (4♂, ROM), 29.vii.2003, M. Buck (6♂, DEBU); Point Pelee National Park (Essex County), 25-30.vii.2003, Paiero and Cheung (1♀, 1♂ DEBU), 26-27.vii.2016, R. Ferrari and T.M. Onuferko (7♀, 10♂, PCYU); Rondeau Park, 29.vii.-14.viii.2003, S.M. Paiero and S.A. Marshall (3♀, DEBU), 14.viii.2003, S.M. Paiero (1♀, DEBU).

**USA:** **Kansas:** 0.5 mi N & 3.3 mi E Crestline (Cherokee County), 26.vi.1965, G.F. Hevel (1♂, USNM); Breidenthal Biological Reserve (15 mi SE Lawrence, Douglas County), 30.vi.1979, R.J. McGinley (1♂,

USNM); **Maryland:** 4 mi SE Salisbury (Wicomico County), 30.viii.2007, M. Buck (1♀, DEBU); Blackwater National Wildlife Refuge (Dorchester County), 12.viii.2015, S.W. Droege (1♂, BIML); **New Jersey:** Edwin B. Forsythe National Wildlife Refuge, 26-27.viii.2008, A. Mortens and D. Conrad (1♀, BIML); **New York:** Gardiners Island (Suffolk County), 17-23.viii.1918 (1♂, AMNH), 04.viii.2007, J.S. Ascher, R.G. Goelet, and J.G. Rozen (1♂, AMNH), 25.viii.2008, R.G. Goelet (1♀, AMNH); **North Carolina:** Kill Devil Hills, 30.vi.1950, K.V. Krombein (1♀, AMNH), 04.vii.1950, K.V. Krombein (1♀, AMNH); **North Dakota:** Sheldon, 25.vii.1949, O.A. Stevens (1♀, AMNH); **South Carolina:** Carolina Sandhills National Wildlife Refuge (Chesterfield County), 07.ix.2006, S.W. Droege (1♀, BIML); **Virginia:** Chincoteague National Wildlife Refuge (Accomack County), 1-2.vii.2006, S.W. Droege (1♀, 2♂, BIML).

### *Epeolus minimus* (Robertson, 1902)

Figures 8b, 13d, 15b, 16a, 18a;

Plate 1, Figure J; Plate 2, Figure J; Plate 3, Figure J;

Map 10

*Triepeolus minimus* Robertson, 1902. Entomol. News 13: 81 (♀).

*Argyroselenis minima* Robertson, 1903. Can. Entomol. 35: 284.

**Primary type specimen.** Holotype ♀ (INHS, catalog number: 62276). **Collection information.** USA: Illinois: Carlinville, C. Robertson.

*Epeolus beulahensis* Cockerell, 1904. Ann. Mag. Nat. Hist. 13: 40 (♀), **new synonymy**

**Primary type specimen.** Holotype ♀ (USNM, catalog number: 534040). **Collection information.** USA: New Mexico: Beulah, 11.vii.????, Cockerell.

*Epeolus lutzi* Cockerell, 1921. Am. Mus. Novit. 23: 16 (♂), **new synonymy**

**Primary type specimen.** Holotype ♂ (AMNH, catalog number: 25098). **Collection information.** USA: Colorado: Walsenburg, 14.vi.1919.

*Epeolus lutzi dimissus* Cockerell, 1921. Am. Mus. Novit. 23: 16 (♀), **new synonymy**

**Primary type specimen.** Holotype ♀ (AMNH, catalog number: 25099). **Collection information.** USA: Colorado: Leadville, 03-05.viii.1919.

*Epeolus arciferus* Cockerell (in Cockerell and Sandhouse, 1924). Proc. Calif. Acad. Sci. (4) 13: 319 (♀), **new synonymy**

**Primary type specimen.** Holotype ♀ (CAS, catalog number: 01614). **Collection information.** USA: California: Pacific Grove (Monterey County), ix.1920, F.E. Blaisdell.

*Epeolus pilatei* Cockerell (in Cockerell and Sandhouse, 1924). Proc. Calif. Acad. Sci. (4) 13: 320 (♀), **new synonymy**

**Primary type specimen.** Holotype ♀ (CAS, catalog number: 01615). **Collection information.** USA: California: San Pedro, 25.x.1909, G.R. Pilate.

*Epeolus eastwoodae* Cockerell, 1937. Pan-Pac. Entomol. 13: 149 (♂).

**Primary type specimen.** Holotype ♂ (CAS, catalog number: 04651). **Collection information.** USA: California: Cuyler's Cove (San Miguel Island), 27.vii.1937, Cockerell.

### Diagnosis

Among Canadian species, *E. minimus* most closely resembles *E. olympiellus*, and the two can be difficult to distinguish from one another where their ranges overlap. *Epeolus minimus* can be readily distinguished from all other *Epeolus* in Canada except *E. olympiellus* by the following combination of features: F2 of female at least 1.2 × as long as wide; mesoscutum with paramedian band (if not entirely obscured by pale tomentum); mesopleuron closely and evenly punctate; axilla with lateral margin relatively straight, axilla with tip clearly separated from lateral margin of mesoscutellum and not extending much beyond midlength of mesoscutellum; axilla (except perhaps tip) and mesoscutellum all black; and T2 with fascia with anterolateral extensions of tomentum. *Epeolus minimus* typically exhibits reddish orange colouration on the labrum (apically or entirely), antenna, and quite extensively on the legs. In *E. olympiellus*, the fasciae of T3 and T4 are typically entirely broken or greatly narrowed laterally, a state not observed in specimens of *E. minimus*.

### Redescription

**FEMALE:** Length 7.7 mm; head length 2.0 mm; head width 2.6 mm; fore wing length 6.2 mm.

**Integument colouration.** Mostly black; notable exceptions as follows: partially to entirely ferruginous on mandible, labrum, antenna, pronotal lobe, tegula, axilla, legs, and pygidial plate. Mandible with apex and preapical tooth darker than all but extreme base. Flagellum brown and (except F1) faintly lighter than partially dark brown (otherwise orange) scape, pedicel, and F1, generally due to extensive pilosity on flagellum. Axilla only with tip orange in the *E. minimus* holotype (axilla all black in the *E. beulahensis* holotype).

Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black. *Pubescence.* Face with tomentum densest around antennal socket. Tomentum mostly rubbed off on clypeus of the *E. minimus* holotype, but dense in the *E. beulahensis* holotype. Upper paraocular and frontal areas, and vertexal area mostly exposed. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with paramedian band. Mesopleuron in both the *E. minimus* and *E. beulahensis* holotypes with dense tomentum, except for two sparsely hairy to entirely bare circular patches (one behind pronotal lobe, a larger one occupying much of ventrolateral half of mesopleuron). Metanotum with tomentum uninterrupted, uniformly off white. T1 with median quadrangular black discal patch enclosed by pale tomentum, except for medial separation at apex. T2 with fascia separated medially and with anterolateral extensions of equally dense tomentum. T3 and T4 with fasciae complete, but somewhat narrowed medially. T5 with two large patches of pale tomentum lateral to and separate from pseudopygidial area. T5 with pseudopygidial area lunate, its apex at least twice as wide as medial length, defined by silvery setae on impressed disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by 2/5 MOD.

*Surface sculpture.* Punctures dense. Labrum with larger and sparser punctures ( $i=1-2d$ ) than clypeus ( $i<1d$ ). Small impunctate spot present lateral to lateral ocellus (dull in the *E. minimus* holotype, but shiny in the *E. beulahensis* holotype). Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally ( $i<1d$ ), less so laterally ( $i=1-2d$ ). Mesopleuron largely obscured by tomentum, but ventrolateral half densely punctate ( $i<1d$ ) to rugose where exposed; mesopleuron with punctures more or less equally dense throughout where exposed. Metasomal terga with punctures very fine, dense ( $i\approx 1d$ ), evenly distributed on disc.

*Structure.* Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel present. Scape with greatest length  $1.7 \times$  greatest width. F2 noticeably longer than wide (L/W ratio = 1.4). Preoccipital ridge not joining hypostomal carina, from which it is separated by 1.5 MOD at its terminal. Mesoscutellum moderately bigibbous. Axilla intermediate in size, its lateral margin nearly half as long as mesoscutellar width (L/W ratio = 0.40) and tip not extending much beyond midlength of mesoscutellum; axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 its medial length; axilla with lateral margin relatively straight and without carina. Fore wing with three submarginal cells. Pygidial plate apically truncate.

MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, not noticeably longer than wide (L/W ratio = 1.1); S4 and S5 with much longer silvery to coppery subapical hairs; pygidial plate apically rounded, with large deep punctures more or less evenly spaced throughout, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure J.

**Male genitalia.** Plate 3, Figure J.

### Discussion

This species, originally placed in *Triepeolus*, is very widely distributed in North America. Following its transfer to the now defunct genus *Argyroselenis* Robertson, the first record of its correct transfer to the genus *Epeolus* I have seen in the literature is in Mitchell (1962), but the change in taxonomic status was not listed as a new combination. Given its variability, as well as its similarity to *E. banksi* (in eastern USA), *E. olympiellus* (in western North America), and a Californian species that has yet to be formally recognized, *E. minimus* has been the subject of much taxonomic confusion. Brumley (1965) proposed 10 unpublished synonymies of *E. minimus*, but discussed several intraspecific groups that could not be separated logically or consistently. Although opting to consider them as conspecific, Brumley (1965) acknowledged that further study may indicate that some of these groups represent distinct species. Barcode sequencing to date has shown there to be at least three valid species in the “*minimus* group”, one of which (*E. olympiellus*) does not appear to occur east of the Rocky Mountains. With few exceptions (related to intraspecific variation in size and colour), the *E. beulahensis* holotype agrees with the present redescription based on the *E. minimus* holotype, which compares and contrasts the two specimens. In Cockerell’s (1904) original description, no comparisons of the *E. beulahensis* holotype were made to *E. minimus*. Cockerell (1904) suggested that *E. beulahensis* is closely allied to *E. autumnalis* (a very different species). Although barcode sequences are currently lacking for specimens from the two type localities of *E. beulahensis* and *E. minimus* (in Beulah, New Mexico and Carlinville, Illinois, respectively), the same BIN was assigned to specimens ranging widely from Yukon to Colorado and east to southern Ontario.

Additionally, Cockerell (1921) described this species under the names *E. lutzii* and *E. lutzii dimissus*. I have examined the types of both specimens, which exhibit the following features associated with *E. minimus*: labrum ferruginous apically; legs, except foreleg, orange from trochanters to tarsi; T2 with lobe-like anterolateral extensions; and T3 and T4 with fasciae complete. The

type localities (both in Colorado) fall within the range of sequenced specimens.

Brumley (1965) discussed coastal and insular Californian types of *Epeolus* in the “*minimus* group”, for which the names *E. arciferus* Cockerell, *E. eastwoodae* Cockerell, and *E. pilatei* Cockerell have been applied. *Epeolus eastwoodae* has since been synonymized under *E. minimus* by Rust (1984). The three type specimens from California, which I have examined, are very similar to one another, and their integument (including that of the pronotal lobe) is virtually all black. However, the pattern of pubescence on the metasoma is like that of the *E. minimus* holotype (the fasciae of T3 and T4 are complete or narrowly interrupted medially, and not broken or conspicuously narrowed laterally). There is continuous variation in the degree of reddish orange colouration of the integument among sequenced specimens. *Epeolus minimus* from Canada should exhibit reddish orange colouration on at least one of the following: labrum, antenna (scape, pedicel, and F1 in part), and legs. One sequenced specimen (CCDB-28312 A02) from Abbots Lagoon, California closely resembles the holotypes of *E. arciferus* and *E. pilatei*, and the three specimens were collected at the same time of year (between September and October). This coastal Californian specimen did not barcode differently from sequenced specimens identified as *E. minimus*.

**HOST RECORDS:** Graenicher (1906) reported *E. minimus* in association with *C. eulophi* Robertson based on detailed observations of a female *Epeolus* that repeatedly examined and entered the nest of a female *Colletes*. No comments were provided with respect to the confidence with which the specimens of either genus were identified to species.

**FLORAL RECORDS:** Collection records on Discover Life (Ascher and Pickering 2016) indicate the following floral associations: *Chrysothamnus viscidiflorus* (Hook.) Nutt. (Asteraceae), *Grindelia squarrosa* (Pursh) Dunal (Asteraceae), *Helianthus petiolaris* Nutt. (Asteraceae), *Heterotheca villosa* (Pursh) Shinnars (Asteraceae), *Mulgedium oblongifolium* (Nutt.) Reveal (Asteraceae), *Potentilla hippiana* Lehm. (Rosaceae), and *Solidago* L. (Asteraceae). Labels of examined voucher specimens further indicate associations with *Chrysopsis* (Nutt.) Elliot (Asteraceae), *Dalea candida* Michx. ex Willd. (Fabaceae), *D. purpurea* Vent., *Melilotus albus* Medik. (Fabaceae), *Malacothrix* DC. (Asteraceae), *Sphaeralcea coccinea* (Nutt.) Rydb. (Malvaceae), *Solidago canadensis* L., and *S. rigida* L.

**Distribution in Canada:** Known to occur in most of Canada except parts of the Atlantic and high Arctic regions (Map 10).

**DNA barcoded material.** Available. BOLD:AAD3554. Specimens examined and sequenced.—CANADA: **Alberta:** Medicine Hat, 13.vi.2007, J. Gibbs and C. Sheffield (1♂, PCYU); Onefour, 23.vii.2010, N. de Silva (1♂, PCYU); **Ontario:** Caledon (Forks of the Credit Provincial Park), 14.vii.2003, J. Grixti (1♂, PCYU); King, 14.vii.2003, A. Gravel (1♀, PCYU); **Saskatchewan:** Sands Hills (7 km W Piapot), 04.vii.2009, D. Larson (3♂, PCYU); **Yukon:** Takhini River (west dunes 6.8 km NNE Kusawa Lake outlet), 21.vii.2009, L. Mennell (1♂, RSKM).

USA: **California:** Abbots Lagoon (Point Reyes National Seashore, Marin County), 04.x.2011, J. Powell (1♂, EMEC); **Colorado:** (1♀, PCYU); Near Wolf Creek (Mineral County), 28.vii.2007, J. Gibbs and C. Sheffield (1♀, PCYU); **Idaho:** (1♀, PCYU); Daniels Reservoir (Oneida County), 25.vii.1995, F.D. Parker (1♀, BBSL), 11.vii.1997, F.D. Parker (1♂, BBSL); **Utah:** 5 mi S Long Valley Junction (Kane County), 04.ix.2008, T.L. Griswold (1♀, BBSL).

**Non-barcoded material examined.** CANADA: **Alberta:** Gleichen, 30.vii.1929, G.F. Manson (1♀, CNC), 30.vii.1929, H.L. Seamans (1♀, CNC); Lethbridge, 18.viii.1917, Sladen (1♀, CNC); Medicine Hat, 20.viii.1916, Sladen (4♀, 1♂, CNC), 01.viii.1917, Sladen (2♀, CNC), 15.viii.1917, Sladen (2♂, CNC), 17.viii.1917, Sladen (5♀, 7♂, CNC); Peace River, 12.vii.1932, L.S. Russell (1♀, CNC); **British Columbia:** Clinton (Fish Hatchery on Loon L. Rd.), 11.vii.1969 (1♀, ROM); Kamloops, 13.viii.1948, L.C. Curtis (1♀, CNC); Langford, 14.vii.1960, D. Evans (1♀, CNC), 13.vii.1961, D. Evans (1♀, CNC); Maple Bay (Vancouver Island), 12.vii.1933, J. McDunnough (2♀, CNC); Nicola, 03.viii.1923, E. R. Buckell (1♀, CNC); Salmon Arm, 04.vii.1914, F.W.L. Sladen (1♀, CNC), 26.vi.1925, A.A. Dennys (2♀, CNC), 27.vi.1925, A.A. Dennys (1♀, 1♂, CNC); Vernon, 25.vii.1917, Sladen (3♀, CNC), 28.vii.1920, M.H. Ruhmann (1♀, CNC); **Manitoba:** Aweme, 21.viii.1923, R.M. White (1♂, CNC); Birds Hill, 27.viii.1916, J.B. Wallis (1♀, CNC); Blumenort, 09.vii.1968, T. Harcus (1♂, ROM); Brandon, 11.vii.1916, Sladen (1♂, CNC); Carmen, 30.vii.1968, T. Harcus (1♂, ROM); Delta, 19.vi.1968, T. Harcus (1♂, ROM); La Salle, 10.vii.1973, T.D. Galloway (1♂, DEBU); Riding Mountain National Park of Canada (3 km E Clear Lake), 20.viii.1979, S. and J. Miller (1♀, CNC); Selkirk, 07.viii.1917 (1♀, CNC); Turtle Mountain Forest Reserve (International Peace Garden), 07.viii.1958, J.G. Chillcott (1♂, CNC); Winnipeg, 02.viii.1916, J.B. Wallis (1♀, CNC); **Northwest Territories:** Fort Simpson, 22.vii.1950, D.P. Whillans (1♀, CNC); Fort Smith, 18.viii.1950, J.B. Wallis (2♀, CNC), 27.viii.1950, J.B. Wallis (2♀, CNC); Norman Wells, 13.vii.1949, W.R.M.

Mason (1♀, CNC), 23.vii.1949, W.R.M. Mason (1♀, CNC); **Ontario:** Caledon (Forks of the Credit Provincial Park), 15.vii.1968, P. MacKay (1♀, ROM), 15.vii.2002, J. Grixti (1♂, PCYU), 30.vii.2002, J. Grixti (1♀, PCYU); Dyer's Bay, 08-29.vii.1952, D.H. Pengelly (3♀, 2♂, CNC), 13.viii.1953, D.H. Pengelly (1♂, CNC), 30.vii.1953, D.H. Pengelly (1♂, CNC); King, 14.vii.2003, J. Grixti (1♂, PCYU); Leaside, 07.vii.1959 (1♀, ROM); Norquay Prov. Rec. Area (Portage La Prairie), 10.viii.1970 (1♀, ROM); Rainy River, 05.vii.1960, S.M. Clark (1♀, CNC), 03.viii.1960, S.M. Clark (1♀, CNC); **Quebec:** Mont-Joli, 13.viii.1948, J.R. McGillis (1♂, CNC), 31.vii.1954, J.R. McGillis (1♂, CNC), 01.viii.1954, J.R. McGillis (1♂, CNC); **Saskatchewan:** Christopher Lake, 08-15.vii.1959, A. and J. Brooks (2♀, 1♂, CNC); Elbow, 12.vii.1960, A.R. Brooks (1♂, CNC); Great Sand Hills, 04.vi.1988, M. Polak (1♀, CNC), 11.vii.2010, D. Larson (3♂, PCYU); Harris Res. (10 km S Maple Creek), 15.ix.2004, D. Larson (1♀, PCYU), 16.ix.2004, D. Larson (2♀, PCYU); Heglund Island, 31.vii.2010, D. Larson (1♂, PCYU); Prince Albert, 23.vii.1959, A. and J. Brooks (1♀, 1♂, CNC); Rockglen, 03.viii.1955, C.D. Miller (1♀, CNC); Rutland, 02.viii.1940, A.R. Brooks (1♀, CNC); Sands Hills (7 km W Piapot), 04.vii.2009, D. Larson (3♂, PCYU); **Yukon:** Whitehorse, 04.vii.1948, M.T. Hughes (1♀, CNC), 06.vii.1948, W.R.M. Mason (1♀, CNC).

**USA: California:** 1 mi SE Manila (Humboldt County), 20.viii.1975, J. Powell (1♂, EMEC); Goat Rock State Beach – Sonoma Coast State Park (Sonoma County), 22.viii.1968, M.E. Irwin (2♀, UCR); Hermosa Valley Park, 30.ix.1984, R. Rogers (1♀, UCR); Morro Bay (San Luis Obispo County), 18.viii.1990, J. Powell (1♂, EMEC); Oso Flaco Lake (San Luis Obispo County), 29.vi.1967, M.E. Irwin, T. Cronin, and S. Larisch (1♀, UCR); S Spur Road (Santa Barbara County), 25.vi.2005, G.R. Ballmer (1♂, UCR); San Pedro Naval fuel reserve site (Los Angeles County), 28.iii.1995, R. Rogers and R. Mattoni (1♂, UCR); **Florida:** Lee County, 10.xi.1983, L. Packer (1♀, PCYU); **Idaho:** Ketchum (Blaine County), 24.vi.2007, J. Gibbs and C. Sheffield (1♀, PCYU); **Illinois:** Argonne National Laboratory (DuPage County), 11.vii.1967, J. Wagner (1♂, FMNH); **Montana:** 17 km N. Billings (Yellowstone County), C.D. Michener (1♀, KUNHM); **Oregon:** Tumalo Reservoir, 23.vi.1954, G.F. Knowlton (1♂, KUNHM); **South Dakota:** Badlands National Park (Pennington County), 19.vi.2012, S.W. Droege (1♀, BIML).

#### *Epeolus olympiellus* Cockerell, 1904

Figures 1b, 2b, 3c, 14b, 15c, 16b, 18b, 19, 20;

Plate 1, Figure K; Plate 2, Figure K; Plate 3, Figure K;

Map 11

*Epeolus olympiellus* Cockerell, 1904. Ann. Mag. Nat. Hist. 13: 41 (♂).

**Primary type specimen.** Holotype ♂ (USNM, catalog number: 534051). **Collection information.** USA: Washington: Olympia, 02.vii.1896, T. Kincaid.

*Epeolus tricolor* Viereck, 1905. Can. Entomol. 37: 280 (♀), **new synonymy**

**Primary type specimen.** Holotype ♀ (ANSP, catalog number: 10123). **Collection information.** CANADA: British Columbia: Vancouver.

*Epeolus humillimus* Cockerell, 1918. Ann. Mag. Nat. Hist. (9) 1: 160 (♂), **new synonymy**

**Primary type specimen.** Holotype ♂ (USNM, catalog number: 534047). **Collection information.** USA: Washington: Pullman, 02.viii.1908, W.M. Mann.

*Epeolus rufomaculatus* Cockerell and Sandhouse, 1924. Proc. Calif. Acad. Sci. (4) 13: 314 (♀), **new synonymy**

**Primary type specimen.** Holotype ♀ (CAS, catalog number: 01609). **Collection information.** USA: Utah: Logan, 14.vii.1922, E.P. Van Duzee.

*Epeolus rubrostrictus* Cockerell and Sandhouse, 1924. Proc. Calif. Acad. Sci. (4) 13: 318 (♀), **new synonymy**

**Primary type specimen.** Holotype ♀ (CAS, catalog number: 01613). **Collection information.** CANADA: British Columbia: Nanaimo (Nanaimo Biological Station), 24.vi.1920, E.P. Van Duzee.

#### Diagnosis

Among Canadian species, *Epeolus olympiellus* most closely resembles *E. minimus*. In *E. olympiellus*, T3 and T4 are with fasciae that may be entirely broken or greatly narrowed laterally, whereas in *E. minimus* T3 and T4 are with fasciae that are complete or only broken medially. The labrum, antenna, and legs of *E. olympiellus* are extensively dark and lack the bright reddish orange colouration typical of Canadian *E. minimus*. For an extensive list of similarities to *E. minimus* and comments with regard to separation from other species in Canada, see diagnosis for *E. minimus*.

#### Redescription

**MALE:** Length 7.5 mm; head length 2.2 mm; head width 2.9 mm; fore wing length 6.0 mm.

**Integument colouration.** Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, antenna, pronotal lobe, tegula, and legs. Mandible with apex darker than all but extreme base. Preapical tooth as dark as mandibular apex (difficult to see in the *E. olympiellus* holotype; described from the *E. humillimus*



holotype). Antennae, except left scape and pedicel, missing in the *E. olympiellus* holotype. Flagellum of most similar sequenced specimen brown and (except F1) faintly lighter than dark brown scape and pedicel, generally due to extensive pilosity on flagellum. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs, except tarsi, more extensively brown or black than reddish orange. **Pubescence.** Face with tomentum densest around antennal socket. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with paramedian band. Mesopleuron with upper half densely hairy, except patch beneath base of fore wing (hypoepimeral area); ventrolateral half nearly bare. Metanotum with tomentum uninterrupted except for median bare patch on apical half, uniformly pale yellow. T1 with median quadrangular black discal patch enclosed by pale tomentum, except for medial separation at apex. T2–T5 with fasciae interrupted medially and narrowed before becoming somewhat broader laterally, and T2 with fascia with anterolateral extensions of sparser tomentum. S4 and S5 with long silvery to coppery subapical hairs, which individually are often darker apically.

**Surface sculpture.** Punctures dense. Labrum with areas of sparser punctures ( $i=1-2d$ ) than clypeus ( $i<1d$ ). Small impunctate spot present lateral to lateral ocellus (larger and shinier in the *E. humillimus* holotype than in the *E. olympiellus* holotype). Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula very densely punctate mesally ( $i<1d$ ), less so laterally ( $i=1-2d$ ). Mesopleuron with ventrolateral half densely punctate ( $i<1d$ ) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense ( $i\approx 1d$ ), evenly distributed on disc.

**Structure.** Labrum with pair of small subapical denticles preceded by small discreet ridges. Frontal keel present. Scape with greatest length  $1.6 \times$  greatest width. F2 (missing in the *E. olympiellus* holotype) short in the *E. humillimus* holotype, not noticeably longer than wide ( $L/W$  ratio = 1.1). Preoccipital ridge not joining hypostomal carina, from which it is separated by 1.5 MOD at its terminal. Mesoscutellum moderately bigibbous. Axilla intermediate in size, its lateral margin nearly half as long as mesoscutellar width ( $L/W$  ratio = 0.40) and tip not extending much beyond midlength of mesoscutellum; axilla with tip clearly visible, but unattached to mesoscutellum for less than  $2/5$  its medial length; axilla with lateral margin relatively straight and without carina. Fore wing (on each side) with second submarginal crossvein incomplete. Pygidial plate mostly hidden in the *E. olympiellus* holotype, but apically rounded, with large deep punctures apically. Punctures sparser basally with the interspaces shining in non-type

specimens.

**FEMALE:** Description as for male except for usual secondary sexual characters and as follows: F2 noticeably longer than wide ( $L/W$  ratio = 1.3); T5 with two patches of pale tomentum bordering and separate from pseudopygidial area present only in female; T5 with pseudopygidial area lunate, its apex at least twice as wide as medial length, defined by silvery setae on flat disc of medioapical region elevated from rest of tergum. S4 and S5 with much shorter hairs (S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by  $1/3$  MOD); Pygidial plate apically truncate.

**Male hidden sterna.** Plate 2, Figure K.

**Male genitalia.** Plate 3, Figure K.

### Discussion

*Epeolus olympiellus* is a highly variable species that has been the subject of much taxonomic confusion. Cockerell (1904) believed it to be closely related to *E. interruptus*, but it is much more similar to *E. minimus*.

A female specimen from Vancouver, British Columbia, Canada was described as a new species (*E. tristicolor*) by Viereck (1905), and was said to be related to *E. autumnalis* (a very different species), to which it was said to differ in colour, size, and structure. Although Viereck (1905) acknowledged *E. olympiellus* as a distinct species, no comparisons were made between it and *E. tristicolor*. The holotype of *E. tristicolor* is not as robust (head length 1.9 mm; head width 2.6 mm) as that of *E. olympiellus*, but the two specimens are equally long, partly because T6 of the *E. olympiellus* type specimen is almost completely retracted. Much of the pubescence is rubbed off in the *E. tristicolor* holotype (Figure 19a), but the pattern of the tomentum on the mesosoma and metasoma that is visible is essentially the same.

Cockerell (1918) described a male specimen from Pullman, Washington, USA under the name *E. humillimus*, which was distinguished from *E. olympiellus* by its smaller size, partially ferruginous labrum (light brown markings laterally), and (supposedly) lighter tegula. Since its original description, the metasoma of the *E. humillimus* holotype has been lost, but otherwise the specimen is most similar in size to the *E. tristicolor* holotype (Figure 19a, 19b). In terms of body size, the type specimens of *E. humillimus*, *E. olympiellus*, and *E. tristicolor* fall within the range of variation of sequenced specimens (Figure 19c, 19d, 19g).

In Cockerell and Sandhouse (1924), this species was described again under two names (*E. rubrostrictus* and *E. rufomaculatus*). *Epeolus rubrostrictus* was said to resemble *E. humillimus*, but otherwise no comparisons were made to any of the abovementioned “species”. In the holotype

of *E. rubrostrictus*, the fasciae of T3 and T4 are medially separated and greatly narrowed, respectively, and broken laterally (Figure 19e). Although the apical fasciae of T1–T4 are separated medially in most sequenced specimens, those of T3 and T4 may be laterally complete, narrowed to varying degrees, or entirely broken. Sequenced specimens from the same localities exhibit variation in T3 and T4 pubescence, and were assigned the same BIN. Even in the same specimen (e.g. CCDB-22015 F05), the fascia may be broken on one side and greatly narrowed on the other. By contrast, I have not seen any specimens of the related *E. minimus* in which the metasomal fasciae are broken laterally. The holotype of *E. rubrostrictus* (a female) is only slightly longer (7.9 mm) than that of *E. olympiellus* (a male).

*Epeolus rufomaculatus* was identified as distinct based on the occurrence of two ferruginous maculations in the female on either side of the pseudopygidial area of T5 (Figure 20a). In the holotype (Figure 19f), these were clearly once covered in pale pubescence, but most of this has been rubbed off. In *E. rubrostrictus* and *E. tricolor*, the integument of these equivalent two areas of T5 is mostly obscured by pubescence, but is clearly black. Specimens with either black or red integument underlying these spots were sequenced (Figure 20b, 20c), and all specimens were assigned the same BIN. One female specimen (Figure 19g) resembles both the *E. olympiellus* holotype (Figure 19h), in that the second submarginal crossvein of the right fore wing is incomplete (the left fore wing has three submarginal cells), and the *E. rufomaculatus* holotype, in that T5 is with two large ferruginous maculations. There is continuous variation in the size of the red spot from absent to nearly as large as the spot of pale tomentum obscuring it. I have, however, not seen any specimens of *E. minimus* with ferruginous maculations on T5, so the feature, when present, seems to be unique to females of *E. olympiellus*. The type locality of *E. rufomaculatus* is Logan, Utah, which falls well within the range of sequenced specimens (from Mendocino County, California in the south to Mineral County, Colorado in the east). The holotype of *E. rufomaculatus* is equal in size to that of *E. olympiellus* (length 7.5 mm; head length 2.2 mm; head width 2.9 mm).

**HOST RECORDS:** Sampling a small island off of Vancouver Island, British Columbia, Canada yielded a long series of *E. olympiellus*, and the only (potential host) *Colletes* species caught in the same traps was *C. hyalinus* Provancher (C. Sheffield, personal communication, 2017).

**FLORAL RECORDS:** The label of one examined voucher specimen indicates a floral association with *Ericameria* Nutt. (Asteraceae).

**Distribution in Canada:** British Columbia, west of the

Rocky Mountains (Map 11).

**DNA barcoded material.** Available. BOLD:AAC6215. Specimens examined and sequenced.—USA: **California:** (1♀, PCYU); Hwy 20 (Mendocino County), 05.vii.2007, J. Gibbs and C. Sheffield (1♀, 4♂, PCYU); **Colorado:** Near Wolf Creek (Mineral County), 28.vii.2007, J. Gibbs and C. Sheffield (2♀, 1♂, PCYU); **Idaho:** Ketchum (Blaine County), 24.vi.2007, J. Gibbs and C. Sheffield (2♀, PCYU); **Oregon:** Hwy 26 (Crook County), 28.vi.2007, J. Gibbs and C. Sheffield (1♀, PCYU); Hwy 26 (Wheeler County), 28.vi.2007, J. Gibbs and C. Sheffield (1♀, PCYU); Hwy 97 (Klamath County), 02.vii.2007, J. Gibbs and C. Sheffield (1♂, PCYU); **Washington:** 25 km W Clarkston (Garfield County), 29.v.2007, J. Gibbs and C. Sheffield (1♂, PCYU); **Wyoming:** 25 km ESE Eden (near Killpecker Sand Dunes, Sweetwater County), 24.vii.2012, M.C. Orr (1♀, BBSL); Pacific Creek Road (Teton County), 13.viii.2013, A. Payne (1♀, AMNH).

**Non-barcoded material examined.** CANADA: **British Columbia:** Comox, 08.vii.1933, J. McDunnough (1♂, CNC), 05.vii.1933, J. McDunnough (1♂, CNC); Langford, 13.vii.1961, D. Evans (1♀, CNC), 19.vii.1960 (1♀, CNC); Oliver, 29.viii.1953, D.F. Hardwick (1♀, CNC); Penticton, 23.viii.1920, W. Downes (1♀, 1♂, CNC); The District of Saanich, 17.vi.1926, W. Downes (1♀, CNC); Victoria, 02.vii.1920, W. Downes (1♂, CNC), 07.vii.1923, K.F. Auden (1♂, CNC).

USA: **California:** Hwy 20 (Mendocino County), 05.vii.2007, J. Gibbs and C. Sheffield (3♀, 2♂, PCYU); Sagehen Creek Field Station (Nevada County), 22-24.vi.1985, D.C. Darling (1♀, PCYU); **Colorado:** Near Wolf Creek (Mineral County), 28.vii.2007, J. Gibbs and C. Sheffield (3♀, 4♂, PCYU); **Idaho:** Ketchum (Blaine County), 24.vi.2007, J. Gibbs and C. Sheffield (6♀, PCYU); **Oregon:** Hwy 26 (Wheeler County), 28.vi.2007, J. Gibbs and C. Sheffield (1♀, PCYU); Lane County, 01.vii.2007, J. Gibbs and C. Sheffield (1♂, PCYU).

### *Epeolus pusillus* Cresson, 1864

Figures 3d, 9d, 13a;

Plate 1, Figure L; Plate 2, Figure L; Plate 3, Figure L;

Map 12

*Epeolus pusillus* Cresson, 1864a. Proc. Entomol. Soc. Phil. 2: 398 (♀).

**Primary type specimen.** Holotype ♀ (ANSP, catalog number: 2228). **Collection information.** USA: Massachusetts: no specific locality given, F.G. Sanborn.

### Diagnosis

Among Canadian species, *E. pusillus* most closely

resembles *E. scutellaris*. Both species exhibit the following similarities: axilla large and robust, its tip attaining or surpassing line of pale tomentum marking posterior margin of mesoscutellum, and its lateral margin arcuate; T1 with discal patch very wide; and metasomal fasciae rather thin. Differences are as follows: in *E. pusillus*, mesopleuron of male entirely obscured by white tomentum; at least mesoscutellum entirely black (entirely black to entirely ferruginous in *E. scutellaris*); and T5 with pseudopygidial area of female narrower (apex  $<2 \times$  medial length) than in *E. scutellaris* (apex  $\geq 2 \times$  medial length). In addition to the diagnostic differences included in the key are the following: in contrast to *E. scutellaris*, paramedian band of *E. pusillus* may be quite long, attaining or surpassing  $3/5$  length of entire mesoscutum; and in *E. pusillus*, fascia of T2 always with lobe-like anterolateral extensions of tomentum, whereas in *E. scutellaris* such extensions may be entirely absent.

### Redescription

**FEMALE:** Length 6.9 mm; head length 1.8 mm; head width 2.4 mm; fore wing length 5.0 mm.

**Integument colouration.** Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, antenna, pronotal lobe, tegula, axilla, legs, pygidial plate, and metasomal sterna. Mandible with apex darker than all but extreme base. Preapical tooth faintly lighter than mandibular apex (difficult to see in holotype; described from non-type specimens). Antenna brown except scape, pedicel, and F1 extensively orange. Pronotal lobe and tegula pale ferruginous to amber. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black.

**Pubescence.** Face with tomentum densest around antennal socket. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with paramedian band. Mesopleuron mostly bare (with tomentum rubbed off) in holotype, but tomentum dense in non-type specimens, except for two almost entirely bare patches (one beneath base of fore wing (hypoepimeral area), a larger circular patch occupying much of ventrolateral half of mesopleuron). Metanotum with tomentum uninterrupted, uniformly off white. T1 with discal patch quadrangular and very wide, the basal and apical fasciae only narrowly joined laterally. T1–T3 with apical fasciae partly rubbed off medially and laterally in holotype, but apical fasciae complete (basal fascia of T1 also) and narrowed or narrowly interrupted medially, and T2 with fascia with anterolateral extensions of tomentum in non-type specimens. T4 with fascia complete medially and narrowed laterally. T5 with large, continuous patch of pale tomentum bordering and contacting pseudopygidial area. T5 with pseudopygidial area lunate, its apex less than twice as wide as medial length, defined by silvery

setae on flat disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs not extending beyond apex of sternum by more than  $1/4$  MOD.

**Surface sculpture.** Punctures dense. Labrum with larger punctures than clypeus, but punctures of both more or less equally dense ( $i < 1d$ ). Small impunctate shiny spot present lateral to lateral ocellus. Mesoscutum, mesoscutellum, and axilla coarsely and densely rugose-punctate. Tegula densely punctate mesally ( $i \leq 1d$ ), less so laterally ( $i = 1-2d$ ). Mesopleuron with ventrolateral half densely punctate ( $i \leq 1d$ ) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense ( $i \approx 1d$ ), evenly distributed on disc.

**Structure.** Preapical tooth obtuse. Labrum with pair of small subapical denticles not preceded by carinae. Frontal keel present. Scape with greatest length  $1.9 \times$  greatest width. F2 noticeably longer than wide (L/W ratio = 1.7). Preoccipital ridge not joining hypostomal carina, from which it is separated by about 1.5–2 MOD at its terminal (difficult to see in holotype; described from non-type specimens). Mesoscutellum weakly bigibbous. Axilla large, its lateral margin nearly half as long as mesoscutellar width (L/W ratio = 0.52) and tip extending well beyond midlength of mesoscutellum but not attaining apex; axilla with tip clearly visible, but unattached to mesoscutellum for less than  $2/5$  its medial length; axilla with lateral margin arcuate. Fore wing with three submarginal cells. Pygidial plate apically truncate.

**MALE:** Description as for female except for usual secondary sexual characters and as follows: F2 shorter, but still longer than wide (L/W ratio = 1.2); mesopleuron entirely obscured by white tomentum; S4 and S5 with much longer silvery to coppery subapical hairs; pygidial plate apically rounded, with large deep, well-separated punctures, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure L.

**Male genitalia.** Plate 3, Figure L.

### Discussion

This species exhibits sexual dimorphism in the pubescence of the mesopleuron, which in males is entirely obscured by white tomentum whereas in females there is a sparsely hairy circle occupying much of the ventrolateral half of the mesopleuron, as well as a sparsely hairy patch beneath the base of the fore wing (hypoepimeral area). With regard to the axilla and mesoscutellum, integument colouration is remarkably consistent among specimens. The mesoscutellum is all black, and typically the axilla is black except along the lateral edge, where it is ferruginous. I have come across only a few specimens in

which the axilla is all black. Unless rubbed off, the apical fascia of T2 is with anterolateral extensions of tomentum. Although the pseudopygidial area of the female T5 is proportionally longer in this species compared to that of the similar *E. scutellaris*, it is still in the shape of a lunule. HOST RECORDS: A known *Colletes* host of *E. pusillus* is *C. compactus compactus* Cresson, an association confirmed by Rozen and Favreau (1968). FLORAL RECORDS: Robertson (1929) reported *E. pusillus* on *Bidens* L. (Asteraceae), *Boltonia* L'Hér. (Asteraceae), *Coreopsis* L. (Asteraceae), *Helianthus* L. (Asteraceae), and *Polygonum* L. (Polygonaceae). Mitchell (1962) indicated additional associations with *Aster* (now *Symphotrichum* Nees) (Asteraceae), *Erigeron* L. (Asteraceae), *Eupatorium* L. (Asteraceae), *Haplopappus* Cass. (Asteraceae), *Helenium* L. (Asteraceae), *Melilotus* Mill. (Fabaceae), and *Solidago* L. (Asteraceae). Collection records on Discover Life (Ascher and Pickering 2016) indicate the following floral associations: *Achillea millefolium* L. (Asteraceae), *Erigeron strigosus* Muhl. ex Willd., *Ilex glabra* (L.) A. Gray (Aquifoliaceae), *Limonium carolinianum* (Walter) Britton (Plumbaginaceae), *Ocimum basilicum* L. (Lamiaceae), *Pityopsis falcata* (Pursh) Nutt. (Asteraceae), *P. graminifolia* (Michx.) Nutt., *Pluchea* Cass. (Asteraceae), *Solidago nemoralis* Aiton, and *S. sempervirens* L. Labels of examined voucher specimens further indicate associations with *Melilotus albus* Medik., *Solidago altissima* L., *S. bicolor* L., and *Symphotrichum ericoides* (L.).

**Distribution in Canada:** Central Canada (Map 12).

**DNA barcoded material.** Available. BOLD:AAX7180. Specimens examined and sequenced.—CANADA: **Ontario:** King, 28.viii.2002, V. Kushnir (1♂, PCYU). USA: **Maryland:** Jug Bay Wetlands Sanctuary (Anne Arundel County), 15.ix.2007, S.W. Droege (1♂, BIML); **Utah:** 4.17 mi SE Wig Mountain (Toole County), 26.ix.2005, T.L. Griswold (1♀, BBSL); Beef Basin Rd (N Cottonwood Creek, San Juan County), 03.x.2014, M.C. Orr (1♀, BBSL).

**Non-barcoded material examined.** CANADA: **Ontario:** Caledon, 04.ix.2003, A. Gravel (1♀, PCYU); Caledon (Forks of the Credit Provincial Park), 12.viii.1968, P. MacKay (1♂, ROM), 20.viii.1968, P. MacKay (2♀, ROM), 25.vii.1968, P. MacKay (1♂, ROM), 27.viii.1968, P. MacKay (3♀, ROM), 21.viii.1969, P. MacKay (1♂, PCYU), 26.viii.1969, P. MacKay (1♀, 1♂, ROM), 27.viii.2002, J. Grixti (1♂, PCYU); Grand Bend, 20.viii.1936, A.A. Wood (1♂, CNC); King, 23.viii.2000, J. Grixti (3♂, PCYU), 14.viii.2001, M. Somers (1♂, PCYU), 21.viii.2001, M. Somers (1♂, PCYU),

29.viii.2001, M. Somers (1♂, PCYU), 23.vii.2002, J. Grixti (3♂, PCYU), 17.viii.2002, J. Grixti (1♂, PCYU), 23.viii.2002, V. Kushnir (1♂, PCYU), 28.viii.2002, J. Grixti (1♂, PCYU), 28.viii.2002, V. Kushnir (1♀, 2♂, PCYU), 14.ix.2002, J. Grixti (1♀, PCYU), 06.ix.2003, A. Gravel (1♂, PCYU), 06.ix.2003, J. Grixti (2♀, 1♂, PCYU); Ottawa, 25.viii.1954, W.R.M. Mason (1♂, CNC); Vankleek Hill, 01.ix.1974, J.T. Huber (1♀, DEBU); Windsor (Ojibway Prairie), 22.ix.2001, S.M. Paiero (1♀, DEBU); **Quebec:** Buckingham, Gatineau, 23.ix.1965, B.V. Peterson (1♀, CNC).

USA: **Florida:** Alachua County, 06.v.1955, R.A. Morse (1♂, AMNH); **Illinois:** Olive Branch, 01.ix.1909, Gerhard (1♀, FMNH); **Indiana:** Gibson County, 08.ix.1956 (1♂, USNM); **Maryland:** Anne Arundel County, 20.ix.2004, R. Andrus (1♂, BIML); Assateague Island (Worcester County), 19.ix.2006, S.W. Droege (1♀, 5♂, BIML), 20.ix.2006, S.W. Droege (2♂, BIML); Jug Bay Wetlands Sanctuary (Anne Arundel County), 15.ix.2007, S.W. Droege (1♀, BIML); **Massachusetts:** Suffolk County, 14-15.ix.2010, J. Rykken (2♀, 4♂, BIML); **Mississippi:** Hattiesburg (Forrest County), 08.x.1944, C.D. Michener (1♂, AMNH); **Montana:** Ashland (Rosebud County), 11.viii.1970, D.R. Miller (1♀, USNM); **New Jersey:** Jamesburg, 20.ix.1909, W.T. Davis (1♀, AMNH); **New York:** Lewisboro (Westchester County), 17.ix.1967, M. Favreau (1♀, AMNH), 04.x.1967, M. Favreau (1♀, AMNH); **Oklahoma:** 15 mi S Altus (Jackson County), 02.iv.1979, R.J. McGinley (1♂, USNM); **South Carolina:** Carolina Sandhills National Wildlife Refuge (Chesterfield County), 26.ix.2007, S.W. Droege (1♀, BIML); Hobcaw Barony (5 km E Georgetown, Georgetown County), 11-17.ix.2007, S.M. Paiero (1♂, DEBU).

### *Epeolus scutellaris* Say, 1824

Figures 3e, 13b;

Plate 1, Figure M; Plate 2, Figure M; Plate 3, Figure M;

Map 13

*Epeolus scutellaris* Say, 1824. In Keating, Narr. Long's 2nd Exped., v. 2: 355 (♀), **new neotype designation Primary type specimen.** Neotype ♀ (AMNH). **Collection information.** USA: New York: Keene Valley (Essex County), 12.viii.1917, H. Notman.

*Epeolus vernoniae* Cockerell, 1907. Entomologist 40: 136 (♂).

**Primary type specimen.** Holotype ♂ (AMNH).

**Collection information.** USA: Virginia: Falls Church, 04.ix.????, N. Banks.

### Diagnosis

This species most closely resembles *E. pusillus*, but can be easily distinguished as follows: mesopleuron of male not entirely obscured by white tomentum (unlike in *E. pusillus*), but with sparsely hairy circle occupying much of ventrolateral half; and T5 with pseudopygidial area of female wider (apex  $\geq 2 \times$  medial length) than in *E. pusillus* (apex  $< 2 \times$  medial length). For a comprehensive list of secondary distinguishing features and similarities to *E. pusillus*, see diagnosis for *E. pusillus*.

### Redescription

FEMALE: Length 8.2 mm; head length 2.1 mm; head width 3.0 mm; fore wing length 6.7 mm.

*Integument colouration.* Mostly black; notable exceptions as follows: at least partially ferruginous on mandible, antenna, pronotal lobe, tegula, axilla, mesoscutum, mesoscutellum, and legs. Mandible with apex darker than all but extreme base. Preapical tooth faintly lighter than mandibular apex (difficult to see in the *E. scutellaris* neotype; described from non-type specimens). Antenna brown except scape, pedicel, and F1 extensively orange. Pronotal lobe and tegula pale ferruginous to amber. Mesoscutum with orange spot anterolaterally between pronotal lobe and tegula. Wing membrane subhyaline, apically dusky. Legs more extensively reddish orange than brown or black. *Pubescence.* Face with tomentum densest around antennal socket. Dorsum of mesosoma and metasoma with bands of off-white to pale yellow setae. Mesoscutum with paramedian band. Mesopleuron mostly bare, but tomentum moderately dense ventrally as well as between two almost entirely bare circular patches (one behind pronotal lobe, a larger one occupying much of ventrolateral half of mesopleuron). Metanotum with tomentum uninterrupted, uniformly off white. T1 with discal patch quadrangular and very wide, the basal and apical fasciae at most only narrowly joined laterally (not joined in the *E. scutellaris* neotype and multiple non-type specimens). T1 with basal fascia interrupted medially, T1–T4 with apical fasciae complete and somewhat broader laterally. T5 with large, continuous patch of pale tomentum bordering but not contacting pseudopygidial area. T5 with pseudopygidial area lunate, its apex more than twice as wide as medial length, defined by silvery setae on flat disc of medioapical region elevated from rest of tergum. S5 with apical fimbria of coppery to silvery hairs extending beyond apex of sternum by 1/3 MOD.

*Surface sculpture.* Punctures dense. Labrum with sparser punctures ( $i=1-2d$ ) than clypeus ( $i<1d$ ). Impunctate spot lateral to lateral ocellus absent in the *E. scutellaris* neotype, but dull/textured spot present in non-type specimens. Mesoscutum, mesoscutellum, and axilla

coarsely and densely rugose-punctate. Tegula densely punctate mesally ( $i \leq 1d$ ), less so laterally ( $i=1-2d$ ). Mesopleuron with ventrolateral half densely punctate ( $i \leq 1d$ ) to rugose; mesopleuron with punctures more or less equally dense throughout. Metasomal terga with punctures very fine, dense ( $i \approx 1d$ ), evenly distributed on disc.

*Structure.* Preapical tooth blunt and obtuse. Labral apex with pair of small denticles preceded by carinae. Frontal keel present. Scape with greatest length  $1.8 \times$  greatest width. F2 noticeably longer than wide (L/W ratio = 1.4). Preoccipital ridge not joining hypostomal carina, from which it is separated by less than 1 MOD at its terminal (difficult to see in the *E. scutellaris* neotype; described from non-type specimens). Mesoscutellum moderately bigibbous. Axilla large, its lateral margin more than half as long as mesoscutellar width (L/W ratio = 0.62) and tip attaining apex of horizontal dorsal portion of mesoscutellum; axilla with tip clearly visible, but unattached to mesoscutellum for less than 2/5 its medial length; axilla with lateral margin arcuate. Fore wing with three submarginal cells. Pygidial plate apically truncate. MALE: Description as for female except for usual secondary sexual characters and as follows: F2 shorter, not noticeably longer than wide (L/W ratio = 1.1); S4 and S5 with much longer silvery to coppery subapical hairs; pygidial plate with large deep punctures closely clustered basally and sparser apically, with the interspaces shining.

**Male hidden sterna.** Plate 2, Figure M.

**Male genitalia.** Plate 3, Figure M.

### Discussion

*Epeolus scutellaris* exhibits some variation in the size of the axilla relative to the mesoscutellum, and in this species the axilla may extend farther posteriorly than in any other species of *Epeolus* in Canada. At least the axilla is ferruginous to some degree, whereas the mesoscutellum may range from entirely black to entirely ferruginous. Although in examined specimens from Canada the fascia of T2 is commonly without lobe-like anterolateral extensions of tomentum, specimens from Western North America typically possess them.

The whereabouts of the primary type of *E. scutellaris* is unknown, but in all likelihood it has been destroyed, along with much of Thomas Say's entomological collection (LeConte 1859:v–vi, xix (footnote)). Mawdsley (1993) lists 71 surviving insect specimens housed in the MCZ of 56 species described by Say, upon which Say's original descriptions are probably based, that have yet to be recognized as primary types. Of the four specimens of Hymenoptera listed, all are Ichneumonidae. Specimens identified as *E. scutellaris* in the MCZ were only recently

collected (in 2010). I have not been able to locate any *Epeolus* specimens collected or identified by Say in any other entomological institution, despite extensive searches.

Similar to *E. scutellaris* is at least one undescribed species from Florida with a unique barcode sequence, and potentially another (also from Florida) yet to be sequenced. In an NJ tree of COI sequence data, *E. scutellaris* is grouped closest with the undescribed sequenced species from Florida. Before formally describing any additional similar-looking species, it is sensible to first have a neotype designated for *E. scutellaris* for reference to ensure proper name use is standardized.

*Epeolus scutellaris* was originally described (♀ only) as exhibiting the following features typically associated with the species: the mandible, antenna (excluding F2–F12), axilla, mesoscutellum, and legs are ferruginous; the integument of the body is otherwise black and densely punctate; the axilla is dilated; and the metasomal terga are with pale yellow fasciae. In the original description, this species is said to inhabit the middle states, presumably referring to the Middle Atlantic States. Herein, I designate a neotype female from Keene Valley in Essex County, New York, which falls within Say's (1824) indicated range for this species and matches the original description. The redescription of *E. scutellaris* provided here is based on this neotype specimen.

Mitchell (1962) synonymized *E. vernoniae* under *E. scutellaris*. I have examined the male holotype specimen of *E. vernoniae*, and agree with Mitchell's treatment. The neotype of *E. scutellaris* is the property of the AMNH, the same institution where the holotype of *E. vernoniae* is housed, which should make future comparisons of the two specimens more convenient for researchers.

**HOST RECORDS:** An inferred *Colletes* host of *E. scutellaris*, based on frequent co-occurrence, is *C. simulans armatus* Patton (Ascher *et al.* 2014), although this association has not yet been confirmed.

**FLORAL RECORDS:** Mitchell (1962) indicated floral associations with *Baccharis* L. (Asteraceae), *Bidens* L. (Asteraceae), and *Solidago* L. (Asteraceae). Collection records on Discover Life (Ascher and Pickering 2016) indicate the following associations: *Euthamia graminifolia* (L.) Nutt. (Asteraceae), *Pityopsis falcata* (Pursh) Nutt. (Asteraceae), *Pluchea odorata* (L.) Cass. (Asteraceae), *Solidago nemoralis* Aiton, *S. rugosa* Mill., *S. sempervirens* L., and *Symphyotrichum* Nees (Asteraceae). Labels of examined voucher specimens further indicate associations with *Allium tricoccum* Aiton (Amaryllidaceae), *Cirsium arvense* (L.) Scop. (Asteraceae), *Melilotus albus* Medik. (Fabaceae), *Solidago altissima* L., *S. bicolor* L., and *Symphyotrichum lateriflorum* (L.) Á. Löve and D. Löve.

**Distribution in Canada:** Atlantic and Central Canada (Map 13).

**DNA barcoded material.** Available. BOLD:AAG5250. Specimens examined and sequenced.—CANADA: **Nova Scotia:** Pereau (Kings County), 10.ix.2002, C. Sheffield (1♀, RSKM); **Ontario:** Cumberland (Ottawa: Baseline Rd & Canaan Rd), 14.viii.2016, T.M. Onuferko (1♂, PCYU); Grand Bend (Lambton County), 10.ix.2008, A. Taylor (1♀, PCYU).

USA: **Idaho:** Saint Anthony (Fremont County), 09.viii.2013, A. Payne (2♂, AMNH).

**Non-barcoded material examined.** CANADA: **New Brunswick:** Kouchibouguac, 02.viii.1978, D.B. Lyons (1♂, CNC); Saint Andrews, 11.viii.1957, G.E. Shewell (1♀, CNC); **Nova Scotia:** Avonport (Kings County), 27-28.viii.2000, C. Sheffield (2♀, PCYU), 14.ix.2000, C. Sheffield (1♀, RSKM); Brier Island (Digby County), 13.viii.2002, C. Sheffield (1♀, 1♂, PCYU); Evang. Beach (Kings County), 10.ix.2000, C. Sheffield (1♀, RSKM); Kemptown (Colchester County), 04.viii.1999, J. Ogden (1♀, PCYU); Kings County, 15.viii.1931, C.E. Atwood (3♂, CNC); Melford, 25.viii.1985, L. Packer (1♂, PCYU); Pereau beach (Kings County), 29.viii.2005, C. Sheffield and S. Westby (1♀, PCYU), 10.ix.2002, C. Sheffield (1♀, PCYU); River Denys Mtn Rd, 24.viii.1985, L. Packer (1♂, PCYU), 01.ix.1985, L. Packer (1♂, PCYU); Valley Mills (Cape Breton Island), 08.ix.1985, L. Packer (1♀, PCYU); Weymouth, 3-10.viii.1900 (1♀, 1♂, CNC); Wreck Cove (Cape Breton Island), 30.viii.1981, L. Packer (1♀, PCYU); **Ontario:** Albion Hills Conservation Area, 21.viii.2012, S. Dumesh (1♂, PCYU); Bobcaygeon (Emily Creek, Peterborough County), 18.viii.1975, F. Quan (1♂, ROM); Brighton, 02.ix.1954, J.C. Martin (1♂, CNC); Burketon, 30.viii.1954, C.D. Miller (1♀, CNC); Caledon, 02.ix.2003, J. Grixti (1♂, PCYU); Caledon (Forks of the Credit Provincial Park), 08.viii.1968, P. MacKay (1♂, ROM), 12.viii.1968, P. MacKay (1♂, ROM), 18.viii.1969, P. MacKay (1♀, PCYU), 18.viii.1969, P. MacKay (1♀, ROM), 21.viii.1969, P. MacKay (1♀, ROM), 27.viii.1968, P. MacKay (1♀, PCYU), 27.viii.1968, P. MacKay (2♀, 1♂, ROM), 08.ix.2003, J. Grixti (1♂, PCYU), 13.ix.2002, J. Grixti (1♀, PCYU), 13.viii.2003, A.I. Gravel (1♂, PCYU), 18.ix.2003, J. Grixti (2♀, PCYU); Conc. 11 near Hume Rd (Puslinch), 10.ix.2002, P. Hebert (1♀, PCYU); Dunnville, 03.viii.1954, C.D. Miller (1♂, CNC); King (1♂, PCYU), 06.ix.2003, J. Grixti (2♀, 1♂, PCYU), 08.viii.2001, M. Somers (2♂, PCYU), 12.ix.2000, J. Grixti (1♀, PCYU), 23.vii.2002, J. Grixti (1♂, PCYU), 23.viii.2000, V. Kushnir (1♂, PCYU), 23.viii.2002, V. Kushnir (1♂, PCYU), 28.viii.2002, J. Grixti (2♀, 2♂, PCYU), 28.viii.2002, V. Kushnir (3♀, 1♂, PCYU),

21.viii.2001, M. Somers (4♂, PCYU), 29.viii.2001, M. Somers (1♂, PCYU); Lake of the Woods (Harris Hill), 3-4.viii.1960, Kelton and Whitney (1♂, CNC); Manester Tract (St. Williams), 01.ix.1992, P.J. Carson (1♂, PCYU); Normandale, 04.ix.1954, C.D. Miller (1♀, CNC); Orono, 03.ix.1925, N.K. Bigelow (1♀, ROM); Ottawa, 25.viii.1954, W.R.M. Mason (1♀, 1♂, CNC); Peel Reg. Mun Hart House Farm (near Cheltenham), 19.ix.1992, D.C. Darling (1♂, ROM); Queen's University Biological Station (Main HQ), 02.ix.2001, A. Zayed (4♀, PCYU); Spencerville, 20.viii.1938, G.H. Hammond (1♀, CNC); Thousand Islands National Park, 05.ix.1976, Reid (1♀, CNC); Toronto (York University Campus), 31.viii.2006, E. Willis (1♀, PCYU); **Quebec:** 8 km SE Rigaud, 08.ix.1985, J.S. Noyes (1♀, CNC); Fort-Coulonge, 20-23.viii.1917, J.I. Beaulne (2♂, CNC); Hull (Gatineau), 13.ix.1965 (1♀, CNC); Mont Ste. Marie, 20.ix.1965, J.R. Vockeroth (1♀, CNC).

USA: **Maine:** Blue Hill, 22.viii.2012, E. Venturini (1♂, BIML); Columbia Falls, 21.viii.2013, (1♀, BIML); Jonesboro, 20.viii.2013, E. Venturini (1♀, BIML); **Maryland:** Assateague Island (Worcester County), 19.ix.2006, S.W. Droege (4♂, BIML); **Michigan:** Alger County, 1-2.ix.2011, J. Gulbransen and C. Heyd (1♀, BIML); **New Jersey:** Montvale (Bergen County), 12.viii.1949, B.L. and J.G. Rozen (1♂, AMNH); **North Carolina:** Black Mountains (1♂, AMNH); **Vermont:** Chittenden (Rutland County), 15.viii.1916 (1♀, 2♂, AMNH); **Wisconsin:** Friendship (Adams County), vi.1965, O. Perk (1♀, FMNH).

## Acknowledgements

The idea of a written key to the species of *Epeolus* in Canada was conceived by Laurence Packer (PCYU). I thank Laurence Packer for his advice, assistance, and comments on multiple drafts of the manuscript, as well as for granting me access to his impressive *Epeolus* collection and superior imaging system, which was purchased through the auspices of Canadensys with funds from the Ontario Research Fund and the Canadian Foundation for Innovation. I thank all institutions listed in the methods and their curatorial staff for providing me with specimens for study (on site, via loans, or both). I am especially grateful to the following individuals who have provided me with a large amount of material for study and/or granted me permission to sequence various specimens of interest: Sean Brady and Brian Harris (USNM), Sophie Cardinal (CNC), Michael Engel and Jennifer Thomas (KUNHM), Terry Griswold (BBSL), Steve Marshall (DEBU), Jerome Rozen and Corey Smith (AMNH), and Cory Sheffield (RSKM). Several specimens used in this study were collected at Point Pelee National Park, and I am grateful to Parks Canada for granting me a permit to collect there. I especially thank Park Ecologist Tammy Dobbie for her assistance during field work. Sam Droege, Rafael Ferrari, and Laurence Packer reviewed/tested the key, and I am grateful for their comments. I thank the CJA I Hymenoptera section editor John T. Huber (CNC) and an anonymous reviewer for their constructive and thorough reviews, which helped improve the manuscript. The specimens used in this study were collected by a very large number of individuals, and I am thankful for their contributions to furthering the knowledge of *Epeolus*. This project was supported through Laurence Packer's discovery grant funded by the Natural Sciences and Engineering Research Council of Canada (NSERC).



19a



19b



19c



19d



19e



19f



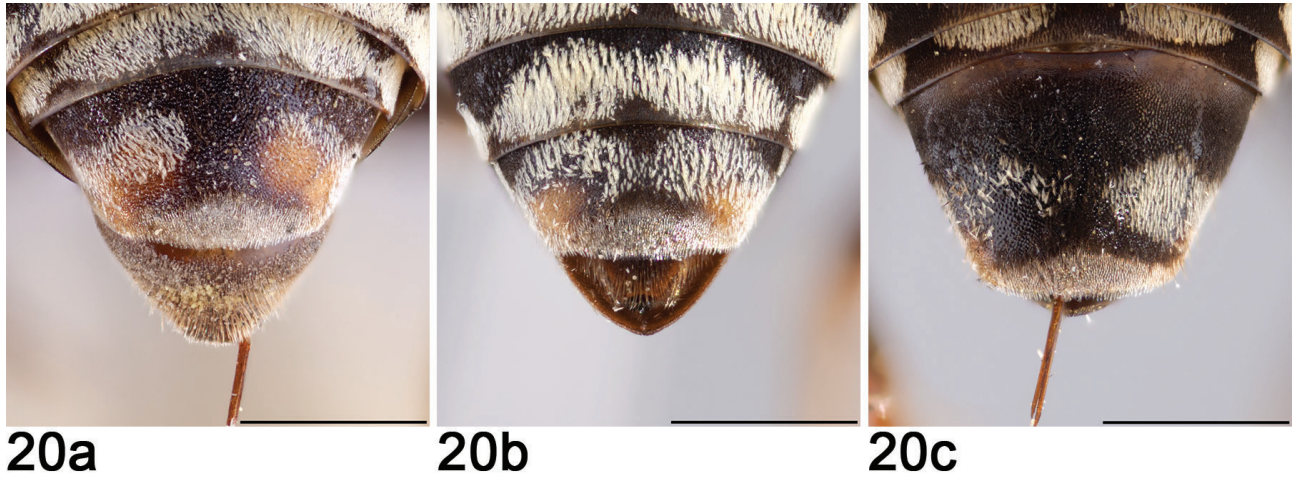
19g



19h

**Figure 19.** A comparison of the holotypes of a) *E. tristicolor*, b) *E. humillimus*, c) *E. rubrostictus*, f) *E. rufomaculatus*, and h) *E. olympiellus* (the species under which the preceding four are being synonymized) to three barcoded specimens (c, d, and g) of *E. olympiellus* illustrating the variability in the “characteristic” features displayed by the type specimens. Scale bars = 3 mm.





**Figure 20.** T5 of female (dorsal view) a) *E. rufomaculatus* holotype (synonymized herein under *E. olympiellus*) and b) barcoded *E. olympiellus* showing ferruginous integument underlying patches of pale tomentum, and c) barcoded *E. olympiellus* showing black integument underlying patches of pale tomentum. Scale bars = 1 mm.



**Plate 1. Female (top) and male (bottom) lateral images. Scale bars = 3 mm.**  
**A. *Epeolus ainsliei* Crawford, 1932**

**B. *Epeolus americanus* (Cresson, 1878)**



**C. *Epeolus autumnalis* Robertson, 1902**

**D. *Epeolus bifasciatus* Cresson, 1864**



**Plate 1. Female (top) and male (bottom) lateral images cont'd. Scale bars = 3 mm.**  
F. *Epeolus compactus* Cresson, 1878  
E. *Epeolus canadensis* Mitchell, 1962



G. *Epeolus ilicis* Mitchell, 1962

H. *Epeolus interruptus* Robertson, 1900



**Plate 1. Female (top) and male (bottom) lateral images cont'd. Scale bars = 3 mm.**

**I. *Epeolus lectoides* Robertson, 1901**

**J. *Epeolus minimus* (Robertson, 1902)**

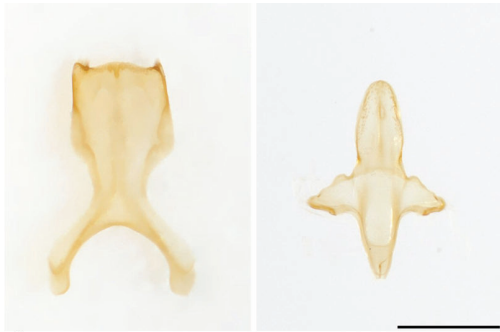


**K. *Epeolus olympiellus* Cockerell, 1904**

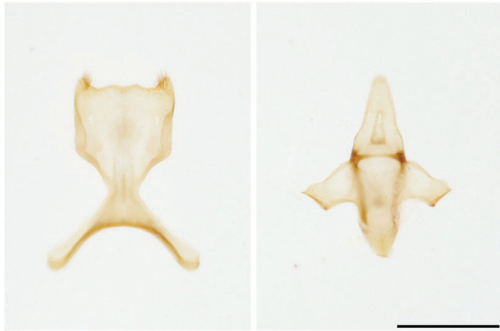
**L. *Epeolus pusillus* Cresson, 1864**



**Plate 1. Female (top) and male (bottom) lateral images cont'd. Scale bars = 3 mm.**  
*M. Epeolus scutellaris* Say, 1824



**A**

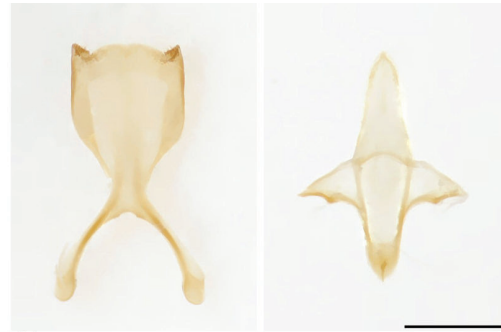


**B**

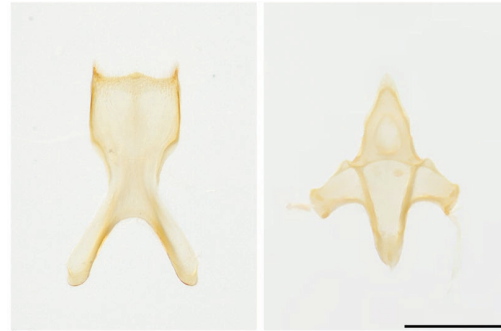
**Plate 2 - Male S7 (left) and S8 (right),  
Scale bars = 0.5 mm.**

A. *Epeolus ainsliei* Crawford, 1932

B. *Epeolus americanus* (Cresson, 1878)



**C**



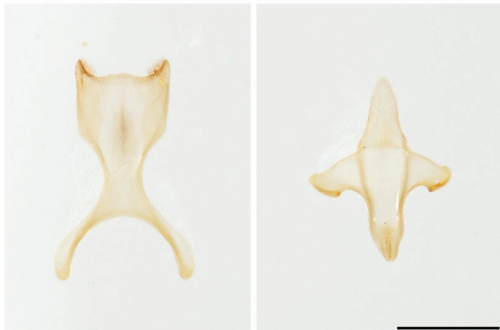
**D**

C. *Epeolus autumnalis* Robertson, 1902

D. *Epeolus bifasciatus* Cresson, 1864



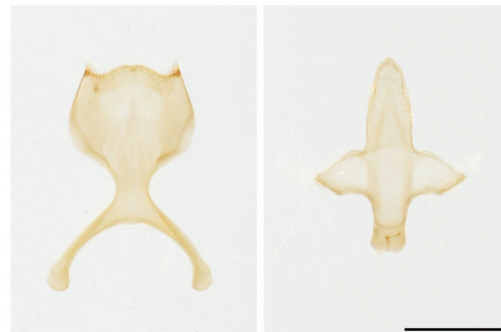
**E**



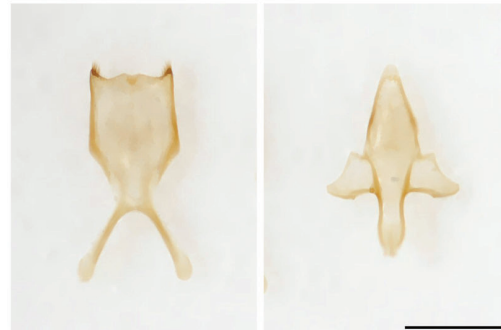
**F**

E. *Epeolus canadensis* Mitchell, 1962

F. *Epeolus compactus* Cresson, 1878



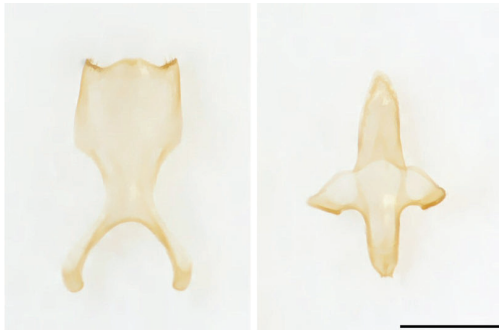
**G**



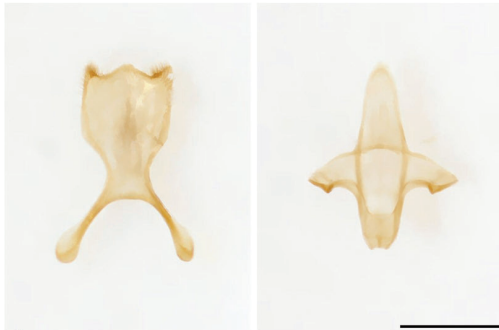
**H**

G. *Epeolus ilicis* Mitchell, 1962

H. *Epeolus interruptus* Robertson, 1900



I



J

Plate 2 - Male S7 (left) and S8 (right)  
cont'd, Scale bars = 0.5 mm.

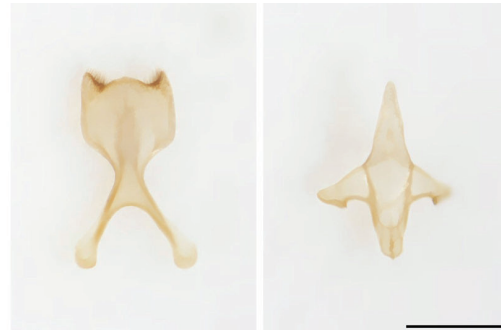
I. *Epeolus lectoides* Robertson, 1901

J. *Epeolus minimus* (Robertson, 1902)

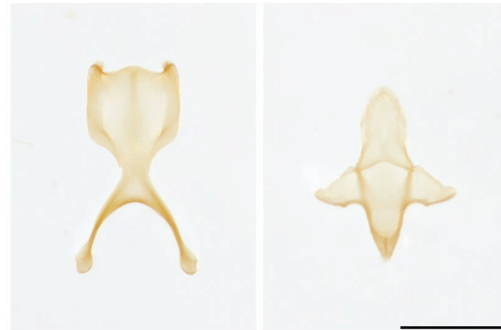


M

M. *Epeolus scutellaris* Say, 1824



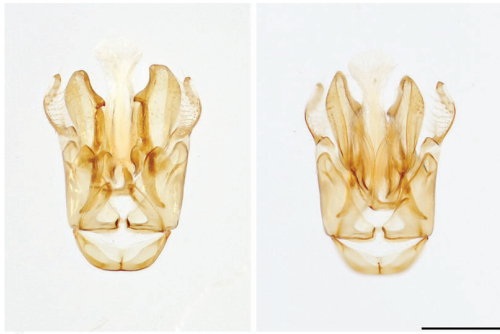
K



L

K. *Epeolus olympiellus* Cockerell, 1904

L. *Epeolus pusillus* Cresson, 1864



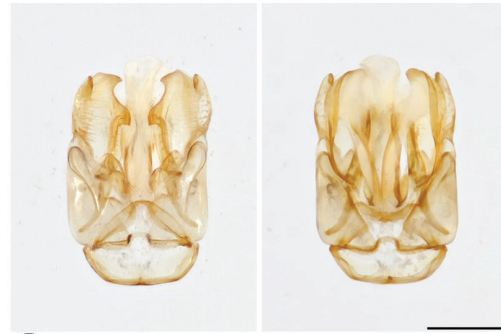
**A**



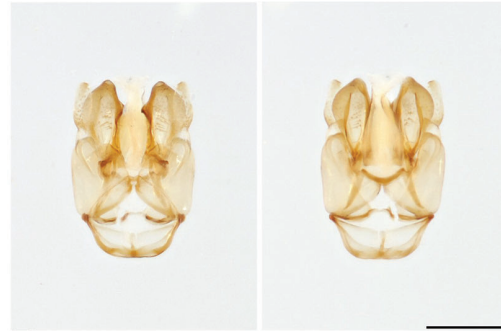
**B**

**Plate 3 - Male genitalia, ventral view (left), dorsal view (right), Scale bars = 0.5 mm.**

A. *Epeolus ainsliei* Crawford, 1932  
B. *Epeolus americanus* (Cresson, 1878)

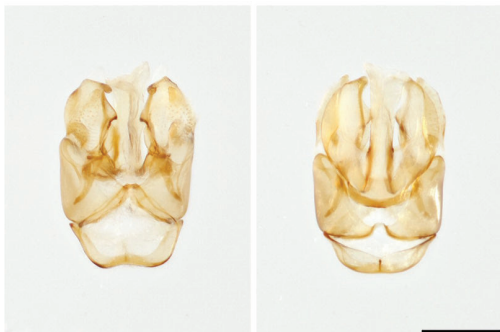


**C**



**D**

C. *Epeolus autumnalis* Robertson, 1902  
D. *Epeolus bifasciatus* Cresson, 1864

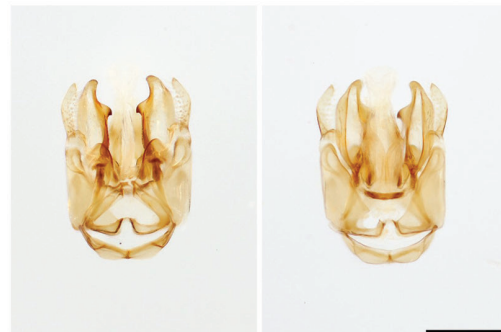


**E**



**F**

E. *Epeolus canadensis* Mitchell, 1962  
F. *Epeolus compactus* Cresson, 1878



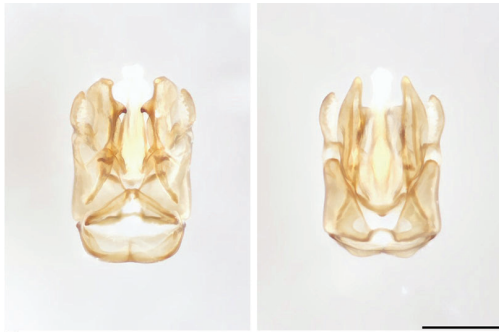
**G**



**H**

G. *Epeolus ilicis* Mitchell, 1962  
H. *Epeolus interruptus* Robertson, 1900





I

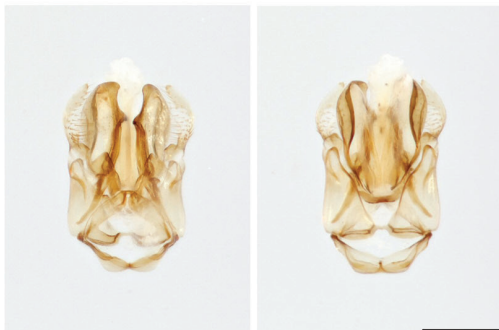


J

**Plate 3 - Male genitalia, ventral view (left), dorsal view (right) cont'd, Scale bars = 0.5 mm.**

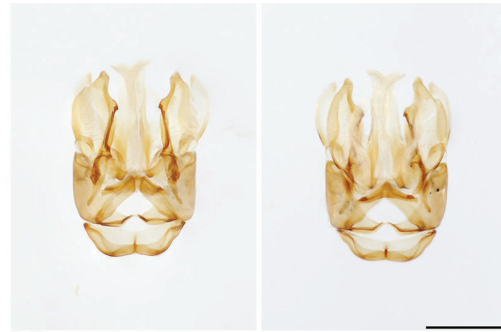
I. *Epeolus lectoides* Robertson, 1901

J. *Epeolus minimus* (Robertson, 1902)

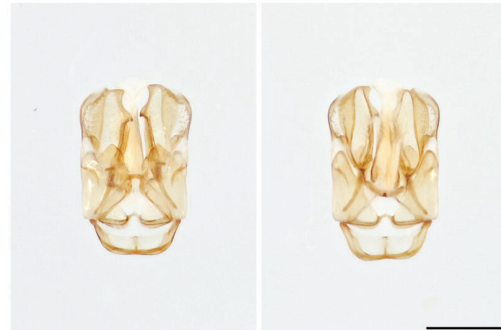


M

M. *Epeolus scutellaris* Say, 1824



K

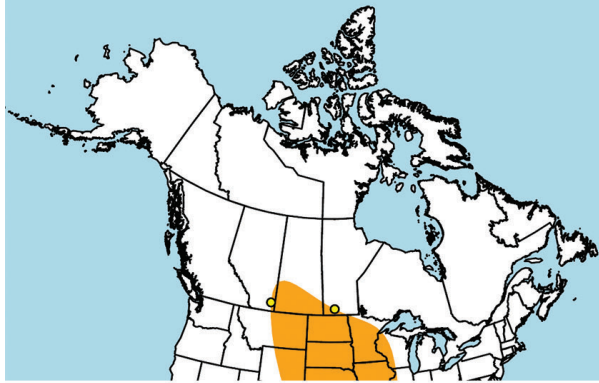


L

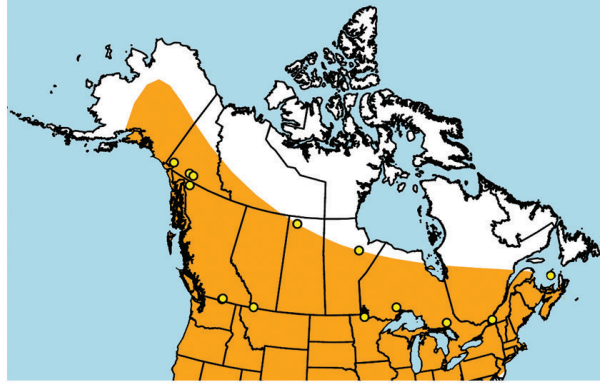
K. *Epeolus olympiellus* Cockerell, 1904

L. *Epeolus pusillus* Cresson, 1864

1. *Epeolus ainsliei*



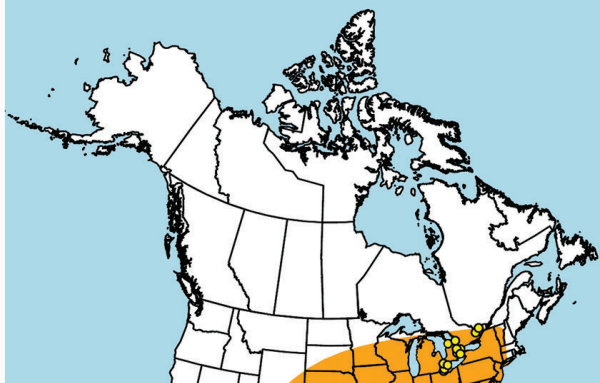
2. *Epeolus americanus*



3. *Epeolus autumnalis*



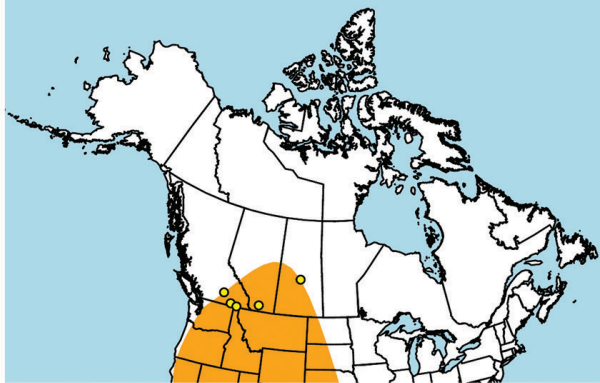
4. *Epeolus bifasciatus*



5. *Epeolus canadensis*



6. *Epeolus compactus*



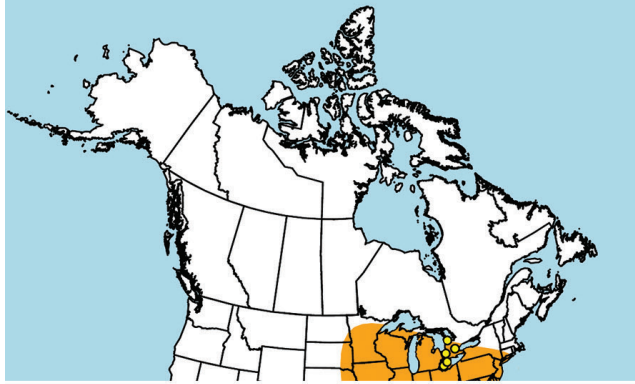
7. *Epeolus ilicis*



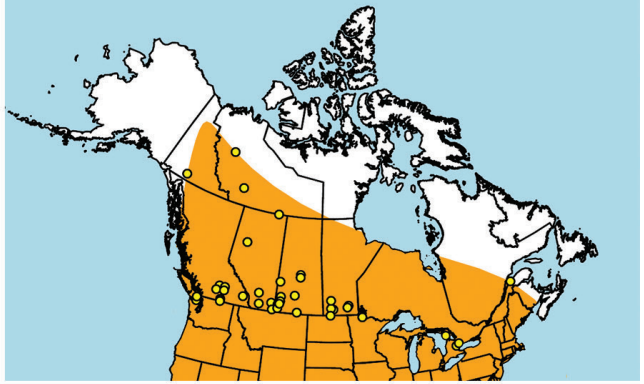
8. *Epeolus interruptus*



9. *Epeolus lectoides*



10. *Epeolus minimus*



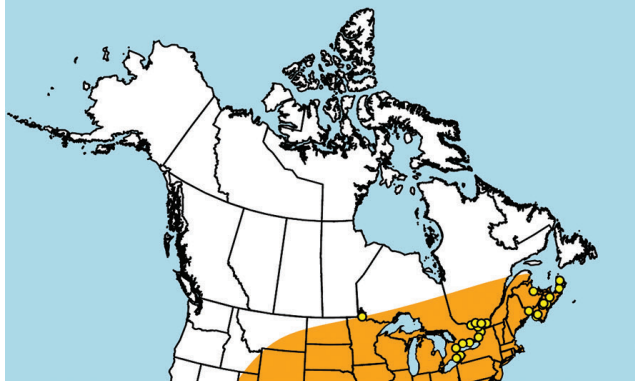
11. *Epeolus olympiellus*



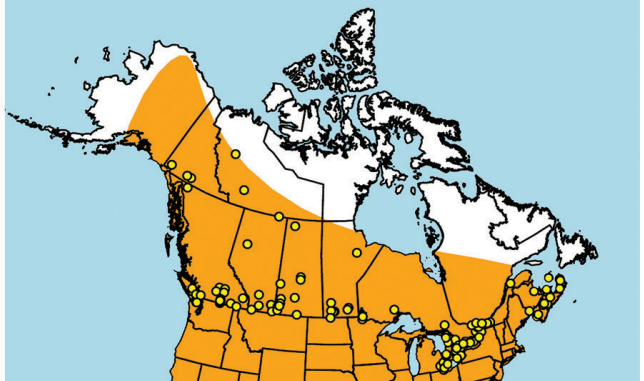
12. *Epeolus pusillus*



13. *Epeolus scutellaris*



14. All Canadian *Epeolus* spp.



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