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Four submarginal cells on a forewing of *Melitoma taurea* (Say) (Hymenoptera: Apidae), and a summary of known records of atypical and variable numbers of submarginal cells

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Abstract. A specimen of *Melitoma taurea* (Say) (Hymenoptera: Apidae) was captured on Hart-Miller Island, Chesapeake Bay, Baltimore County, Maryland. The specimen possessed the typical three submarginal cells on the right forewing but exhibited four submarginal cells on the left forewing due to the presence of an additional submarginal crossvein dividing the second submarginal cell. The presence of four submarginal cells is a rare occurrence in bees. Besides documenting this occurrence, this paper presents a summary of known published and previously unpublished records of atypical and variable numbers of submarginal cells. Published records were found for 66 species: Colletidae (1), Andrenidae (28), Halictidae (19), and Apidae (18). In four instances, published records were also found at the genus or subgenus level. Previously unpublished records are reported for 29 species: Colletidae (1), Andrenidae (5), Halictidae (13), and Apidae (10). Previously unpublished records are also shown for six specimens that are only identified to genus or subgenus. Twelve-and-one-third percent of the specimens with atypical numbers of submarginal cells would normally have had two submarginal cells; 87.7% would normally have had three submarginal cells. Approximately, 49.4% of the specimens had atypical numbers on one wing, and approximately 50.6% had atypical numbers on both wings. Of the normally two submarginal cell specimens, 80.0% gained and 20.0% lost one submarginal crossvein. Of the normally three submarginal cell specimens, 1.4% gained one submarginal crossvein and 98.6% lost one or more submarginal crossveins.

Key words. submarginal crossvein, wing venation.

Introduction

Although there are tribes (e.g. Allodapini [Apidae: Xylocopinae], Neolarrini [Apidae: Nomadinae], and Meliponini [Apidae: Apinae]) where certain species may possess either no or only one submarginal cell on the forewing (Michener 2007), for the overwhelming majority of bee species, all individuals of a particular species usually possess either two or three submarginal cells (i.e. two or three submarginal crossveins) (Tofilski 2011). Three submarginal cells is the ancestral condition (Tofilski 2011). Submarginal crossveins have been lost independently in numerous taxa (Tofilski 2011). This has resulted in species possessing two submarginal cells. The lost crossveins are usually the first and/or second submarginal crossveins, although it is not always possible to tell which of the two crossveins is missing (Michener 2007). Each of the six North American bee families contains species that have either two or three submarginal cells (Tofilski 2011). Occasionally, anomalies occur where a two submarginal cell species produces a specimen with one or both forewings expressing three submarginal cells, or vice versa. Incomplete variations (e.g. partially formed crossveins) can also be expressed. Here I report on a specimen exhibiting four submarginal cells, as well as summarize published and previously unpublished records of atypical and variable numbers of submarginal cells.

Materials and Methods

I conducted a bee bowl (pan trap) survey of Hart-Miller Island, Chesapeake Bay, Baltimore County, Maryland, based on the methods in Droege (2008). The survey yielded 4446 specimens representing five families, 27 genera, and at least 86 species (Scarpulla 2013). Only one specimen of *Melitoma taurea* (Say) (Hymenoptera: Apidae), a female, was collected during this survey. The specimen was captured on 20 July 2009 in Transect 1, the sandy path and edge of the sandy beach.

Laboratory processing and photography took place at the United States Geological Survey's Bee Inventory and Monitoring Lab at the Patuxent Wildlife Research Center, Beltsville, Maryland [current location of the lab is Laurel, Maryland]. I examined the *M. taurea* specimen using a Leica WILD M3Z stereo dissecting scope (20×/13 oculars, 6.5–40× objective) for identification to species using the Discover Life *Melitoma* IDnature guide (Orr et al. 2011). For achieving the best photographic lighting conditions, Brooke Alexander placed the specimen within a polystyrene foam cooler and then photographed the wings by using a Canon EOS 5D camera equipped with a Canon MP-E 65 mm 1–5× Macro Photo Lens (*f* 5.0, ISO 100, shutter speed 200) and a Canon MT-24EX Macro Twin Lite flash. The camera was mounted on a StackShot STKS-C macro rail system (Cognisys Inc., 459 Hughes Drive, Traverse City, MI 49696). The 60-µ individual images (left forewing 74, right forewing 32) were stacked using Zerene Stacker (Zerene Systems LLC, 629 Cherrywood Loop, Richland, WA 99354-1807).

Although being fully aware that many published records of atypical and variable numbers of submarginal cells would likely be buried in the text of obscure taxonomic papers and unlikely to be indexed or searchable, I initiated a search for published records using AGRICOLA, BioOne, EBSCO*host*, Google, Google Scholar, Ingenta Connect, ScienceDirect, Scopus, and Web of Science. Additionally, I made a request to the "Bee Inventory, Monitoring, and ID" listserve (http://groups.yahoo.com/neo/groups/beemonitoring/info) for any previously unpublished records of atypical and variable numbers of submarginal cells.

The forewing terminology used in this paper is based on Michener (2007). The relevant terms are the first, second, and third submarginal cells (i.e. 1st SM, 2nd SM, and 3rd SM) and the first, second, and third submarginal crossveins (i.e. 1st SMCV, 2nd SMCV, and 3rd SMCV). In the cited literature, the three submarginal crossveins have various alternative designations. A cross reference is provided in Table 1.

Table 1. Vein terminology used in this paper (based on Michener (2007)).

Vein terminology used in this paper	**Alternative terminology used by authors in the literature cited below**
first submarginal crossvein (1st SMCV)	2nd abscissa of Rs 1st transverse cubital vein 1st transverse cubitus cubital transverse vein I 1st intercubitus vein 1st cubital nervure 1st transverse cubital nervure vein *rm* radio-medial cross-vein
second submarginal crossvein (2nd SMCV)	1 (or 1st) r-m 2nd transverse cubital vein 1rs-m cubital transverse vein II 2nd intercubitus vein 2nd cubital nervure 2nd transverse cubital nervure vein III_5
third submarginal crossvein (3rd SMCV)	2 (or 2nd) r-m 3rd transverse cubital vein 2rs-m

Table 2 lists the codens used for specimen repositories cited in the manuscript. The codens are based on Evenhuis (2007), except for BIML, CNBL, ISIC, and PCYU. Additionally, the following private collections are cited in the text: Michael S. Arduser, Henning Bang Madsen, Joan Milam, John Plant, Claus Rasmussen, Eugene J. Scarpulla, and Maximilian Schwarz.

The details reported for the *M. taurea* specimen, and for the previously unpublished specimen records in the Results section, follow this standardized format: sex; collection date; collection location;

latitude; longitude; collection method; collector (coll.); determiner (det.); specimen repository; specimen identification number (if one exists); left wing; right wing; and contributor.

Table 2. Codens for cited specimen repositories (primarily based on Evenhuis [2007]).

Coden	Museum
BIML	Bee Inventory and Monitoring Lab, Patuxent Wildlife Research Center, United States Geological Survey, Laurel, Maryland, USA
CAES	Connecticut Agricultural Experiment Station, New Haven, Connecticut, USA
CNBL	Cariveau Native Bee Lab, University of Minnesota, University of Minnesota, St. Paul, Minnesota, USA
CNC	Canadian National Collection of Insects, Arachnids, and Nematodes, Ottawa, Ontario, Canada
INHS	Illinois Natural History Survey, Champaign, Illinois, USA
ISIC	Iowa State Insect Collection, Iowa State University, Ames, Iowa, USA
JBWM	J. B. Wallis/R. E. Roughley Museum of Entomology, University of Manitoba, Winnipeg, Manitoba, Canada
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru
PCYU	Packer Collection at York University, York University, Toronto, Ontario, Canada
UMSP	University of Minnesota Insect Collection, University of Minnesota, St. Paul, Minnesota, USA
UNMC	Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico, USA
USNM	United States National Entomological Collection, Smithsonian National Museum of Natural History, Washington, District of Columbia, USA

Results

The Hart-Miller Island *Melitoma taurea* specimen

The Hart-Miller Island *Melitoma taurea* specimen exhibited the typical 3 SM (Mitchell 1962) on the right forewing (Fig. 1) but displayed 4 SM on the left forewing (Fig. 2). This could also be thought of as aberrant wing venation, with the left forewing possessing an additional SMCV dividing the 2nd SM. The additional vein traversed between the marginal cell and the 1st medial cell.

Melitoma taurea (Say) (Apidae)

♀; 20 July 2009; USA, Maryland, Baltimore Co., Chesapeake Bay, Hart-Miller Island, Transect 1; 39.2524°; –76.3722°; bee bowl; coll. and det.: Eugene J. Scarpulla; Scarpulla collection; USGS_DRO205857; left: 4 SM (additional SMCV dividing the 2nd SM); right: 3 SM (normal [Mitchell 1962]).

Published records of atypical or variable numbers of submarginal cells

A search in the published literature yielded the following records of atypical and variable numbers of submarginal cells. All records of non-managed or non-laboratory-reared specimens (i.e. excluding the specimens from managed or laboratory-reared *Apis mellifera* Linnaeus) involved either 2 SM or 3 SM (See the Discussion section for an explanation of intermediate conditions). Current taxonomy is based on Ascher and Pickering (2017a), except as noted. Table 3 provides a summary of the published records.

Family Colletidae

Leioproctus (*Minycolletes*) *abnormis* (Cockerell)

[reported as *Leioproctus* (*Leioproctus*) *abnormis* (Cockerell) in Michener (2007)]

Polymorphic; either 2 SM or 3 SM (Michener 2007).

Figure 1. *Melitoma taurea*. Female; USGS_DRO205857; right forewing with typical 3 SM. Photographed by Brooke Alexander, BIML.

Figure 2. *Melitoma taurea*. Female; USGS_DRO205857; left forewing with atypical 4 SM. (The distorted appearance is due to the wing being partially folded over.) Photographed by Brooke Alexander, BIML.

Family Andrenidae

Andrena (*Callandrena* s. lat.) *asteris* Robertson

Typically, 3 SM; less than 5% of specimens with only 2 SM in one or both wings (LaBerge 1967).

Andrena (*Callandrena* s. lat.) *asteris* Robertson

[reported as genus *Pterandrena asteris* Robertson in Robertson (1902a); *Pterandrena* = *Callandrena* per Gusenleitner and Schwarz (2002)]

Typically, 3 SM; missing 2nd SMCV (Robertson 1902a; J. C. Crawford in Pierce 1909).

Table 3. Published records of species exhibiting atypical or variable numbers of submarginal cells.

Family	Species
Colletidae	*Leioproctus* (*Minycolletes*) *abnormis* (Cockerell)
Andrenidae	*Andrena* (*Callandrena* s. lat.) *asteris* Robertson
	Andrena (*Callandrena* s. lat.) *asteroides* Mitchell
	Andrena (*Callandrena* s. lat.) *crawfordi* Viereck
	Andrena (*Callandrena* s. lat.) *gardineri* Cockerell
	Andrena (*Callandrena* s. lat.) *krigiana* Robertson
	Andrena (*Callandrena* s. lat.) *simplex* Smith
	Andrena (*Cnemidandrena*) *denticulata* (Kirby)
	Andrena (*Euandrena*) *geranii* Robertson
	Andrena (*Euandrena*) *segregans* Cockerell
	Andrena (*Gonandrena*) *flocculosa* LaBerge and Ribble
	Andrena (*Gonandrena*) *integra* Smith
	Andrena (*Gonandrena*) *platyparia* Robertson
	Andrena (*Larandrena*) *miserabilis* Cresson
	Andrena (*Micrandrena*) *nigrae* Robertson
	Andrena (*Micrandrena*) *personata* Robertson
	Andrena (*Rhacandrena*) *brevipalpis* Cockerell or *A.* (*R.*) *robertsonii* Dalla Torre
	Andrena (*Scaphandrena*) *arabis* Robertson
	Andrena (*Scrapteropsis*) *biareola* LaBerge
	Andrena (*Scrapteropsis*) *imitatrix* Cresson
	Andrena (*Scrapteropsis*) *stipator* LaBerge
	Andrena (*Scrapteropsis*) *unicostata* LaBerge
	Andrena (*Thysandrena*) *ferrugineipes* LaBerge
	Andrena (*Trachandrena*) *forbesii* Robertson
	Andrena (*Trachandrena*) *hippotes* Robertson
	Perdita (*Alloperdita*) *bradleyi* Viereck
	Perdita (*Alloperdita* Viereck) spp.
	Perdita (*Xerophasma*) *celadona* Griswold and Miller
	Perdita (*Xerophasma*) *vespertina* Griswold and Miller
	Pseudopanurgus compositarum (Robertson)
Halictidae	*Augochlorella aurata* (Smith)
	Halictus (*Hexataenites*) *sexcinctus* (Fabricius)
	Halictus (*Seladonia*) *subauratus* (Rossi)
	Lasioglossum (*Ctenonomia*) *bakeri* Pauly
	Lasioglossum (*Dialictus*) *anomalum* (Robertson)
	Lasioglossum (*Dialictus*) *lionotum* (Sandhouse)
	Lasioglossum (*Dialictus*) *occidentale* (Crawford)
	Lasioglossum (*Dialictus*) *parvum* (Cresson)
	Lasioglossum (*Dialictus*) *versatum* (Robertson)
	Lasioglossum (*Dialictus* Robertson) sp.
	Lasioglossum (*Hemihalictus*) *lucidulum* (Schenck)

Family	Species
Halictidae, cont'd.	*Lasioglossum* (*Hemihalictus*) *lustrans* (Cockerell)
	Lasioglossum (*Lasioglossum*) *sisymbrii* (Cockerell)
	Lasioglossum (*Sphecodogastra*) *calceatum* (Scopoli)
	Sphecodes antennariae Robertson
	Sphecodes confertus Say
	Sphecodes cressonii (Robertson)
	Sphecodes niger Hagens
	Sphecodes pimpinellae Robertson
	Sphecodes stygius Robertson
	Temnosoma Smith spp.
Apidae	*Apis* (*Apis*) *mellifera* Linnaeus
	Epeolus ainsliei Crawford
	Epeolus minimus (Robertson)
	Epeolus olympiellus Cockerell
	Eucera (*Eucera*) *tuberculata* (Fabricius)
	Melecta (*Melecta*) *luctuosa* (Scopoli)
	Nomada flavoguttata (Kirby)
	Nomada mesopotamica Roig Alsina
	Nomada obliterata Cresson
	Nomada panamensis Michener
	Nomada roberjeotiana Panzer
	Nomada rufipes Fabricius
	Nomada sexfasciata Panzer
	Nomada stoeckherti Pittioni
	Nomada trapidoi Michener
	Xylocopa (*Koptortosoma*) *caerulea* (Fabricius)
	Xylocopa (*Koptortosoma*) *insularis* Smith
	Xylocopa (*Koptortosoma*) *unicolor* Smith
	Xylocopa (*Koptortosoma* Gribodo) "Cyaneoderes group" spp.

Andrena (*Callandrena* s. lat.) *asteroides* Mitchell
Typically, 3 SM; rarely with 2 SM in one or both wings (LaBerge 1967).

Andrena (*Callandrena* s. lat.) *crawfordi* Viereck
Typically, 3 SM; missing 2nd SMCV (J. C. Crawford in Pierce 1909).

Andrena (*Callandrena* s. lat.) *gardineri* Cockerell
Typically, 3 SM; rarely with 2 SM (LaBerge 1967).

Andrena (*Callandrena* s. lat.) *krigiana* Robertson
Typically, 3 SM; rarely 2 SM in one wing (LaBerge 1967).

Andrena (*Callandrena* s. lat.) *krigiana* Robertson
[reported as genus *Pterandrena krigiana* Robertson in Robertson (1902a); *Pterandrena* = *Callandrena* per Gusenleitner and Schwarz (2002)]
Typically, 3 SM; missing 2nd SMCV (Robertson 1902a; J. C. Crawford in Pierce 1909).

Andrena (*Callandrena* s. lat.) *simplex* Smith

[reported as genus *Pterandrena solidaginis* Robertson in Robertson (1902a); *Pterandrena* = *Callandrena* per Gusenleitner and Schwarz (2002)]

Typically, 3 SM; missing 2nd SMCV (Robertson 1902a; J. C. Crawford in Pierce 1909).

Andrena (*Cnemidandrena*) *denticulata* (Kirby)

Typically, 3 SM; one specimen with only 2 SM, the 2nd SM and 3rd SM combined (Schenck 1856).

Andrena (*Euandrena*) *geranii* Robertson

Typically, 3 SM; missing 2nd SMCV, hence only 2 SM (Robertson 1902a; J. C. Crawford in Pierce 1909).

Andrena (*Euandrena*) *segregans* Cockerell

Typically, 3 SM; one ♂ with 2 SM in left wing (LaBerge 1977).

Andrena (*Gonandrena*) *flocculosa* LaBerge and Ribble

Typically, 3 SM; one ♀ with 2 SM (LaBerge and Ribble 1972).

Andrena (*Gonandrena*) *integra* Smith

Typically, 3 SM; ♀s: 5% with 2 SM in both wings; ♂s: 7% with 2 SM in both wings; 18.6% with 2 SM in one wing (right:left = ~50:50). (LaBerge and Ribble 1972).

Andrena (*Gonandrena*) *platyparia* Robertson

Typically, 3 SM; missing 2nd SMCV, hence only 2 SM (Robertson 1902a; J. C. Crawford in Pierce 1909).

Andrena (*Gonandrena*) *platyparia* Robertson

[reported as *Andrena* (*Gonandrena*) *nigrifrons* (Cresson) in LaBerge and Ribble (1972); junior homonym per Gusenleitner and Schwarz (2002)]

Typically, 3 SM; ♂s: 10% with one wing and 16% with both wings having 2 SM; ♀s: ~5% of the specimens with these anomalies (LaBerge and Ribble 1972).

Andrena (*Larandrena*) *miserabilis* Cresson

[reported as genus *Opandrena bipunctata* Robertson in Robertson (1902a); junior synonym per Ribble (1967)]

Typically, 3 SM; missing 2nd SMCV, hence only 2 SM (Robertson 1902a; J. C. Crawford in Pierce 1909).

Andrena (*Micrandrena*) *nigrae* Robertson

[reported as *Andrena illinoensis* Robertson in Robertson 1902a, and in J. C. Crawford in Pierce 1909]

Typically, 3 SM; missing 2nd SMCV, hence only 2 SM (Robertson 1902a; J. C. Crawford in Pierce 1909).

Andrena (*Micrandrena*) *personata* Robertson

[reported as genus *Opandrena personata* Robertson in Robertson (1902a)]

Typically, 3 SM; missing 2nd SMCV, hence only 2 SM (Robertson 1902a; J. C. Crawford in Pierce 1909).

Andrena (*Rhacandrena*) *brevipalpis* Cockerell or *Andrena* (*Rhacandrena*) *robertsonii* Dalla Torre

[reported as genus *Opandrena robertsonii* Robertson in Robertson (1902a); could refer to either of the above species per LaBerge (1977)]

Typically, 3 SM; missing 2nd SMCV, hence only 2 SM (Robertson 1902a; J. C. Crawford in Pierce 1909).

Andrena (*Scaphandrena*) *arabis* Robertson

Typically, 3 SM; missing 2nd SMCV, hence only 2 SM (Robertson 1902a; J. C. Crawford in Pierce 1909).

Andrena (*Scrapteropsis*) *biareola* LaBerge

Typically, 2 SM; ♀: one specimen from Samuel Spring, Napa Co., California with 3 SM in both wings (LaBerge 1971).

Andrena (*Scrapteropsis*) *imitatrix* Cresson

[reported as genus *Trachandrena claytoniae* Robertson in Robertson (1902a); synonym per Gusenleitner and Schwarz (2002)]

Typically, 3 SM; missing 2nd SMCV, hence only 2 SM (Robertson 1902a; J. C. Crawford in Pierce 1909). One specimen missing 2nd SMCV, hence only 2 SM on one wing (Robertson 1903).

Andrena (*Scrapteropsis*) *stipator* LaBerge
Typically, 3 SM; one ♂ specimen with 2 SM in one wing (LaBerge 1971).

Andrena (*Scrapteropsis*) *unicostata* LaBerge
Typically, 3 SM; ♂s: a tendency towards having only 2 SM in one or both wings; five of 13 ♂s with 2 SM in one or both wings (LaBerge 1971).

Andrena (*Thysandrena*) *ferrugineipes* LaBerge
Typically, 3 SM; one ♂ with 2 SM in left wing (LaBerge 1977).

Andrena (*Trachandrena*) *forbesii* Robertson
[reported as genus *Trachandrena forbesii* (Robertson) in Robertson (1902a)]
Typically, 3 SM; missing 2nd SMCV, hence only 2 SM (Robertson 1902a; J. C. Crawford in Pierce 1909).

Andrena (*Trachandrena*) *hippotes* Robertson
[reported as genus *Trachandrena hippotes* (Robertson) in Robertson (1902a)]
Typically, 3 SM; missing 2nd SMCV, hence only 2 SM (Robertson 1902a; J. C. Crawford in Pierce 1909).

Perdita (*Alloperdita*) *bradleyi* Viereck
Typically, with an intercalary cell and therefore a variation of 3 SM cells (Michener 2007).
Holotype: left wing with 3 SM, where the 1st SMCV forks near its base resulting in the intercalary 3rd SM; right wing with 2 SM; seven specimens: "Most, if not all" with 3 SM in one or both wings as in the type, however some with the fork nearer the middle of the 1st SMCV (Viereck 1907).

Perdita (*Alloperdita* Viereck) spp.
Typically have an intercalary cell and therefore a variation of 3 SM. The intercalary cell variable in size and even absent occasionally (Timberlake 1956; Michener 2007).

Perdita (*Xerophasma*) *celadona* Griswold and Miller
Typically, 3 SM (a small triangular, petiolate SM intercalated between two regular SM). The intercalated SM occasionally missing on one or both wings. The size of the intercalated cell variable. Three ♀ specimens with the cell missing on one wing (Griswold and Miller 2010).

Perdita (*Xerophasma*) *vespertina* Griswold and Miller
Typically, 3 SM (a small triangular, petiolate SM intercalated between two regular SM); intercalated submarginal cell occasionally missing on one or both wings. Riverside, Nevada: three ♀s and one ♂ missing the cell on the left wing only; one ♀ incompletely missing the cell on the right wing only; two ♀s incompletely missing the cell on the right and missing it on the left; one ♀ incompletely missing the cell on the left; four ♂s missing the cell on both wings. Mesquite, Nevada: One ♂ missing the 3rd SM on both wings (Griswold and Miller 2010).

Pseudopanurgus compositarum (Robertson)
Typically, 2 SM (Mitchell 1960); one specimen with 3 SM (Robertson 1922).

Family Halictidae

Augochlorella aurata (Smith)
[reported as genus *Oxystoglossa confusa* (Robertson) in Robertson (1902b); synonym per Ascher and Pickering 2017a]
Typically, 3 SM (Mitchell 1960); one specimen with the 1st SMCV missing on one wing; a second with both the 1st SMCV and the 2nd SMCV missing on one wing (Robertson 1902b).

Halictus (*Hexataenites*) *sexcinctus* (Fabricius)
Typically, 3 SM; illustration of a ♀ forewing with only 2 SM, missing the 1st SMCV; out of 44 ♀s, two with 2 SM on both wings; out of 46 ♂s, two with 2 SM on one wing (Peters 1969).

Halictus (*Seladonia*) *subauratus* (Rossi)
Typically, 3 SM; found with 2 SM (Peters 1969).

Lasioglossum (*Ctenonomia*) *bakeri* Pauly

Unknown whether 2 SM or 3 SM is the norm; only two specimens: ♂ holotype with 2 SM on both wings without the 2nd SMCV; ♂ paratype with 3 SM on both wings (Pauly 2001). Three SM is the norm in *Ctenonomia* and there are no known species with 2 SM (Pauly, pers. comm., 20 April 2017). Pauly thinks the holotype is simply aberrant.

Lasioglossum (*Dialictus*) *anomalum* (Robertson)

Typically, 2 SM (Mitchell 1960, Gibbs 2010b).

Mitchell (1960) made the then genus *Chloralictus* Robertson a synonym of *Dialictus* Robertson since he felt that 2 SM versus 3 SM was an unreliable character to separate the two genera.

Seven specimens: six with 3 SM (2nd SMCV present) on one wing; one with 3 SM present on both wings (Gibbs 2010a).

Lasioglossum (*Dialictus*) *lionotum* (Sandhouse)

[reported as *Lasioglossum* (*Dialictus*) *asteris* (Mitchell) in Gibbs (2010a, 2010b); junior synonym per Gibbs (2011)]

Polymorphic, 2nd SMCV either present or absent, hence either 2 SM or 3 SM (Gibbs 2010a). Often, 2nd SMCV incomplete or absent (Gibbs 2010b).

Lasioglossum (*Dialictus*) *occidentale* (Crawford)

Typically, 2 SM (Gibbs 2010b). One ♂ specimen: one wing with 3 SM, one wing with 2 SM (Sandhouse 1923).

Lasioglossum (*Dialictus*) *parvum* (Cresson)

Specimens commonly lack the 2nd SMCV; all the ♂ specimens and 75% of the ♀ specimens with 2 SM, some showing stubs of the 2nd SMCV; in many examples, 2 SM found on one wing and 3 SM on the other of the same specimen (Baker 1906).

Polymorphic, 2nd SMCV either present or absent, hence either 2 SM or 3 SM (Gibbs 2010a). Ratio: 2 SM on both wings, 2 SM and 3 SM (one on each wing), and 3 SM on both wings is approximately = 4:1:1 (Gibbs, pers. comm., 18 May 2017).

Lasioglossum (*Dialictus*) *versatum* (Robertson)

[reported as genus *Chloralictus versatus* Robertson in Robertson (1902b)]

Typically, with 3 SM (Mitchell 1960); one specimen with the 2nd SMCV "wanting," hence only 2 SM (Robertson 1902b).

Lasioglossum (*Dialictus* Robertson) sp.

One West Indian species: either 2 SM or 3 SM; occasionally an individual specimen with 2 SM on one wing and 3 SM on the other (Michener et al. 1994). [These are most likely Baker's *L.* (*D.*) *parvum* mentioned above (Gibbs, pers. comm., 23 April 2017).]

Lasioglossum (*Hemihalictus*) *lucidulum* (Schenck)

Typically, 3 SM; found with 2 SM (Peters 1969).

Lasioglossum (*Hemihalictus*) *lustrans* (Cockerell)

Typically, 2 SM; one ♂ specimen with the 2nd SMCV present on both wings, hence 3 SM (Gibbs 2010a).

A small proportion of specimens with the 2nd SMCV present on both wings (Gibbs et al. 2013), particularly from more northern parts of the species range: Michigan (Dickinson Co.) and Wisconsin (Marinette Co.: Dunbar barrens; Monroe Co.).

Lasioglossum (*Lasioglossum*) *sisymbrii* (Cockerell)

One ♂ collected by Sheffield on Mt. Kobau, South Okanagan Grasslands Protected Area, near Osoyoos (Western Interior Basin Ecozone [= Southern Interior Ecoprovince] of British Columbia) on 8 August 2014; a non-metallic *Lasioglossum* s. str. with 2 SM (missing 1st SMCV) on both wings, instead of the normal 3 SM (Sheffield and Heron 2017).

Lasioglossum (*Sphecodogastra*) *calceatum* (Scopoli)

[reported as genus *Evylaeus cylindricus* (Fabricius) in Robertson (1902b)]

Typically, 3 SM (Mitchell 1960); one specimen from Pérez of Bordeaux with the 2nd SMCV "wanting," hence only 2 SM (Robertson 1902b).

Sphecodes antennariae Robertson

[Reported as genus *Dialonia antennariae* (Robertson), gen. nov. for *Sphecodes antennariae* Robertson in Robertson (1903)]

Typically, 2 SM, i.e. lacking the 1st SMCV in five specimens (Robertson 1903).

Sphecodes confertus Say

[Reported as genus *Drepanium falciferum* Robertson, gen. nov. for *Sphecodes falcifer* Patton in Robertson (1903)]

Typically, 3 SM; 1st SMCV missing in one specimen, hence only 2 SM (Robertson 1903).

Sphecodes cressonii (Robertson)

[Reported as genus *Sphecodium cressonii* Robertson, gen. nov. and sp. nov. in Robertson (1903)]

Typically, 3 SM; 1st SMCV missing in two specimens, hence only 2 SM (Robertson 1903).

Sphecodes niger Hagens

Typically, 3 SM (Peters 1969); a population of *S. niger* observed by Wolf in 1946–1949 in a *Lasioglossum* (*Dialictus*) *morio* (Fabricius) colony, about half of all ♂ *Sphecodes* had only 2 SM, while all ♀s had normal venation (H. Wolf, pers. comm., in Peters 1969).

Sphecodes pimpinellae Robertson

Typically, with 2 SM or 3 SM; type specimen with 3 SM, but three others with 2 SM; the character considered to be unstable for the species (Mitchell 1960).

Variable with 2 SM rather than 3 SM; Connecticut specimens, some with partial loss of SMCVs in one or both wings (Zarrillo et al. 2016).

Sphecodes pimpinellae Robertson

[Reported as genus *Sphecodium pimpinellae* (Robertson), gen. nov. for *Sphecodes pimpinellae* Robertson in Robertson (1903)]

Typically, 3 SM; 1st SMCV missing in three specimens; 1st SMCV missing in known ♂ specimens (Robertson 1903).

Sphecodes stygius Robertson

[Reported as genus *Machaeris stygia* (Robertson), gen. nov. for *Sphecodes stygius* Robertson in Robertson (1903)]

Typically, 3 SM; 1st SMCV missing in two specimens, hence only 2 SM (Robertson 1903).

Temnosoma Smith spp.

Typically, 3 SM (except *T. sphaerocephalum* [Schrottky] that only has 2 SM); species other than *T. sphaerocephalum* occasionally with only 2 SM (Michener 2007).

Family Apidae

Apis (*Apis*) *mellifera* Linnaeus

Typically, 3 SM (Michener et al. 1994). Experimental effects of undernourishment of larvae: 116 specimens: 19.82% ± 2.50 with incomplete development of the 2nd SMCV resulting in the 2nd SM and 3rd SM being partially conjoined (Alpatov 1928).

Drones from a virgin queen of mixed Italian honey bees, *A. m. ligustica* Spinola: occasional partial or complete division of the 3rd SM by "protrusion" of veinlets between the 2nd SMCV and 3rd SMCV (Akahira and Sakagami 1959).

Wing vein teratology study: specimens with the following: reduction of the 1st SMCV to a stub thereby joining the 1st SM and 2nd SM; an incomplete 2nd SMCV and partial merging of the 2nd SM and 3rd SM; an open forked 2nd SMCV forming an incomplete supernumerary SM; a closed forked 2nd SMCV forming a complete supernumerary SM (a small fourth cell); and spurs on the 2nd SMCV and 3rd SMCV that nearly met, almost dividing the 3rd SM in two (Porporato et al. 2014).

Epeolus ainsliei Crawford

Typically, 3 SM; specimens examined by Onuferko (2017): the 2nd SMCV or 3rd SMCV partially or entirely missing in one or both wings.

Epeolus minimus (Robertson)

Typically, 3 SM; specimens examined by Onuferko (2017): the 2nd SMCV or 3rd SMCV partially or entirely missing in one or both wings.

Epeolus olympiellus Cockerell

Typically, 3 SM; holotype with 2nd SMCV incomplete on both forewings (Onuferko 2017); specimens examined by Onuferko (2017): the 2nd SMCV or 3rd SMCV partially or entirely missing in one or both wings.

Eucera (*Eucera*) *tuberculata* (Fabricius)

Typically, 2 SM; illustration of a ♂ forewing possessing a 2nd SMCV and 3 SM (Peters 1969).

Melecta (*Melecta*) *luctuosa* (Scopoli)

[reported as *Melecta* (*Melecta*) *punctata* (Fabricius) in Peters (1969) and in Hirsch [1999] (2000)]

Typically, 3 SM; illustration of a ♂ forewing lacking 2nd SMCV and with only 2 SM; of 31 ♀s, one specimen having both wings with only 2 SM; of 23 ♂s, four with only 2 SM (three specimens with 2 SM on both wings, and one specimen with 2 SM on one wing only) (Peters 1969).

Two ♀s collected in northern Poland with only 2 SM (Hirsch [1999] 2000).

Nomada flavoguttata (Kirby)

Often with 2 SM instead of the typical 3 SM (Peters 1969).

Nomada mesopotamica Roig Alsina

Typically, 3 SM; three of 19 specimens with 2 SM (one with 2nd SMCV reduced on both wings; two with 1st SMCV reduced) (Roig Alsina 2009).

Nomada obliterata Cresson

Typically, ♀s with 2 SM; rarely with 3 SM, but usually on one wing only (Droege et al. 2010).

Nomada panamensis Michener

Typically, 3 SM; 2nd SMCV sometimes absent (Alexander 1994).

Nomada roberjeotiana Panzer

Often with 2 SM instead of the typical 3 SM (Peters 1969).

Nomada roberjeotiana Panzer

[reported as *Nomada montana* (Mocsáry) in Peters (1969); synonym of *N. roberjeotiana* Panzer per BWARS (2017)]

Sometimes with 3 SM instead of the typical 2 SM (Peters 1969). Note that these characters are just the opposite of *N. roberjeotiana* as stated above in Peters (1969).

Nomada rufipes Fabricius

Often with 2 SM instead of the typical 3 SM (Peters 1969).

Nomada sexfasciata Panzer

Typically, 3 SM; illustration of a ♀ forewing lacking 2nd SMCV and with only 2 SM (Peters 1969).

Nomada stoeckherti Pittioni

Sometimes with 3 SM instead of the typical 2 SM (Peters 1969).

Nomada trapidoi Michener

Michener's specimens: number of submarginal cells varied by sex; ♂s with 3 SM; ♀s with 2 SM (Michener 1954).

Xylocopa (*Koptortosoma*) *caerulea* (Fabricius)

Typically, 3 SM; 2nd SM "frequently wanting" (Smith 1874).

Xylocopa (*Koptortosoma*) *insularis* Smith

Typically, 3 SM; ♂s from Sarawak, Borneo, with the 1st SMCV "obliterated" (Smith 1858).

Xylocopa (*Koptortosoma*) *unicolor* Smith

2nd SM is obsolete in both sexes; ♂s show a trace of 1st SMCV (Smith 1861).

Smith (1874) examined two ♂s and ten ♀s "always, apparently" without a 2nd SM.

Xylocopa (*Koptortosoma* Gribodo) "Cyaneoderes group" spp.

[reported as *Xylocopa* (*Cyaneoderes* Ashmead) (Hurd and Moure 1963)]

Fourteen names applied in the former subfamily *Cyaneoderes* (Hurd and Moure 1963); currently, six recognized species: *X. abbotti* (Cockerell), *X. bangkaensis* Friese, *X. caerulea* (Fabricius), *X. incompleta* Ritsema, *X. insularis* Smith, and *X. tumida* Friese (Mawdsley 2016). Forewing with 2 SM or 3 SM; if 3 SM, 1st SMCV usually incomplete; number of submarginal cells variable; species often exhibit just 2 SM; the frequency of 2 SM individuals was high in the specimens examined by Hurd and Moure (1963); they postulated that natural selection might be producing a 2 SM group in the Xylocopini.

Previously unpublished specimen records of atypical or variable numbers of submarginal cells

The following previously unpublished records of atypical and variable numbers of submarginal cells were submitted by colleagues and members of the "Bee Inventory, Monitoring, and ID" listserve. Each specimen record is shown as a separate paragraph, except when a series of records are closely related by date, location, or personnel, in which case they are shown in the same paragraph. Table 4 provides a list of the previously unpublished records. Tables 5 and 6 summarize the data and show that 12.3% (n = 10) of the specimens with atypical numbers of submarginal cells (n = 81) would normally have had 2 SM; 87.7% (n = 71) would normally have had 3 SM. Approximately 49.4% (n = 40) of the specimens had atypical numbers on one wing, and approximately 50.6% (n = 41) had atypical numbers on both wings. Of the normally 2 SM specimens, 80.0% (n = 8) gained and 20.0% (n = 2) lost one SMCV. Of the normally 3 SM specimens, 1.4% (n = 1) gained one SMCV and 98.6% (n = 70) lost one or more SMCV.

Family Colletidae

Colletes robertsonii Dalla Torre

♀; 13–14 July 2015; USA, Minnesota, Pipestone Co., Terrace WMA; 44.03038°; –96.17125°; 3.25-oz elevated bee bowls; coll.: Ashley Fulton and Karin J. Jokela; det.: Crystal L. Boyd; UMSP; UMSP_BEE_115120; left: 3 SM (normal [Mitchell 1960]); right: 2 SM (partial 2nd SMCV extending posteriorly ~67% the distance from the marginal cell); Crystal L. Boyd, pers. comm.

Family Andrenidae

Andrena (*Andrena*) *tridens* Robertson

♂; 06–25 April 2006; USA, West Virginia, Hardy Co., 3 mi NE Mathias; 38.9166667°; –78.8166667°; malaise traps (bycatch from sawfly studies); coll.: David R. Smith; det.: Samuel W. Droege; BIML; USGS_DRO068906; left: 2 SM; right: 3 SM (normal [Mitchell 1960]); Jane J. Whittaker, pers. comm. (specimen examined by Scarpulla).

Andrena (*Euandrena*) *bicolor* Fabricius

♀; 12 August 2015; Denmark, Strandegaard; coll.: Projekt Beefarm; det.: Henning Bang Madsen; Madsen collection; left: 2 SM; right: 2 SM (3 is the normal [Mitchell 1960]); Henning Bang Madsen via Claus Rasmussen, pers. comm.

Andrena (*Micrandrena*) *subopaca* Nylander

♂; 27 May 2017; Denmark, Teglværkshuse; ~55.41°; 12.07°; coll. and det.: Henning Bang Madsen; Madsen collection; left: 3 SM (normal [Mitchell 1960]); right: 2 SM; Henning Bang Madsen via Claus Rasmussen, pers. comm.

Andrena (*Simandrena*) *nasonii* Robertson

♀; 6 June 2013; USA, Massachusetts, Hampden Co., Springfield, JACABB, unmowed-treatment A; elev.: 73 m; 42.0970°; –72.4939°; bee bowl; coll.: Susannah B. Lerman; det.: Joan Milam; Milam collection;

Table 4. Previously unpublished specimen records of atypical or variable numbers of submarginal cells. SM-N = normal number of SM; SM-L = number of SM on left wing; SM-R = number of SM on right wing; AW = number of atypical wings.

Family	Species	Sex	SM-N	SM-L	SM-R	AW
Colletidae	*Colletes robertsonii* Dalla Torre	F	3	3	2	1
Andrenidae	*Andrena* (*Andrena*) *tridens* Robertson	M	3	2	3	1
	Andrena (*Euandrena*) *bicolor* Fabricius	F	3	2	2	2
	Andrena (*Micrandrena*) *subopaca* Nylander	M	3	3	2	1
	Andrena (*Simandrena*) *nasonii* Robertson	F	3	2	2	2
	Andrena (*Trachandrena* Robertson) sp.	M	3	2	3	1
	Calliopsis (*Calliopsis*) *andreniformis* Smith	F	2	1	1	2
	Liphanthus sp.	F	2	2	3	1
Halictidae	*Augochlora* (Say) sp.	F	3	2	3	1
	Halictus (*Protohalictus*) *rubicundus* (Christ)	F	3	2	3	1
	Halictus (*Seladonia*) *confusus* Smith	F	3	3	2	1
		F	3	2	2	2
		F	3	2	3	1
		F	3	2	2	2
		F	3	2	2	2
		F	3	2	3	1
		F	3	3	3[a]	1[a]
		F	3	2	2	2
		F	3	3	2	1
		F	3	3	2	1
		F	3	2	2	2
		F	3	2	3	1
	Lasioglossum (*Dialictus*) *admirandum* (Sandhouse)	F	3	3[b]	3	1[b]
	Lasioglossum (*Dialictus*) *anomalum* (Robertson)	F	2	3	2	1
		M	2	1	1	2
		F	2	3	2	1
	Lasioglossum (*Dialictus*) *laevissimum* (Smith)	F	3	2	3	1
	Lasioglossum (*Dialictus*) *zephyrum* (Smith)	F	3	1	1	2
	Lasioglossum (*Evylaeus* s. lat. Robertson) sp.	M	3	3	2	1
	Lasioglossum (*Hemihalictus*) *hewetti* (Cockerell)	F	3	3	2	1
	Lasioglossum (*Leuchalictus*) *leucozonium* (Schrank)	F	3	2	3	1
	Lasioglossum (*Sphecodogastra*) *seillean* Gibbs and Packer	F	3	3	2	1
	Lipotriches (*Afronomia* Pauly, *Austronomia* Michener, or *Macronomia* Cockerell) sp.	M	3	2	3	1
	Sphecodes antennariae Robertson	F	3	3	2	1
		F	3	2	2	2
		F	3	2	1	2
		F	3	2	3	1
	Sphecodes coronus Mitchell	F	3	2	3	1

Family	Species	Sex	SM-N	SM-L	SM-R	AW
Halictidae, cont'd	*Sphecodes pimpinellae* Robertson	F	3	2	3	1
		M	3	2	2	2
		F	3	3[c]	3[d]	2[c, d]
		F	3	2	2	2
		F	3	3	2	1
	Sphecodes puncticeps Thomson	F	3	2	2	2
Apidae	*Anthophorula* (*Anthophorula*) *completa* (Cockerell)	M	3	2	3	1
	Melitoma taurea (Say)	F	3	4	3	1
	Nomada flavoguttata (Kirby)	M	3	2	2	2
		M	3	2	2	2
		F	3	2	2	2
		M	3	1	2	2
		M	3	2	1	2
		M	3	2	2	2
		M	3	2	2	2
		F	3	1	1	2
		M	3	2	2	2
		F	3	2	2	2
		M	3	2	2	2
		M	3	2	2	2
		M	3	2	2	2
		M	3	3	2	1
		M	3	[e]	2	[e]
		M	3	3	2	1
		M	3	2	2	2
		M	3	3	2	1
		M	3	2	2	2
		M	3	2	3	1
		M	3	2	2	2
		M	3	2	2	2
		F	3	3	2	1
		M	3	2	2	2
		F	3	3	2	1
		M	3	2	2	2
	Nomada obliterata Cresson	F	2	2	3	1
	Nomada stoeckherti Pittioni	F	2	2	3	1
		F	2	3	2	1
		M	2	3	3	2
		F	2	3	3	2
	Nomada Scopoli sp.	U[f]	U[f]	1	1	2
	Tetraloniella (*Tetraloniella*) *salicariae* (Lepeletier)	M	3	2	3	1

Family	Species	Sex	SM-N	SM-L	SM-R	AW
Apidae, cont'd	*Xylocopa* (*Koptortosoma*) *caerulea* (Fabricius)	F	3	2	2	2
		F	3	2	2	2
		M	3	2	2	2
	Xylocopa (*Koptortosoma*) *coronata* Smith	F	3	2	2	2
		M	3	2	2	2
	Xylocopa (*Neoxylocopa*) *orthogonaspis* Moure	F	3	2	3	1
	Xylocopa (*Xylomelissa*) *lugubris* Gerstäcker	M	3	2	3	1

[a] = 2nd SM atypically triangular, with the point touching the marginal cell
[b] = dot of extra sclerotization and small extra veins present on the distal side of the 3rd SMCV [exterior to the 3rd SM], anterior to where the 3rd SMCV meets the 2nd medial cell
[c] = 2nd SM very narrow, only two vein widths wide; all veins dark in color
[d] = 2nd SMCV faintly-colored, and separated from the 1st SMCV by no more than one vein width, thus the 2nd SM extremely narrow
[e] = missing wing
[f] = specimen unavailable for species identification, sexing, or normal number of SM

Table 5. Numbers of previously unpublished specimens exhibiting atypical numbers of submarginal cells. (Table 4 specimens bearing superscripts are not included in this analysis.)

Normal Condition	Number of Atypical Specimens	Atypical Number of Submarginal Cells							
		One Wing (n = 40)				Two Wings (n = 41)			
		1 SM	2 SM	3 SM	4 SM	1 SM	1 SM/ 2 SM	2 SM	3 SM
2 SM	10	0	(normal)	6	0	2	0	(normal)	2
3 SM	71	0	33	(normal)	1	2	3	32	(normal)

Table 6. Percentages of previously unpublished atypical specimens exhibiting atypical numbers of submarginal cells. (Table 4 specimens bearing superscripts are not included in this analysis.)

Normal Condition	Percentage of Atypical Specimens	Atypical Number of Submarginal Cells							
		One Wing (49.4%)				Two Wings (50.6%)			
		1 SM	2 SM	3 SM	4 SM	1 SM	1 SM/ 2 SM	2 SM	3 SM
2 SM	12.3%	0%	(normal)	60.0%	0%	20.0%	0%	(normal)	20.0%
3 SM	87.7%	0%	46.5%	(normal)	1.4%	2.8%	4.2%	45.1%	(normal)

left: 2 SM (missing the 1st SMCV); right: 2 SM (partially missing the 2nd SMCV) (3 SM is the normal [Mitchell 1960]); Joan Milam, pers. comm. (photo examined by Scarpulla).

Andrena (*Trachandrena* Robertson) sp.

♂; 25 April–10 May 2006; USA, West Virginia, Hardy Co., 3 mi NE Mathias; 38.9166667°; –78.8166667°; malaise traps (bycatch from sawfly studies); coll.: David R. Smith; det.: Samuel W. Droege; Scarpulla collection; USGS_DRO069083; left: 2 SM (2nd and 3rd SM conjoined; incomplete 2nd

SMCV, extending slightly more than halfway from the posterior margin of the marginal cell); right: 3 SM (normal [Michener 2007]); Jane J. Whittaker, pers. comm.

Calliopsis (*Calliopsis*) *andreniformis* Smith

♀; 6 September 1922; USA, Minnesota, Watonwan Co., Madelia; coll.: C. N. Ainslie; det.: A. F. Shinn; confirmed: Crystal L. Boyd; ISIC; ISIC_100078; left: 1 SM; right: 1 SM (both wings with incomplete 1st SMCV, extending anteriorly ~80% of the distance from the 1st medial cell) (2 SM normal [Mitchell 1960]); Crystal L. Boyd, pers. comm.

Liphanthus Reed sp. (an undescribed species per Packer, pers. comm., 27 September 2018)

♀; 27 November 2017; Chile, Region VII, Road to Laguna Teno, elev.: 1849 m; –35.12498°; –70.48891°; coll.: Samuel W. Droege and Laurence Packer; det.: Laurence Packer; PCYU; left: 2 SM (normal); right: 3 SM (2nd SMCV added); of 28 specimens collected (PCYU: 25; BIML: 3), only one was atypical.; Laurence Packer, pers. comm.

Family Halictidae

Augochlora (Say) sp. (likely an undescribed species per Rasmussen, pers. comm., 30 June 2014)

♀; 6 October 1970; Peru, Pucallpa; coll.: Renan Garcia; det.: Claus Rasmussen; MUSM; left: 2 SM; right: 3 SM (normal [Mitchell 1960]); Claus Rasmussen, pers. comm. (photo examined by Scarpulla).

Halictus (*Protohalictus*) *rubicundus* (Christ)

♀; 26 July 1989; Canada, Manitoba, Lyleton, 4.4 km E; coll.: W. B. Preston; det.: Jason Gibbs; JBWM; left: 2 SM (missing 2nd SMCV); right: 3 SM (normal [Mitchell 1960]); Jason Gibbs, pers. comm.

Halictus (*Seladonia*) *confusus* Smith

♀; 12–14 August 2014; USA, Minnesota, St. Louis Co., open bog; Start: 47.166964°, –92.732307°; 3.25-oz elevated bee bowls (4 each of yellow, blue, and white); coll.: Gerda Nordquist and Kristen Olson; det.: Crystal L. Boyd and Amy Arndorfer; UMSP; MN-DNR_155786; left: 3 SM (normal [Mitchell 1960]); right: 2 SM (1st SMCV absent); Crystal L. Boyd, pers. comm.

♀; 26–27 May 2015; USA, Minnesota, Pipestone Co., Winter Wildlife Management Area; 44.13456°; –96.36904°; 3.25-oz elevated bee bowls; coll.: Ashley Fulton and Karin J. Jokela; det.: Crystal L. Boyd; UMSP; UMSP_BEE_113167; left: 2 SM (1st SMCV extending anteriorly 25% of the distance from the 1st medial cell); right: 2 SM (missing 1st SMCV); Crystal L. Boyd, pers. comm. ♀; same information except: UMSP_BEE_113268; left: 2 SM (1st SMCV absent); right: 3 SM. ♀; same information except: UMSP_BEE_113271; left: 2 SM, right: 2 SM (both wings 1st SMCV extending anteriorly 10% of the distance from the 1st medial cell). ♀; same information except: UMSP_BEE_113317; left: 2 SM; right: 2 SM (both wings missing 1st SMCV). ♀; same information except: UMSP_BEE_113394; left: 2 SM (missing 1st SMCV); right: 3 SM. ♀; same information except: Terrace Wildlife Management Area; 44.03038°; –96.17125°; UMSP_BEE_113065; left: 3 SM; right: 3 SM (2nd SM atypically triangular, with the point touching the marginal cell). ♀; same information except: Lac qui Parle Co., Bail Out Wildlife Management Area; 44.84752°; –96.28242°; UMSP_BEE_113748; left: 2 SM; right: 2 SM (both wings missing 1st SMCV). ♀; same information except: Swift Co., Clair Rollings Wildlife Management Area; 45.29003°; –95.62591°; UMSP_BEE_113844; left: 3 SM; right: 2 SM (missing 1st SMCV). ♀; same information except: Yellow Medicine Co., Mound Spring Prairie Scientific and Natural Area; 44.74177°; –96.42908°; UMSP_BEE_113597; left: 3 SM; right: 2 SM (missing 1st SMCV). ♀; same information except: 9–10 September 2015; Murray Co., Salt & Pepper Wildlife Management Area; 43.95021°; –96.02563°; UMSP_BEE_122470; left: 2 SM; right: 2 SM (both wings missing 1st SMCV).

♀; 5 August 2015; USA, Maryland, Prince George's Co., USDA Beltsville Agricultural Research Center, in front of BIML, Building 308; 39.035090°; –76.874023°; bee bowl; coll.: Michael Fizdale; det.: Eugene J. Scarpulla; Scarpulla collection; USGS_DRO 429803; left: 2 SM (missing 1st SMCV); right: 3 SM; Michael Fizdale, pers. comm.

Lasioglossum (*Dialictus*) *admirandum* (Sandhouse)

♀; 15–16 June 2015; USA, Minnesota, Nobles Co., West Graham Wildlife Management Area; 43.80083°; –95.53262°; 3.25-oz elevated bee bowls; coll.: Ashley Fulton and Karin J. Jokela; det.: Crystal L. Boyd;

UMSP; UMSP_BEE_114381; left: 3 SM (dot of extra sclerotization and small extra veins present on the distal side of the 3rd SMCV [exterior to the 3rd SM], anterior to where the 3rd SMCV meets the 2nd medial cell); right: 3 SM (normal [Mitchell 1960]); Crystal L. Boyd, pers. comm. (sketch examined by Scarpulla).

Lasioglossum (*Dialictus*) *anomalum* (Robertson)

♀; 10–13 May 2010; USA, Connecticut, New Haven, Cheshire, Boulder Knoll Farm; elev.: 90 m; 41°28.13′; –072°52.26′›; bee bowl; coll.: Tracy A. Zarrillo; det.: John S. Ascher; CAES; UCMS_ENT00044323; left: 3 SM; right: 2 SM (normal [Mitchell 1960]); Tracy A. Zarrillo, pers. comm.

♂; 8 September 2013; USA, Minnesota; 43°50′42.66″ 91°47′6.31″; on *Symphyotrichum oolentangiense* (Riddell) G. L. Nesom (Asteraceae) (skyblue aster); coll.: Scott Leddy; det.: Jason Gibbs; JBWM; left: 1 SM; right: 1 SM (missing 1st SMCV on each wing; slight nub visible on anterior margin of each SM); Jason Gibbs, pers. comm.

♀; 8 August 2016; USA, Minnesota; Ramsey Co., Battle Creek Regional Park; elev.: 295 m; 44.9384°; –92.9933°; bee bowl; coll.: Elaine Evans; det.: Jason Gibbs; CNBL; 2016hc5647; left: 3 SM (2nd SMCV added); right: 2 SM; Crystal L. Boyd, pers. comm.

Lasioglossum (*Dialictus*) *laevissimum* (Smith)

♀; 9 July 1959; USA, Minnesota, St. Louis Co., Eagles Nest; coll.: V. W. Balduf; det.: Jason Gibbs; INHS; INHS_318012; left: 2 SM (2nd SMCV missing); right: 3 SM (normal [Mitchell 1960]); Crystal L. Boyd, pers. comm.

Lasioglossum (*Dialictus*) *zephyrum* (Smith)

♀; 12 September 2011; USA, Connecticut, Fairfield Co., Bethel, Holbrook Farm, 45 Turkey Plain Road; 41°20.741′; –073°24.935′; netted from *Galinsoga* Ruiz and Pav. sp. (Asteraceae) (gallant soldier); coll.: Ellen Bulger and Krystian Madrid; det.: Jason Gibbs; CAES; UCMS_ENT00052638; left: 1 SM; right: 1 SM (both wings missing 2nd SMCV; both wings with only a partial spur of the 3rd SMCV extending ~40% the distance from the 2nd medial cell; 3 SM is the normal [Mitchell 1960]); Tracy A. Zarrillo, pers. comm. (photos examined by Scarpulla).

Lasioglossum (*Evylaeus* s. lat. Robertson) sp.

♂; 1–2 August 2012; USA, Wyoming, Yellowstone National Park, COM1; 44.7628°; –110.4726°; bee bowl; coll.: Yellowstone National Park staff; det.: Catherine E. Stragar; Scarpulla collection; USGS_DRO 328954; left: 3 SM (normal [Mitchell 1960]); right: 2 SM (missing 2nd SMCV); Catherine E. Stragar, pers. comm.

Lasioglossum (*Hemihalictus*) *hewetti* (Cockerell)

♀; 11 February 2010; Mexico, Chiapas, Ocosingo; elev.: 1118 m; 16.89°; –92.27°; coll.: D. Sánchezm; det.: Jason Gibbs; JBWM; left: 3 SM (normal [Gibbs, pers. comm.]); right: 2 SM (missing 2nd SMCV); Jason Gibbs, pers. comm.

Lasioglossum (*Leuchalictus*) *leucozonium* (Schrank)

♀; 26 May 2017; Denmark, Give, Rækkebjerge; 55.77112392°; 9.05901958°; sweep net; coll. and det.: Claus Rasmussen; Rasmussen collection; left: 2 SM (missing 2nd SMCV); right: 3 SM (normal [Mitchell 1960]); Claus Rasmussen, pers. comm.

Lasioglossum (*Sphecodogastra*) *seillean* Gibbs and Packer

♀; paratype; 27 May 1949; Canada, Newfoundland, Harmon Field; coll.: F. G. DiLabio; det.: Jason Gibbs and Laurence Packer; CNC; left: 3 SM (normal); right: 2 SM (missing 2nd SMCV); Jason Gibbs, pers. comm.

Lipotriches (*Afronomia* Pauly, *Austronomia* Michener, or *Macronomia* Cockerell) sp.

Both Michener (2007) and Eardley et al. (2010) state that ♂s of these three subgenera cannot be separated.

♂; 27 November 2016; South Africa, Mpumalanga, Skukuza, Kruger National Park, in village scrub-lined street; –24.9857°; 31.581°; bee bowl; coll. and det.: Sam Droege; BIML; USGS_DRO 482042; left: 2 SM (missing 2nd SMCV); right: 3 SM (normal [Michener 2007]); Sam Droege, pers. comm. (specimen examined by Scarpulla).

Sphecodes antennariae Robertson

♀; 11 September 1995; USA, Wisconsin, Dane Co., Black Earth, T8N R6E Sect. 27, DNR study; sweep net; coll. and det.: Michael S. Arduser; Arduser collection; left: 3 SM (2nd SM very narrowly triangular); right: 2 SM (missing 2nd SMCV; typically, 3 SM [Arduser, pers. comm.]); Michael S. Arduser, pers. comm. ♀; same information except: left: 2 SM; right: 2 SM (both wings missing 2nd SMCV). ♀; same information except: 26 August 1999; USA, Wisconsin, Grant Co., McNamee Prairie, T8N R3W Sect. 35, DNR study; left: 2 SM (missing 2nd SMCV); right: 1 SM (missing 1st and 2nd SMCVs; no spur veins or other indications of SMCVs). ♀; same information except: 31 August 1999; USA, Wisconsin, Pepin Co., Schaull's Bluff Prairie, T25N R13W Sect. 29, DNR study; left: 2 SM (a minute spur vein coming off the marginal cell where the 1st SMCV would have been); right: 3 SM (2nd SM with veins parallel, not converging above).

Sphecodes coronus Mitchell

♀; 2–3 June 2016; USA, Maryland, Anne Arundel Co., Harwood, Riddle Sand and Gravel, sand mine; 38.8693°; –76.671°; bowl trap; coll.: Dejen Mengis; det.: Sam Droege; BIML; USGS_DRO 471826; left: 2 SM (partial 1st SMCV, 2 spurs: one weak spur extends posteriorly ~30% the distance from the marginal cell, the other spur extends anteriorly ~25% the distance from the 1st medial cell); right: 3 SM (normal [Mitchell 1956]).; Sam Droege, pers. comm. (specimen examined by Scarpulla).

Sphecodes pimpinellae Robertson

♀; homotype; 16 June 1923; USA, North Carolina, Bryson City; coll.: J. C. Crawford; Arduser collection; left: 2 SM (missing 2nd SMCV); right: 3 SM (normal [Arduser, pers. comm.]); Michael S. Arduser, pers. comm.

♂; 29 July 1995; USA, Illinois, Madison Co., Poag Road, sand prairie; netted at the extrafloral nectaries of *Chamaecrista fasciculata* (Michx.) Greene var. *fasciculata*, partridge pea (Fabaceae); coll. and det.: Michael S. Arduser; Arduser collection; left: 2 SM; right: 2 SM (both wings missing 2nd SMCV); Michael S. Arduser, pers. comm.

♀; 16 August 1996; USA, Wisconsin, Iowa Co., T8N R4E, Sect. 30, dry hill prairie, DNR study; sweep net; coll. and det.: Michael S. Arduser; Arduser collection; left: 3 SM (2nd SM very narrow, only two vein widths wide; all veins dark in color); right: 3 SM (2nd SMCV faintly-colored and separated from the 1st SMCV by no more than one vein width, thus the 2nd SM extremely narrow); Michael S. Arduser, pers. comm.

♀; 14 May 2002; USA, Missouri, Atchison Co., Star School Hill Prairie; netted; coll.: Tom Nagel; Arduser collection; left: 2 SM; right: 2 SM (both wings missing 2nd SMCV); Michael S. Arduser, pers. comm.

♀; 18–19 May 2016; USA, Maryland, Caroline Co., S of Goldsboro, MD Rte. 313, Councell pit, roadside; 39.0233°, –75.7883°; bowl trap; coll.: Dejen Mengis; det.: Sam Droege; BIML; USGS_DRO 471376; left: 3 SM; right: 2 SM (missing 1st SMCV); Sam Droege, pers. comm. (specimen examined by Scarpulla).

Sphecodes puncticeps Thomson

♀; 26 May 2017; Denmark, Give, Rækkebjerge; 55.77112392°; 9.05901958°; sweep net; coll. and det.: Claus Rasmussen; Rasmussen collection; left: 2 SM; right: 2 SM (both wings missing 1st SMCV; typically, 3 SM [Rasmussen, pers. comm.]); Claus Rasmussen, pers. comm.

Family Apidae

Anthophorula (*Anthophorula*) *completa* (Cockerell)

♂; 10–24 August 2009; USA, New Mexico, Socorro Co., Sevilleta National Wildlife Refuge; 34.3325°; –106.6328°; blue funnel trap (Buchmann style); coll. and det.: Karen W. Wright; UNMC; left: 2 SM (missing 2nd SMCV); right: 3 SM (normal [Timberlake 1947]); Karen W. Wright, pers. comm.

Nomada flavoguttata (Kirby)

All specimens: 3 SM (normal [Peters 1969]); det.: Maximilian Schwarz (except as noted); Schwarz collection; Maximilian Schwarz, pers. comm. (all specimens examined by Scarpulla).

♂; 4 June 1938; Germany, München, Schleissheim; coll.: Hartl; left: 2 SM; right: 2 SM (both wings missing 2nd SMCV).

♂; 21 May 1940; Germany, Bayern, Thaldorf; coll.: Stöckhert; left: 2 SM (incomplete 3rd SMCV, 2 spurs: posterior spur extends anteriorly ~40% the distance from the 2nd medial cell; anterior spur extends posteriorly ~20% the distance from the marginal cell); right: 2 SM (2nd SMCV only a very weak spur extending anteriorly ~50% the distance from the 2nd medial cell).

♀; 22 May 1940; Germany, München, Kapuzinerhölzl; coll.: Stöcklein; left: 2 SM; right: 2 SM (both wings missing 2nd SMCV). ♂; same information except: left: 1 SM (missing 2nd SMCV; 1st SMCV only a spur extending posteriorly ~70% the distance from the marginal cell); right: 2 SM (missing 2nd SMCV). ♂; same information except: left: 2 SM (missing 1st SMCV); right: 1 SM (missing 2nd SMCV; 1st SMCV only a spur extending posteriorly ~40% the distance from the marginal cell). ♂; same information except: left: 2 SM (1st SMCV only a spur extending posteriorly ~60% the distance from the marginal cell); right: 2 SM (1st SMCV merely a nub on the posterior margin of the marginal cell). ♂; same information except: det.: E. Stöckhert; left: 2 SM (1st SMCV only a spur extending posteriorly ~40% the distance from the marginal cell); right: 2 SM (1st SMCV only a spur extending posteriorly ~70% the distance from the marginal cell).

♀; 25 April 1949; Österreich [Austria], Niederösterreich, St. Valentin; coll.: Hamann; left: 1 SM; right: 1 SM (both wings missing 2nd SMCV; both wings 1st SMCV but a spur extending posteriorly ~50% from the marginal cell).

♂; 5 May 1952; [Hungary], Ürbő pta. [Ürbőpuszta]; on *Brassica* L. (Brassicaceae); coll.: L. and M. Móczár; left: 2 SM (2nd SMCV only a spur extending posteriorly ~40% the distance from the marginal cell); right: 2 SM (2nd SMCV only a very weak spur extending posteriorly ~30% the distance from the marginal cell).

♀; 25 April 1954; Austria, Steyrermühl - Talholz; on *Tussilago* L. (Asteraceae); coll.: Karl Kusdas; left: 2 SM (missing 2nd SMCV); right: 2 SM (2nd SMCV only two weak spurs: one extending posteriorly ~20% the distance from the marginal cell; one extending anteriorly ~20% the distance from the 2nd medial cell). ♂; same information except: left: 2 SM; right: 2 SM (both wings missing 2nd SMCV).

♂; 21 April 1955; Austria, Oberösterreich, Linz, Gründberg Hohlweg; on *Tussilago farfara* L., coltsfoot; coll.: Karl Kusdas; left: 2 SM; right: 2 SM (both wings missing 2nd SMCV). ♂; same information. ♂; same information except: left: 3 SM; right: 2 SM (missing 2nd SMCV). ♂; same information except: 28 April 1955; left: missing wing; right: 2 SM (missing 2nd SMCV).

♂; 5 May 1955; Austria, Oberösterreich, Linz, Mönchgraben; on *Potentilla verna* [now *P. neumanniana*] Rchb., spring cinquefoil (Rosaceae); coll.: Karl Kusdas; left: 3 SM; right: 2 SM (missing 2nd SMCV). ♂; same information except: left: 2 SM; right: 2 SM (both wings missing 2nd SMCV); ♂; same information except: no plant data; left: 3 SM; right 2 SM (missing 2nd SMCV).

♂; 24 April 1956; Austria, Mühlviertel, Schwertberg; on *Tussilago farfara*; coll.: K. Kusdas; left: 2 SM; right: 2 SM (both wings missing 2nd SMCV).

♂; 3 May 1956; Austria, Oberösterreich, Linz, St. Florian, Rohrbach; on Löwenzahn [*Taraxacum officinale* F. H. Wigg., common dandelion (Asteraceae)]; coll.: Karl Kusdas; left: 2 SM (missing 2nd SMCV); right 3 SM.

♂; 24 May 1957: Hungary, Bakony, Gézah; coll.: Sólymosné; left: 2 SM; right: 2 SM (both wings missing 2nd SMCV).

♂; 5 May 1961; Austria, Salzburg; Parsch; auf Waldblösse [in forest clearing]; coll.: P. P. Babiy; left: 2 SM; right: 2 SM (both wings missing 2nd SMCV).

♀; 23 April 1962; Austria, Linz, Schiltenberg; coll.: Maximilian Schwarz; left: 3 SM; right: 2 SM (missing 2nd SMCV). ♂; same information except: left: 2 SM; right: 2 SM (both wings missing 2nd SMCV)

♀; 12 July1975; Marokko [Morocco], Atlas Mountains, Oukaimeden, 2700–2900 m; coll.: J. Gusenleitner; left: 3 SM; right: 2 SM (2nd SMCV extends posteriorly only ~50% the distance from the marginal cell).

♂; 22–23 May 1981; Algeria, El-Kseur, F.t d'Akfadou [forest of Akfadou]; Spedizione "Algeria '81" ["Algeria '81" Expedition], coll.: Bóffa, Casale, Giachino, Pagilano, Risi, Scaramozzino; left: 2 SM; right: 2 SM (both wings missing 2nd SMCV).

Nomada obliterata Cresson

♀; 31 May 2011; USA, Georgia, Cobb Co. Chattahoochee River National Recreation Area; 33.9119°; –84.4483°; bee bowl; coll. Melina L. Durán; det.: Sam Droege; USNM; USGS_DRO212145; left: 2 SM (normal [Mitchell 1962]); right: 3 SM (1st SMCV added); Brian Harris and Sam Droege, pers. comm.

Nomada stoeckherti Pittioni

♀; 8 July 1964; Austria, Burgenland, Neusiedl; by hand; coll.: J. Schmidt; det.: Maximilian Schwarz; Schwarz collection; left: 2 SM (normal [Peters 1969]); right: 3 SM (2nd SMCV added); Maximilian Schwarz, pers. comm. ♀; same information except: left: 3 SM (2nd SMCV added); right: 2 SM. ♂; same information except: left: 3 SM; right: 3 SM (both wings 2nd SMCV added). ♀; same information except: Austria, Burgenland, Neusiedlsee; coll.: Karl Kusdas; left: 3 SM; right: 3 SM (both wings 2nd SMCV added) (all specimens examined by Scarpulla).

Nomada Scopoli sp.

sex unrecorded; 24 May 2017; United Kingdom, Oxford, Wytham Woods; 51.771786°, –1.337671°; netted; coll. and det.: Steven Falk; specimen discarded; left: 1 SM; right: 1 SM (both wings without 1st SMCV and 2nd SMCV [Without knowing the species, it's not possible to know whether 2 SM or 3 SM was the normal condition.]); Laura A. Russo, pers. comm.

Tetraloniella (*Tetraloniella*) *salicariae* (Lepeletier)

♂; 30 August 1984; Germany, Baden-Württemberg, Vogtsburg im Kaiserstuhl; 48.079202°; 7.656548°; handheld insect net; coll. and det.: John Plant; Plant collection; left: 2 SM (missing 2nd SMCV); right: 3 SM (normal [Michener 2007]); John Plant, pers. comm.

Xylocopa (*Koptortosoma*) *caerulea* (Fabricius)

♀; April–December 1996; Indonesia, Java, Buitenzorg [Bogor]; col.: D. G. Fairchild; USNM (temporarily at BIML); left: 2 SM; right: 2 SM (both wings missing 1st SMCV); 3 SM is the normal (Smith 1874).

♀; [reported as *X. caeruleiformis* Meade-Waldo on det. label]; Singapore; coll.: Baker; USNM (temporarily at BIML); left: 2 SM; right: 2 SM (both wings missing 1st SMCV).

♂; [reported as *X. caeruleiformis* Meade-Waldo on det. label]; Singapore; coll.: Baker; USNM (temporarily at BIML); left: 2 SM; right: 2 SM (both wings missing 1st SMCV).

Xylocopa (*Koptortosoma*) *coronata* Smith

♀; [labeled as *X.* (*Maiella*) *coronata coronata* Smith]; June–July 1953; Indonesia, N. Moluccas [North Maluku], S. Batjan [Bacan]; coll.: A. M. R. Wegner; det.: M. A. Lieftinck; USNM (temporarily at BIML); left: 2 SM; right: 2 SM (both wings 1st SMCV merely a weak spur extending posteriorly ~20% the distance from the marginal cell, then becoming ephemeral); 3 SM is the normal (Hurd and Moure 1963).

♂; [labeled as *X.* (*Maiella*) *coronata combinata* Ritsema]; September–October 1953; Indonesia, C. Moluccas [North Maluku], Obi Island, Laiwui; coll.: A. M. R. Wegner; det.: M. A. Lieftinck; USNM (temporarily at BIML); left: 2 SM (partial 1st SMCV extending posteriorly ~25% the distance from the marginal cell; right: 2 SM (partial 1st SMCV extending posteriorly ~40% the distance from the marginal cell).

Xylocopa (*Neoxylocopa*) *orthogonaspis* Moure

♀; paratype; [labeled as manuscript name *Xylocopa gonaspis* Moure (Mawdsley, pers. comm., 16 July 2017)]; March 1894; Montserrat, Plymouth; from C. V. Riley; det.: J. S. Moure; USNM (temporarily at BIML); left: 2 SM (partial 1st SMCV extending anteriorly ~75% the distance from the 1st medial cell and a very small nub extending posteriorly from the marginal cell); right: 3 SM (normal [Hurd and Moure 1963]).

Xylocopa (*Xylomelissa*) *lugubris* Gerstäcker

♂; 30 November 2016; South Africa, Mpumalanga, Kruger National Park; –25.3086°; 31.5187°; hand net; coll.: Sam Droege; det.: Jonathan Mawdsley; temporarily at BIML; USGS_DRO 480030; left: 2 SM (partial 2nd SMCV, 2 spurs: one spur extends posteriorly ~30% the distance from the marginal cell, the other spur extends anteriorly ~30 % the distance from the 1st medial cell); right: 3 SM (normal [Hurd and Moure 1963]).

In addition to the above actual specimens, other researchers responded with the following information:

John S. Ascher (pers. comm., 30 May 2017) reported *Pseudopanurgus* (*Pseudopanurgus*) *bradleyi* Timberlake (Andrenidae) as an unpublished junior synonym of *Protandrena bancrofti* Dunning (Andrenidae) on Discover Life (Ascher and Pickering 2017b) based on his study of the *P. bradleyi* male holotype at the Cornell University Insect Collection. He proposed that *P. bradleyi* is actually *P. bancrofti* with the submarginal cells reduced from 3 SM to 2 SM.

Jason Gibbs (pers. comm., 18 May 2017) stated that the 2 SM type of *Lasioglossum* (*Dialictus*) *stictaspis* (Sandhouse) is in the *L.* (*D.*) *tegulare* (Robertson) species group, and therefore is probably just a deviant form of a 3 SM species. He felt that this is also probably true of *L.* (*D.*) *subcyaneum* (Ashmead). Gibbs has seen occasional mutants in several 3 SM species and felt that they are probably relatively common.

Gordon E. Hutchings (pers. comm., 28 June 2011) reported having a few specimens of *Andrena* Fabricius (Andrenidae) and *Osmia* Panzer (Megachilidae) with a different number of submarginal cells on each wing. Details were unavailable at the time of publication.

Cory S. Sheffield (pers. comm., 23 November 2013) reported capturing an atypical specimen in 2002 during the American Museum of Natural History Bee Course at the Southwestern Research Station in Portal, Arizona. The specimen had 4 SM on one forewing and 3 SM on the other. (At the time of this paper's publication, the specimen, believed to have been a eucerine, had not been relocated in the collection where it had been deposited.)

Douglas A. Yanega (pers. comm., 2 May 2015, 8 May 2017) reported that *Xeromelecta* (*Melectomorpha*) *californica* (Cresson) (Apidae) seems to have 2 SM relatively commonly in one or both wings. In some cases, there was not a complete absence of a submarginal crossvein, but a short spur instead. He has seen a few *Protandrena* s. str. Cockerell species, where one wing has 2 SM instead of 3 SM. Yanega once saw a *Pseudopanurgus* s. str. Cockerell specimen with 3 SM in one wing instead of 2 SM. He further elaborated on the significance of this since the number of submarginal cells was historically treated as a diagnostic genus-level feature in panurgines, and it is possible that there are some described species which are actually synonyms of members of other genera (or subgenera, depending on the classification) and are in reality simply variants. Along this same line, numbers of *Lasioglossum* Curtis were originally described as *Panurgus* Panzer for this reason (e.g. *L.* [*Hemihalictus*] *lustrans*, *L.* [*Dialictus*] *parvum*, and *L.* [*Dialictus*] *biclausum* Gibbs) (Gibbs, pers. comm., 18 May 2017).

Discussion

For the overwhelming majority of bee species, all individuals of a particular species usually possess either 2 SM or 3 SM (Tofilski 2011). While this is the norm for most species, there are exceptions, as seen in the above examples where individuals of one species may have 2 SM or 3 SM, or where an individual bee may possess 2 SM on one wing and 3 SM on the other.

Although this paper tends to simplify the anomaly of atypical or variable numbers of submarginal cells as being either 2 SM or 3 SM in number, in reality there are instances where a submarginal vein is only partially formed, i.e. a stub, spur, veinlet. If this occurs in a 2 SM species, it could be interpreted as almost forming 3 SM. Alternatively, if the same situation occurred in a 3 SM species, it could be interpreted as almost forming 2 SM. In both cases, the result is the same, but the interpretation of the result is dependent on the normal initial state of the wing.

Danforth (1989) evaluated the importance of body size on the evolution of hymenopteran wings. As body size increased, wings were more elongate and narrow; conversely as body size decreased, wings were shorter and broader. He found that the distal-most cells of the forewing (i.e. marginal, 2nd SM, 3rd SM, 1st medial, and 2nd medial) became more elongate with increasing body size and less elongate with decreasing body size. Looking at the 2nd SM, the anterior vein (i.e. Rs) that it shares with the marginal cell showed distal movement of the attachment of 2nd SMCV with increasing body size and proximal movement with decreasing body size; in some small species, the 2nd SM even became triangular. Danforth theorized that this allometric trend could be the factor where taxa with small body size often lack a 2nd SM.

Regarding bees in general, the 2 SM condition resulted from the loss of either the 1st SMCV or 2nd SMCV from the 3 SM condition (Tofilski 2011). From an evolutionary standpoint, this loss of submarginal crossveins occurred independently with and within the various families (Tofilski 2011). In the 2 SM condition, the homology of both the missing crossvein and the remaining crossvein is not often easy to ascertain (Tofilski 2011).

Alpatov (1928) looked at the experimental effects of undernourishment of honey bee larvae. The experiment resulted in 19.82% ± 2.50 (n = 116) of the specimens with incomplete development of the 2nd SMCV, thereby resulting in the 2nd SM and 3rd SM being partially conjoined. Alpatov's experiment

also showed that the undernourished bees had shorter forewings than the sufficiently-fed ones.

Undernourishment in other species of bees could be a potential trigger for incomplete SMCV development, thereby resulting in fewer than normal SMs. Further research could investigate whether non-*Apis* 2 SM individuals of a normally 3 SM species would also exhibit shorter wings. Additional research could also investigate whether the body size of 2 SM individuals of a normally 3 SM species are smaller than their normal 3 SM individuals.

When a particular specimen's forewings are bilaterally asymmetric, this could indicate fluctuating asymmetry. Fluctuating asymmetry is distinguished by small random deviations from an a priori expectation that bilateral symmetry is the norm. Loss or addition of a SMCV could be considered more than a "small" deviation, but will be discussed here as such. Fluctuating asymmetry measures deviations from the norm and may be the result of environmental or genetic stress on an individual during its development (Tomkins and Kotiaho 2001). Clarke and McKenzie (1992) studied the effects of larval overcrowding on *Lucilia cuprina* (Wiedemann) (Diptera: Calliphoridae) and found that fluctuating asymmetry was a good indicator of developmental stress.

Miklasevskaja and Packer (2015) investigated fluctuating asymmetry in males and females of *Xeromelissa rozeni* (Toro and Moldenke) (Colletidae). In addition to measuring seven characters of the maxillary palpi (considered highly functionally essential), they also measured two forewing characters: marginal cell length and apical width of the second cubital cell (both considered less functionally essential). The results showed lower functional asymmetry in the palpus characters and higher in the forewing characters, thereby suggesting that there was a higher selection force on the more functionally essential traits (i.e. the maxillary palpi traits).

Of the previously unpublished specimen records of atypical or variable numbers of submarginal cells (N = 86), 51 were females, 34 were males, and one was unknown. Wcislo (2004) reviewed bee gynandromorphs in the literature and found that there were more examples of females exhibiting cross-sex tendencies than there were examples for males. Since the capture of atypical specimens is dependent upon what sex might be flying at any specific point in time, little can be inferred from these numbers. Interestingly, Wcislo's review also mentions environmental stress as a trigger for gynandromorphism.

Summary

Species in the genus *Melitoma* (Say) (reported as *Melitoma* Lepeletier and Serville in Mitchell [1962]) typically have 3 SM (Mitchell 1962). A search of the literature and an inquiry on the bee monitoring listserve found three other reports of bees with 4 SM (Akahira and Sakagami 1959; Sheffield, pers. comm., 23 November 2013; Porporato et al. 2014). Other than the managed or laboratory-reared honey bee studies (Akahira and Sakagami 1959; Porporato et al. 2014), my specimen of *M. taurea* and Sheffield's unknown specimen, each with 4 SM on one of the forewings, appear to be extremely rare occurrences in the wild.

Published records were found for 66 species: Colletidae (1), Andrenidae (28), Halictidae (19), and Apidae (18). In four instances, published records were also found at the genus or subgenus level (Table 3). Previously unpublished records were reported for 29 species: Colletidae (1), Andrenidae (5), Halictidae (13), and Apidae (10). Previously unpublished records were also reported for six specimens that were only identified to genus or subgenus (Table 4).

Table 7 provides a compilation of the species with published and previously unpublished records of atypical and variable numbers of submarginal cells. The compilation includes four families, 23 genera, and at least 89 species. Although Melittidae and Megachilidae both have species possessing either 2 SM or 3 SM, I found no published or previously unpublished records of any one species having atypical or variable numbers of submarginal cells, except for the anecdotal *Osmia* megachilid information from Hutchings (pers. comm., 2011).

The available records primarily center on three families: Andrenidae, Halictidae, and Apidae. Within these families, the genus with the most records is *Andrena*, followed by *Lasioglossum* and *Nomada*. Interestingly, all three of these genera contain 2 SM and 3 SM species. The fact that these three genera possess submarginal cell anomalies more than others could be the actual situation, but one must be cautious that this also could be an artificial situation where the numbers are only based on reported

specimens of these three extremely abundant and species-rich genera. Additionally, there are several records of *Sphecodes* and *Xylocopa*, both genera primarily containing 3 SM species.

At best, I have compiled a preliminary list of known bee species possessing atypical and variable numbers of submarginal cells. Undoubtedly, there are numerous unpublished specimens in collections worldwide. This has been an attempt to compile what has been published in the literature, as well as adding any known previously unpublished specimens. I encourage others that have additional specimens possessing submarginal cell variations to forward their records to me for compilation. I thank them in advance.

The *M. taurea* specimen is deposited in the author's personal collection.

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Table 7. Compilation of species with published and previously unpublished records of atypical and variable numbers of submarginal cells.

Family	**Genus**	**Subgenus**	**Species**
Colletidae	*Colletes*	—	*robertsonii*
	Leioproctus	(*Minycolletes*)	*abnormis*
Andrenidae	*Andrena*	(*Andrena*)	*tridens*
		(*Callandrena* s. lat.)	*asteris*
			asteroides
			crawfordi
			gardineri
			krigiana
			simplex
		(*Cnemidandrena*)	*denticulata*
		(*Euandrena*)	*bicolor*
			geranii
			segregans
		(*Gonandrena*)	*flocculosa*
			integra
			platyparia

Family	Genus	Subgenus	Species
Andrenidae, cont'd.	*Andrena*, cont'd.	(*Larandrena*)	*miserabilis*
		(*Micrandrena*)	*nigrae*
			personata
			subopaca
		(*Rhacandrena*)	*brevipalpis* or *robertsonii*
		(*Scaphandrena*)	*arabis*
		(*Scrapteropsis*)	*biareola*
			imitatrix
			stipator
			unicostata
		(*Simandrena*)	*nasonii*
		(*Thysandrena*)	*ferrugineipes*
		(*Trachandrena*)	*forbesii*
			hippotes
			sp.
	Calliopsis	(*Calliopsis*)	*andreniformis*
	Liphanthus	—	sp.
	Perdita	(*Alloperdita*)	*bradleyi*
			spp.
		(*Xerophasma*)	*celadona*
			vespertina
	Pseudopanurgus	—	*compositarum*
Halictidae	*Augochlora*	—	sp.
	Augochlorella	—	*aurata*
	Halictus	(*Hexataenites*)	*sexcinctus*
		(*Protohalictus*)	*rubicundus*
		(*Seladonia*)	*confusus*
			subauratus
	Lasioglossum	(*Ctenonomia*)	*bakeri*
		(*Dialictus*)	*admirandum*
			anomalum
			laevissimum
			lionotum
			occidentale
			parvum
			versatum
			zephyrum
			sp.
		(*Evylaeus* s. lat.)	sp.
		(*Hemihalictus*)	*hewetti*
			lucidulum
			lustrans

Family	Genus	Subgenus	Species
Halictidae, cont'd	*Lasioglossum*, cont'd.	(*Lasioglossum*)	*sisymbrii*
		(*Leuchalictus*)	*leucozonium*
		(*Sphecodogastra*)	*calceatum*
			seillean
	Lipotriches	(*Afronomia*, *Austronomia*, or *Macronomia*)	sp.
	Sphecodes	—	*antennariae*
			confertus
			coronus
			cressonii
			niger
			pimpinellae
			puncticeps
			stygius
	Temnosoma		spp.
Apidae	*Anthophorula*	(*Anthophorula*)	*completa*
	Apis	(*Apis*)	*mellifera*
	Epeolus	—	*ainsliei*
			minimus
			olympiellus
	Eucera	(*Eucera*)	*tuberculata*
	Melecta	(*Melecta*)	*luctuosa*
	Melitoma	—	*taurea*
	Nomada	—	*flavoguttata*
			mesopotamica
			obliterata
			panamensis
			roberjeotiana
			rufipes
			sexfasciata
			stoeckherti
			trapidoi
			sp.
	Tetraloniella	(*Tetraloniella*)	*salicariae*
	Xylocopa	(*Koptortosoma*)	*caerulea*
			coronata
			insularis
			unicolor
			"cyaneoderes group" spp.
		(*Neoxylocopa*)	*orthogonaspis*
		(*Xylomelissa*)	*lugubris*

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