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Reinstatement of *Andrena vernalis* Mitchell (Hymenoptera: Andrenidae) from Synonymy with *A. ziziae* Robertson

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Abstract

Andrena (*Micrandrena*) *ziziae* Robertson, 1891 (Hymenoptera: Andrenidae) is a well-known species found in a variety of habitats in the eastern and central United States and adjacent southern Canada. *Andrena* (*Micrandrena*) *vernalis* Mitchell, 1960 was described from five female specimens in the eastern United States and was synonymized with *A. ziziae* by Ribble in 1968. Recently collected specimens from throughout Minnesota have revealed that *A. ziziae sensu* Ribble is actually two species, one of which matches *A. vernalis*. Here, we reinstate *A. vernalis* as a valid species and describe the previously unknown male. We provide diagnostic characters that separate *A. ziziae* and *A. vernalis*, as well as data on the geographic range and floral preferences of both species in Minnesota. *Andrena vernalis* appears to be restricted to high-quality remnant habitats, making it a species of potential conservation concern. These changes will require that previous work on *A. ziziae* be revisited to determine if *A. vernalis* is also present.

Key words: Species complex, specialization, *Zizia*, Apiaceae, taxonomy

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Andrena (*Micrandrena*) *ziziae* Robertson, 1891 (Hymenoptera: Andrenidae) is a small, solitary, ground nesting bee (Ribble 1968). *Andrena ziziae* collects pollen only from plants in the family Apiaceae (Ribble 1968, Wood and Roberts 2018), making it an important pollinator of forb species in the genus *Zizia* and *Thaspium* (Lindsey 1984, Lindsey and Bell 1985). *Andrena ziziae* occurs throughout the eastern and central United States and adjacent southern Canada (Ribble 1968). It can be locally abundant where individuals of its host plants persist, and is found in a variety of habitats, including urban areas (Normandin et al. 2017), tallgrass prairie (Davis et al. 2008), prairie restorations (Harmon-Threatt and Hendrix 2015), powerline strips (Russell et al. 2005), and montane and piedmont areas (Lindsey 1984).

Andrena ziziae was originally described by Robertson (1891). Soon after, Robertson (1897) split *A. ziziae* into two species, describing the second species as *A. personata* Robertson, 1897. *Andrena* (*Micrandrena*) *vernalis* Mitchell, 1960 was described from five female specimens (the males were unknown) from Connecticut (type locality), Ohio, and New York. The characters Mitchell (1960) used to separate females of *A. vernalis* from *A. ziziae* (as well as the closely related *Micrandrena* Ashmead species *A. illinoiensis* Robertson, 1891 and *A. salictaria* Robertson, 1905) were the broader facial fovea and the presence of a unique pleural ridge, which he described as "pleura protuberant below, having a flattened triangular area anterior to mid coxal cavities, delimited by a distinct ridge".

Andrena vernalis was later synonymized with *A. ziziae* by Ribble (1968) as part of a broader revision of the subgenus *Micrandrena*. Ribble (1968) justified the synonymy by stating that there was continuous variation in the structure of the pleural ridge and specimens both with and without the pleural ridge co-occurred throughout the range of *A. ziziae*. However, Ribble (1968) did not examine the holotype of *A. vernalis* before synonymizing the species (though it appears he did examine two paratypes). In addition, the illustrations of the male terminalia of *A. ziziae* in Ribble (1968) differ substantially from the illustrations of Mitchell (1960).

Recent collections throughout Minnesota provided hundreds of specimens of *A. ziziae*, including many specimens that match Mitchell's (1960) description of *A. vernalis*. Examination of these specimens revealed that in addition to the pleural ridge, female specimens matching *A. vernalis* have multiple other consistent morphological characters that separate them from the typical form of *A. ziziae*, indicating that *A. vernalis* is a valid species in its own right. This conclusion is reinforced by the discovery of the male of *A. vernalis*, including both novel specimens and a male collected with the type series. The males of *A. vernalis* have clear and consistent differences in the male terminalia that further cement its status as a valid species.

Here, we resurrect *A. vernalis* from synonymy and provide additional diagnostic characters that separate it from *A. ziziae*. In addition, we provide the first description of the previously unknown male. Although *A. vernalis* appears to occur across the eastern United States, we focus here on Minnesota, where it is important to provide a clear species definition for upcoming ecological studies. Our data suggest that both *A. ziziae* and *A. vernalis* specialize on *Zizia* pollen in Minnesota prairies. However, unlike *A. ziziae*, *A. vernalis* appears to be associated with high-quality remnant habitats, making it essential to further delineate the range and habitat requirements of these two species.

Methods & Materials

The following abbreviations are used for museums and institutions:

INHS	Illinois Natural History Survey, Champaign, IL, USA. Dr. Thomas McElrath.
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge, MA, USA. Dr. Crystal Maier.
MNDNR	Minnesota Department of Natural Resources, St. Paul, MN, USA. Dr. Jessica Petersen.
NCSU	North Carolina State University Insect Museum, Raleigh, NC, USA. Dr. Bob Blinn.
UMSP	University of Minnesota Insect Collection, St. Paul, MN, USA. Dr. Robin Thomson.

We examined 850 specimens for this study. Specimens were largely drawn from a mix of published (Pennarola 2019) and unpublished ecological studies of the Minnesota bee fauna. The type of *A. vernalis* was examined at MCZ and additional non-type specimens were examined from the type locality. Unless otherwise noted, specimens are deposited in the UMSP or the Cariveau native bee lab collection at the University of Minnesota and will later be deposited at UMSP.

Classifications and terminology follow Michener (2007), except wing vein terminology follows Engel (2001). The abbreviations S1…S8 and T1…T7 are used for sterna and terga, respectively. The format and terminology of specimen descriptions are modified and adapted from Mitchell (1960) and Ribble (1968). Specimen images and measurements were taken with an Olympus DP27 camera mounted on an Olympus SZX16 stereomicroscope. Images were stacked with CombineZP software (Hadley 2010). Photographic plates were compiled using Adobe Photoshop 2018 software (Adobe Systems Inc., San Jose, CA). Maps were created using ArcMap software v10.5.1 (ESRI, Redlands, CA).

Pollen analysis. To gain insight into foraging preferences for *A. ziziae* and *A. vernalis*, we used hand nets to collect bees that were actively foraging on *Zizia aptera* and *Z. aurea* from eight prairies throughout western MN. We placed all collected bees into individual 1.5 mL microcentrifuge tubes and cleaned the net before continuing our sampling to reduce pollen contamination. All collected specimens were sacrificed in the freezer, then swabbed for pollen, and later identified to species.

In the lab, we sampled the pollen on each specimen by swabbing the head, thorax, abdomen, and underside of the thorax with a small piece (~8 mm^3) of fuchsin gel (Kearns and Inouye 1993). Next, we melted the fuchsin gel onto a microscope slide and covered it with a cover slip. We then used a compound microscope to count the first 300 pollen grains encountered on the slide (Ritchie et al. 2016), recording the number of *Zizia* pollen grains and the number of pollen grains from other genera. We then calculated the mean number of *Zizia* pollen grains and the mean proportion of *Zizia* pollen grains bees carried on their body for each species. We were not able to differentiate between the pollen of *Z. aurea* and *Z. aptera*.

Results

***Andrena* (*Micrandrena*) *vernalis* Mitchell, new status**

Fig. 1A,C,E, 2A,C,E, 3A,C,E, 4A,C,E, 5A–B, 6A–C, 7, 8A,C, 9

Andrena vernalis Mitchell 1960: 168, ♀. Holotype ♀, USA, CT, Colebrook, 31 May 1922, W.M. Wheeler leg. (MCZ 30485).

Andrena ziziae (in part): Ribble, 1968: 267 (syn. *A. vernalis* with *A. ziziae*).

Diagnosis. Female *A. vernalis* can most easily be separated from *A. ziziae* by the broader facial fovea (Fig. 1A–D) and the more prominent tergal hair bands (Fig. 1E–F). The fovea of *A. vernalis* take up nearly the entire distance between the eye and lateral ocelli (Fig. 1C), whereas the fovea of *A. ziziae* take up only slightly more than

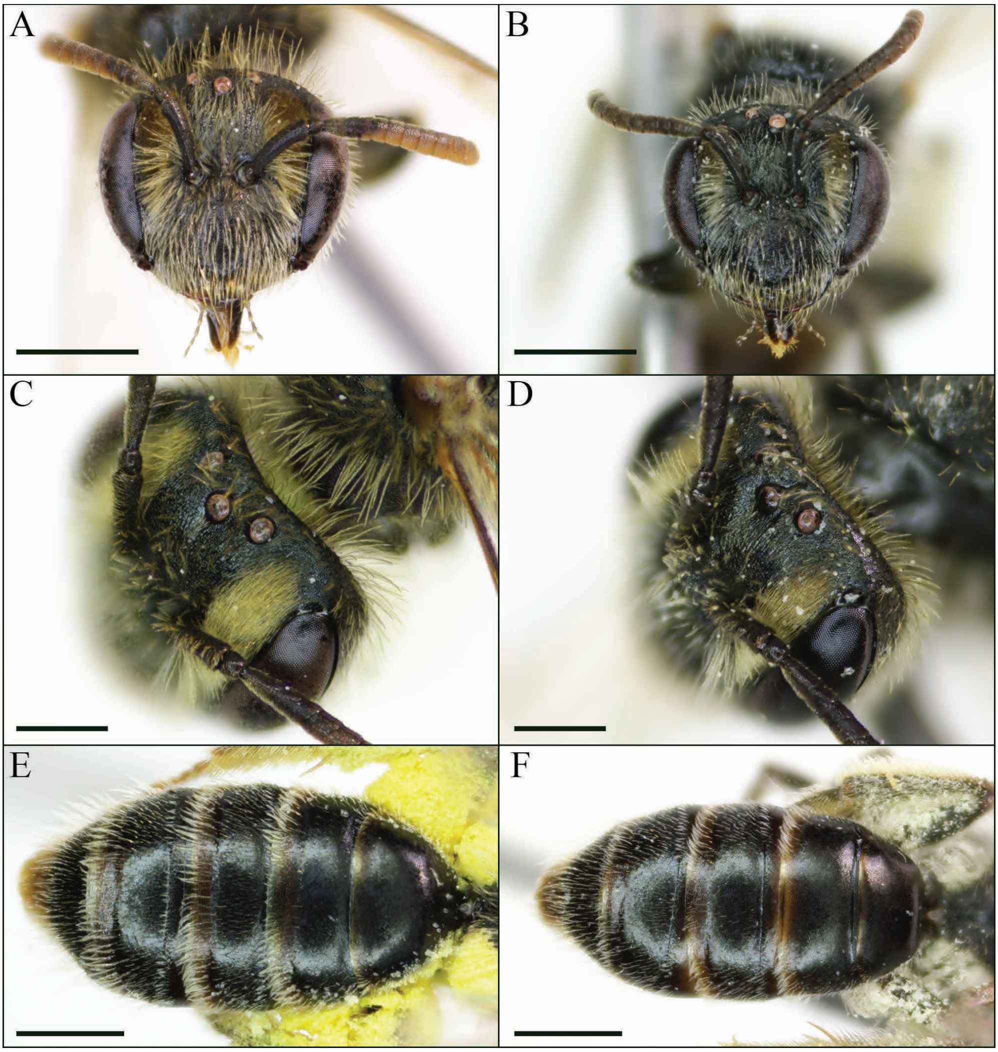

Figure 1. *Andrena vernalis* (left column) and *A. ziziae* (right column) female face and abdominal characters: (A) *A. vernalis* face; (B) *A. ziziae* face; (C) *A. vernalis* facial fovea; (D) *A. ziziae* facial fovea; (E) *A. vernalis* abdomen; (F) *A. ziziae* abdomen. Scale bars: A–B, E–F = 1mm; C–D = 500 µm.

half the distance between the eye and lateral ocelli (Fig. 1D). The apical tergal hair bands of *A. vernalis* are longer (Fig. 1E) than the relatively close-cropped hairs of *A. ziziae* (Fig. 1F), though these hairs can be worn off. In addition, tergal rims of *A. vernalis* are distinctly transparent on nearly the entire apical impressed area (Fig. 1E, 2A), whereas *A. ziziae* have the tergal rims are transparent only at the very apex (Fig. 1F).

Other characters that can help separate female *A. vernalis* from *A. ziziae* include the propodeum of *A. vernalis*, which has a slightly more well-defined triangle with the interior of the triangle rugulose (Fig. 2E). In contrast, the triangle of *A. ziziae* is less well-defined and less strongly sculptured (Fig. 2F). In addition, the Rs vein of *A. vernalis* is generally attached to the marginal cell 2–3 vein widths from the stigma (Fig. 3A) whereas the Rs vein of *A. ziziae* is generally attached about 1 vein width from the stigma (Fig. 3B). However, this character is variable and some *A. ziziae* have the Rs vein attached slightly further, about 2 vein widths (Fig. 3D), overlapping with some

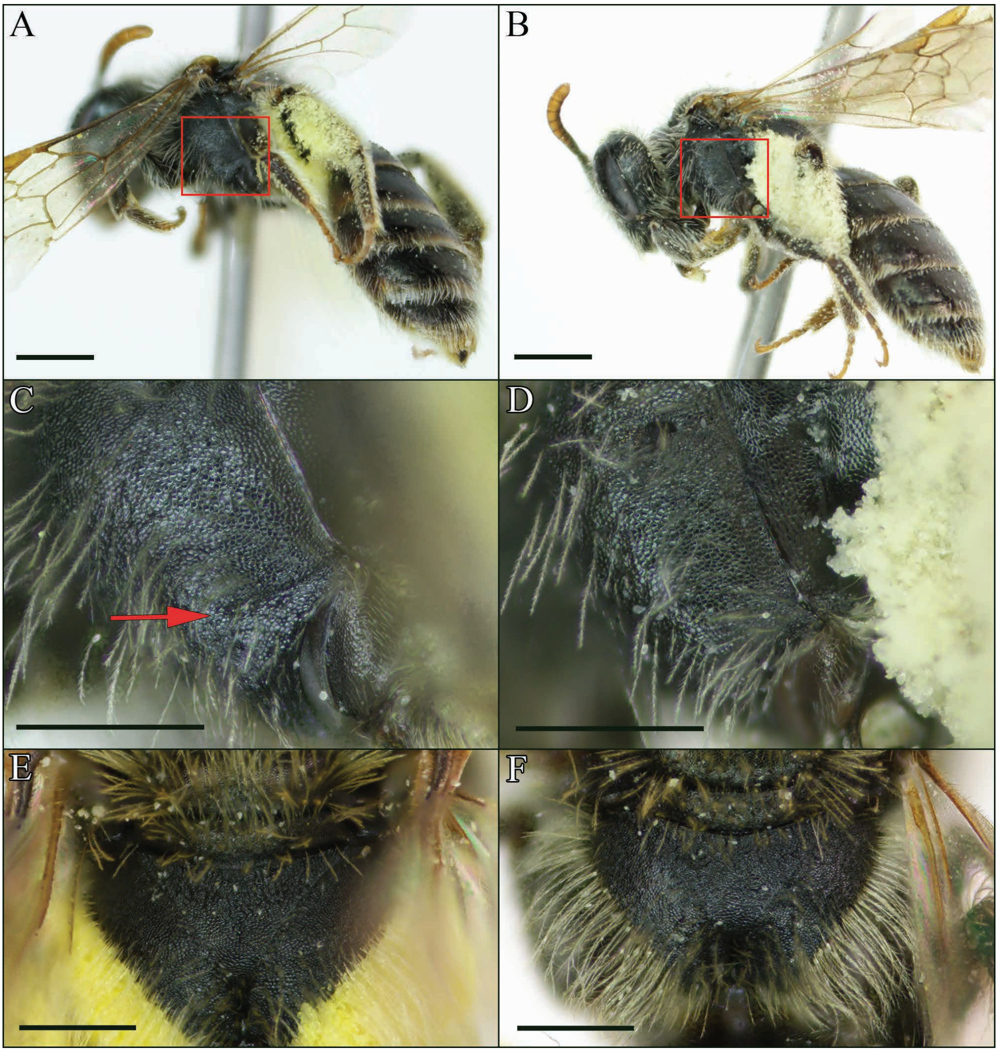

Figure 2. *Andrena vernalis* (left column) and *A. ziziae* (right column) female thoracic characters: (A) *A. vernalis* lateral view; (B) *A. ziziae* lateral view; (C) *A. vernalis* closeup of pleural depression and ridge, indicated by red arrow; (D) *A. ziziae* closeup of smoothly rounded pleura; (E) *A. vernalis* propodeal triangle; (F) *A. ziziae* propodeal triangle. Scale bars: A–B = 1mm; C–E = 500 µm.

A. vernalis that have the Rs vein attached closer to the stigma (Fig. 3C).

Finally, in *A. vernalis*, the pleura directly anterior to the mid-coxa has a depressed subtriangular area delineated by a weakly carinate but distinct ridge (Fig. 2A,C, 9A–B). In contrast, *A. ziziae* has the pleura smoothly rounded (Fig. 2B,D), or at most weakly protruding in this area. While this character is diagnostic, it can be extremely difficult to see, especially since it is typically blocked from view by the midlegs.

Females of *A. vernalis* key out correctly in Mitchell (1960), and they key out to *A. ziziae* in Ribble (1968) and can be separated by the previously mentioned characters.

Male *A. vernalis* can be separated from *A. ziziae* by their broader antennal segments (measured on the anterior side as in Fig. 4B): F3–7 of *A. vernalis* are distinctly broader than long (Fig. 4A,C), whereas in *A. ziziae*, F3–7 are longer than broad or have length and width equal (Fig. 4B,D). In addition, the apical lobes of S7 are truncate in *A. vernalis* (Fig. 5B) and rounded in *A. ziziae* (Fig. 5D),

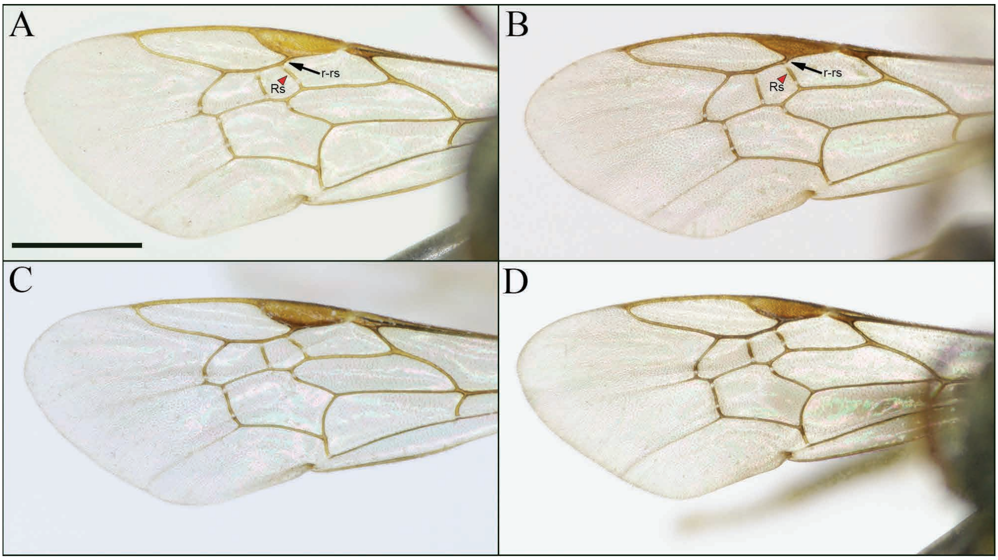

Figure 3. *Andrena vernalis* (left column) and *A. ziziae* (right column) forewings: (A) typical *A. vernalis* female forewing with longer r-rs crossvein (long black arrow) and Rs vein (short red arrow) attached to marginal cell 2–3 vein widths from stigma; (B) typical *A. ziziae* female forewing with shorter r-rs crossvein (long black arrow) and Rs vein (short red arrow) attached to marginal cell about 1 vein width from stigma; (C) *A. vernalis* female forewing with Rs vein attached more closely to stigma, about 2 vein widths; (D) *A. ziziae* female forewing with Rs vein attached further from stigma, about 2 vein widths. Scale bar = 1 mm, all images are at the same scale.

and the dorsal lobes of genitalia are much broader in *A. vernalis* (Fig. 6A) than *A. ziziae* (Fig. 6D).

Additional characters can help separate males of *A. vernalis* and *A. ziziae* but they are subtle and often difficult to discern. Similar to females, male *A. vernalis* have a slightly more well-defined propodeal triangle, the apical rims of the terga are more broadly transparent in *A. vernalis* (Fig. 4E) than *A. ziziae* (Fig. 4F), the Rs wing vein attaches further from the stigma in *A. vernalis* (as in Fig. 3A) than *A. ziziae* (as in Fig. 3B) though this character can be variable, and the pleura directly anterior to the mid-coxa has a depressed subtriangular area delineated by a slightly protruding margin (Fig. 9C–D). Males are difficult to separate from *A. ziziae* and it is recommended that the terminalia be used to confidently identify them.

Males of *A. vernalis* key out to *A. ziziae* in both Mitchell (1960) and Ribble (1968) and can be separated by the previously mentioned characters.

Description of male. Body length: 6.0 mm, range 5.8–6.2 mm; ITD: 1.25 mm (n=7).

Integumental color. Body black without any metallic reflections; clypeus yellow except for two small, sublateral black spots and dark apical rim (Fig. 4A); antennae dark brown above and light brown below (Fig. 4C); wing veins a mix of light and dark brown (Fig. 3E); tibial spurs clearish-white; apical tarsi light brown; basitarsi generally with apex somewhat light brown; apical rims of terga hyaline (Fig. 4E).

Structure. Length and breadth of facial quadrangle about equal; eyes slightly converging below (Fig. 4A); clypeus very slightly convex, projecting slightly below lower margin of eye, shining with faint tessellation, punctures small and obscure, separated by about 2–3 puncture widths, midline of clypeus more sparsely punctate; vertex less than one ocellar diameter; cheeks subequal to eyes in width, rounded posteriorly; malar space linear; F1 subequal to F2+F3; middle flagellomeres broader than long (Fig. 4C); process of labrum very short, about twice as broad as long, broadly truncate and very slightly emarginate medially; mandibles in repose reaching slightly beyond midline of face, with a small but distinct subapical tooth; galea quite short, impunctate, distinctly tessellate and slightly shining.

Pronotal collar without humeral angle; scutum tessellate, only slightly shining, with very obscure punctures separated by 2–4 puncture widths; scutellum tessellate,

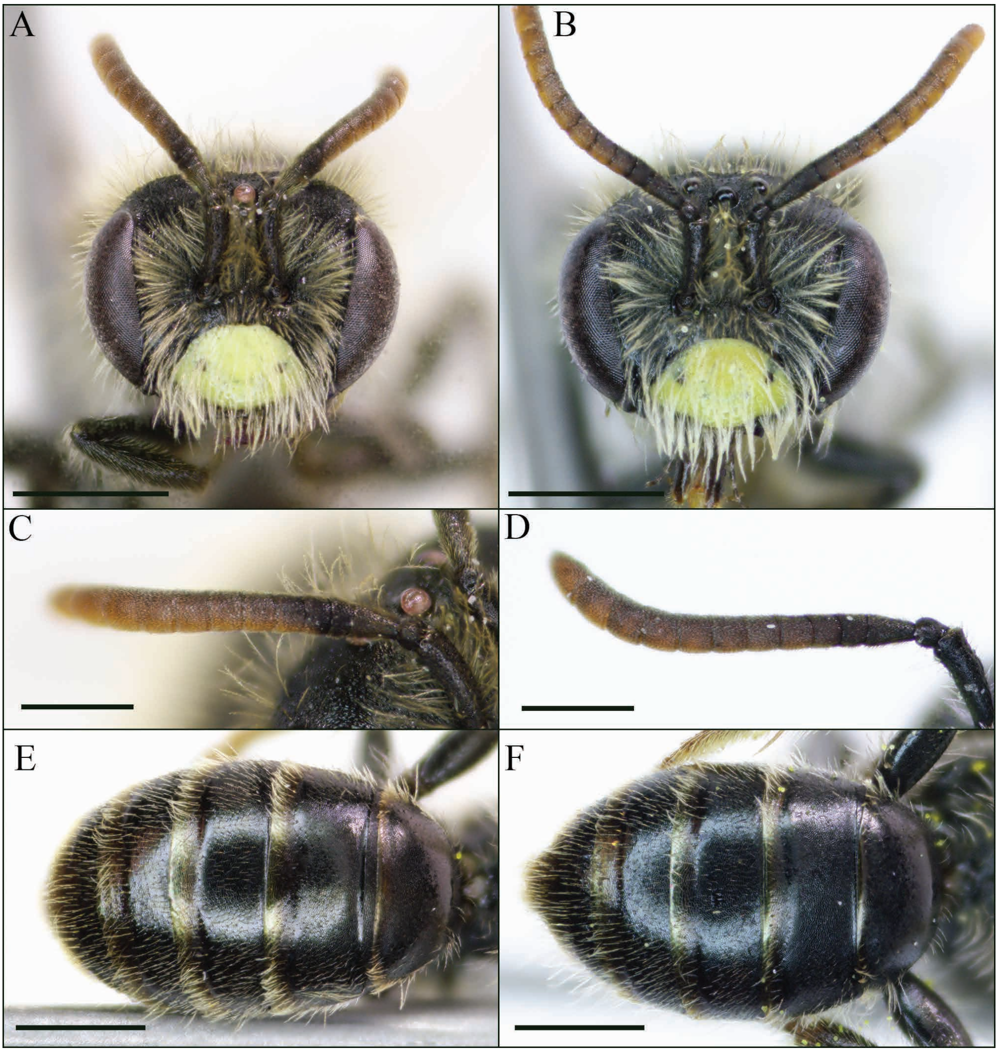

Figure 4. *Andrena vernalis* (left column) and *A. ziziae* (right column) male external characters: (A) *A. vernalis* face; (B) *A. ziziae* face; (C) *A. vernalis* antenna; (D) *A. ziziae* antenna; (E) *A. vernalis* abdomen; (F) *A. ziziae* abdomen. Scale bars: A–B, E–F = 1mm; C–D = 500 µm.

only slightly shining, with very sparse and obscure punctures; pleura granular without evident punctures; area on pleura directly anterior to mid coxae with a slightly depressed subtriangular area delimited by a slightly protruding margin (Fig. 9C–D); dorsal area of propodeum rather broad, nearly horizontal, triangle with a slightly impressed outline, finely roughened, subtly but distinctly contrasting with adjacent areas; all basitarsi slender and elongate, considerably narrower than their respective tibiae; r-rs vein relatively long with Rs vein attached to marginal cell 2–3 vein widths from the stigma; 2nd submarginal cell receiving 1m-cu vein at or slightly beyond middle.

Overall shape of metasoma ovoid, reaching greatest width at T3, equal in width to mesosoma (Fig. 4E); terga smooth and tessellate, slightly shining, punctures indistinct; T1 and T2 slightly duller than the apical terga; apical margins of terga slightly but distinctly impressed, taking up about 1/4 of segment on T2 and T3 (Fig. 4E); pygidial plate broadly triangular with a rounded apex.

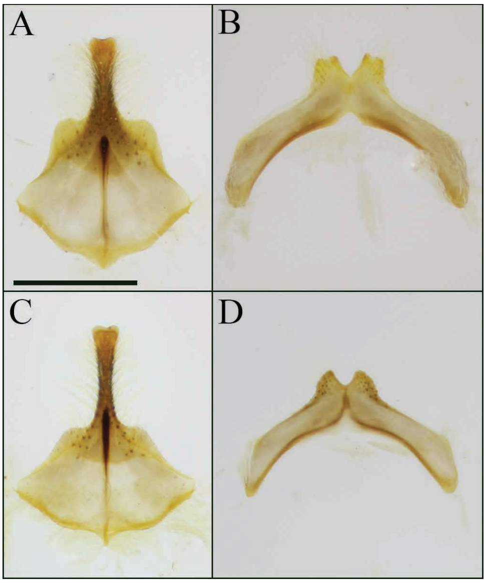

Figure 5. Male S8 and S7: *Andrena vernalis* (A) S8 and (B) S7; *A. ziziae* (C) S8 and (D) S7. Scale bar = 500 µm, all images are at the same scale.

Terminalia. S8 apical portion moderately slender, slightly expanded at tip (Fig. 5A); S7 with apical lobes distinctly truncate, separated by a V-shaped emargination (Fig. 5B); genitalia with dorsal lobes of gonocoxites relatively broad, narrowly separated, slightly diverging apically (Fig. 6A); ventral lobes of gonocoxides narrowed medially, apical halves expanded and strongly bent ventrally, apices slightly overlapping medially, apex of volsella appearing slightly emarginate in ventral view (Fig. 6B); penis valves quite broad medially, filling space between ventral lobes of gonocoxites.

Vestiture. Pubescence entirely whitish; hairs on venter of head rather long, about equal to the length of the cheek+eye; hairs on scutum erect, weakly plumose, not obscuring surface; venter of mesosoma clothed in relatively dense hairs; pubescence on discs of terga relatively short (Fig. 4E); T1 largely lacking discal pubescence; T2 discal hairs with very short and minute, discal hairs moderately longer on more apical terga; apical hair bands weak and generally worn off even in moderately worn specimens; T1 apical hair band limited to a small lateral tuft, T2 apical hair band slightly more extensive but still limited to lateral tufts, T3 apical hair band weak, diffuse, narrowly interrupted medially, T4 apical hair band entire, very weak and diffuse, T5 and T6 lacking apical hair bands (Fig. 4E).

Description of female. Body length: 7.2 mm, range 7.0–7.4 mm; ITD: 1.40 mm (n = 10).

See Mitchell (1960) for full description.

Floral records. Apiaceae (6 ♂ 108 ♀): *Zizia aptera* 6 ♂ 86 ♀, *Z. aurea* 22 ♀. Twenty-six female *A. vernalis* collected in 2018 had their body pollen analyzed. Individuals of *A. vernalis* had on average 287.5 *Zizia* pollen grains on their bodies and 97% of the pollen carried was from *Zizia* (Fig. 7).

Phenology. Active in May and June in Minnesota.

Distribution. In Minnesota, *A. vernalis* has a relatively restricted distribution, especially compared to *A. ziziae*. *Andrena vernalis* has only been found in a band in the south-central area of the state (Fig. 8A,C). Although a comprehensive examination of the range of *A. vernalis* was not performed, based on the specimens examined, it extends to the east coast of the US.

Type material examined. Holotype: ♀, Connecticut: Litchfield Co.: Colebrook, 31 May 1922, W.M. Wheeler leg. (MCZ 30485).

Additional material examined. Total specimens: 7 ♂ 114 ♀. **CONNECTICUT: Litchfield Co.:** Colebrook: 1 ♂ 2 ♀ (MCZ), 31 May 1922, W.M. Wheeler leg.; 2 ♀ (MCZ), 11 Jun 1926, W.M. Wheeler leg. **MINNESOTA: Big Stone Co.:** (45.3065 –96.2874): 1 ♀, 21 Jun 2018, S. Marconie leg., *Zizia aurea*; 2 ♀, 18 Jun 2019, I. Bur leg., *Z. aurea*; (45.3259 –96.3714): 1 ♀, 1 Jun 2018, G. Pardee leg., *Z. aptera*; 1 ♀, 1 Jun 2018, M. Rancour leg., *Z. aptera*; 15 ♀, 1 Jun 2018, S. Marconie leg., *Z. aptera*; 1 ♀, 1 Jun 2018, S. Marconie leg., *Z. aurea*; 6 ♀, 10 Jun 2019, G. Pardee leg., *Z. aptera*; 8 ♀, 10 Jun 2019, I. Bur leg., *Z. aptera*; Larson Slough WPA (45.3612 –96.3119): 1 ♀, 3 Jun 2017, P. Pennarola leg., *Z. aptera*; **Douglas Co.:** Staffanson Prairie (45.8161 –95.7460): 7 ♀, 5 Jun 2018, G. Pardee leg., *Z. aptera*; 7 ♀, 5 Jun 2018, I. Lane leg., *Z. aptera*; 1 ♀, 5 Jun 2018, T. Eicholz leg., *Z. aptera*; **Kandiyohi Co.:** (45.3529 –95.1192): 1 ♀, 25–27 May 2018, J. Brokaw leg.; 1 ♀, 5 Jun 2019, G. Pardee leg., *Z. aurea*; Brenner Lake WPA (45.4006 –95.2463): 5 ♀, 4 Jun 2018, A. Ritchie leg., *Z. aptera*; 4 ♀, 4 Jun 2018, M. Rancour leg., *Z. aptera*; 1 ♀, 7 Jun 2018, G. Pardee leg., *Z. aptera*; 6 ♀, 12 Jun 2019, G. Pardee leg., *Z. aptera*; **Lyon Co.:** Vallers WMA (44.5622 –95.8403): 1 ♀ (MNDNR), 16 Jun 2015, K.J. Jokela leg., *Z. aurea*; **Pope Co.:** (45.6707 –95.5077): 1 ♀, 3 Jun 2019, G. Pardee leg., *Z. aptera*; 2 ♂ 4 ♀, 3 Jun 2019, I. Bur leg., *Z. aptera*; 3 ♀, 11 Jun 2019, G. Pardee leg., *Z. aptera*; 3 ♀, 11 Jun 2019, I. Bur leg., *Z. aptera*; 2 ♀, 11 Jun 2019, I. Bur leg., *Z. aurea*; **Stevens Co.:** (45.4507 –96.1325): 1 ♀, 9 Jun 2017, I. Lane

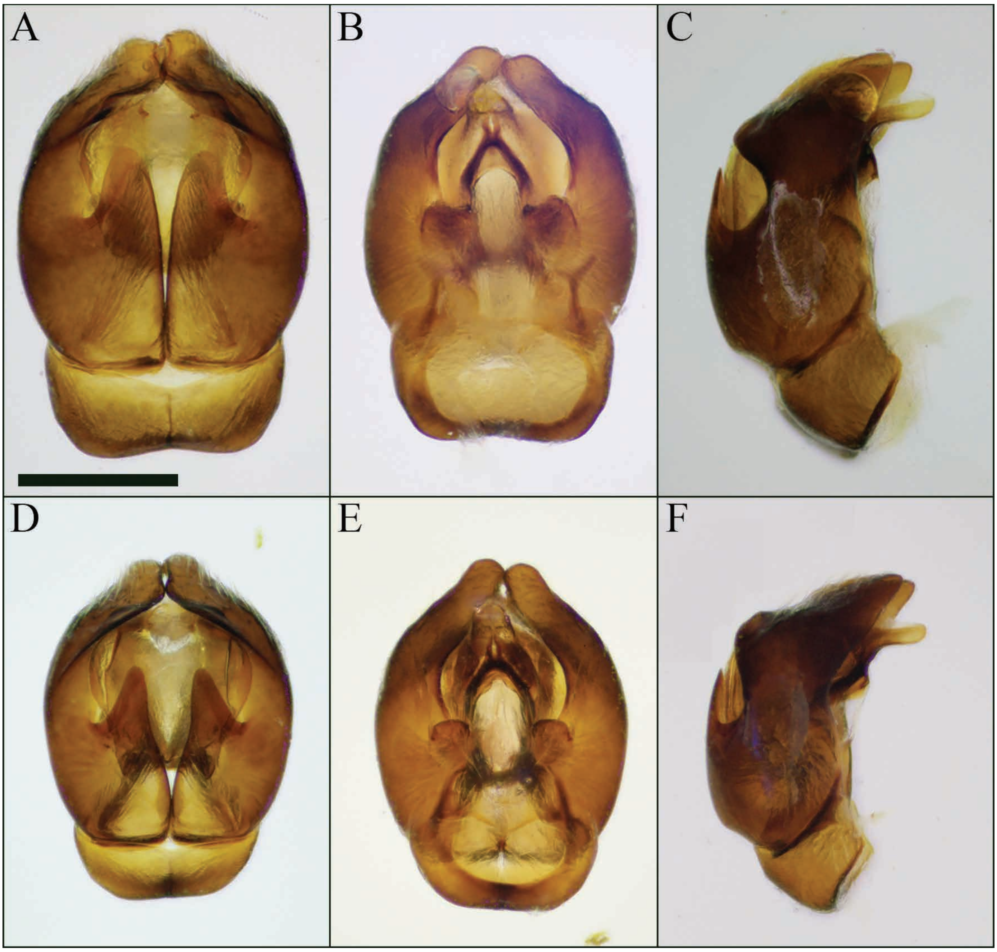

Figure 6: Male genitalia: *Andrena vernalis* (A) dorsal view; (B) ventral view; (C) lateral view; *A. ziziae* (D) dorsal view; (E) ventral view; (F) lateral view. Scale bar = 500 µm, all images are at the same scale.

leg., *Z. aurea*; 4 ♀, 7 Jun 2018, I. Lane leg., *Z. aurea*; 1 ♀, 7 Jun 2018, M. Rancour leg., *Z. aurea*; 3 ♀, 7 Jun 2018, S. Marconie leg., *Z. aurea*; 3 ♀, 7 Jun 2018, T. Eicholz leg., *Z. aurea*; 1 ♀, 18 Jun 2019, I. Bur leg., *Z. aurea*; John Freeman WMA (45.4611 –95.9681): 5 ♀, 6 Jun 2019, G. Pardee leg., *Z. aptera*; 2 ♀, 6 Jun 2019, I. Bur leg., *Z. aptera*; **Swift Co.:** Chippewa Prairie (45.1545 –96.0086): 1 ♀, 31 May 2018, A. Ritchie leg., *Z. aptera*; 4 ♂ 4 ♀, 31 May 2018, I. Lane leg., *Z. aptera*; **Washington Co.:** Belwin Conservancy (44.9445 –92.8169): 1 ♀, 7 Jun 2016, E. Evans leg., *Z. aurea*. **VERMONT: Franklin Co.:** St. Albans: 1 ♀ (MCZ), 21 Jun 1913, W.M. Wheeler leg.

Remarks. Ribble (1968) synonymized *A. vernalis* with *A. ziziae* because he considered *A. vernalis* to merely represent variation within *A. ziziae*. One of the defining characters that Mitchell (1960) used to separate *A. vernalis* was the pleural depression and ridge; Ribble (1968) considered this character too variable, stating:

"Different individuals show a continuous variation in the mesepisternum from the modified type (above) to specimens having a flattened area in front of the coxa. Also, individuals with modified mesepisterna occur throughout most of the range of *ziziae* and are often collected with it. Specimens collected together may be almost identical except for the quite different mesepisterna and intermediates between these two types may occur with them. Males occasionally have weakly depressed areas in front of the middle coxae, but are not unusual in other respects."

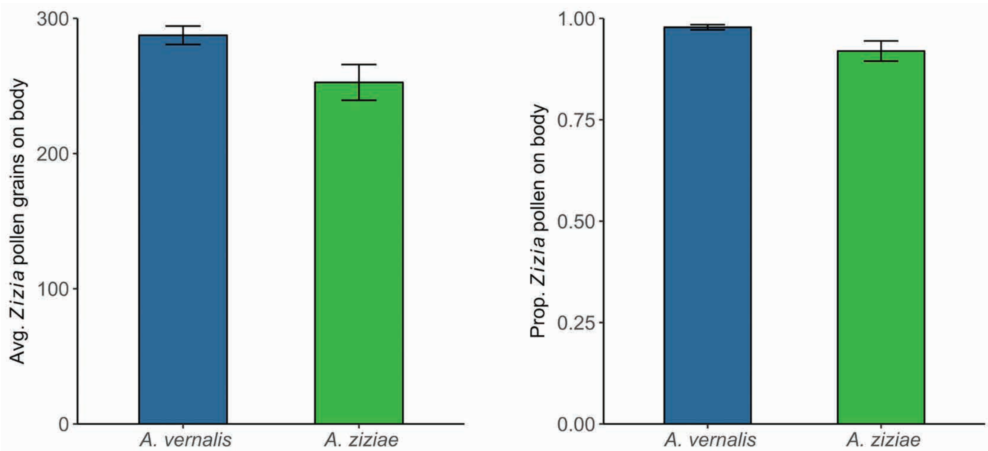

Figure 7. Foraging behavior of *A. vernalis* (blue) and *Andrena ziziae* (green) based on our pollen study. The left panel shows the average number of *Zizia* pollen grains found on individuals of each species and the right panel shows the average proportion of *Zizia* pollen grains found on individuals of each species. Bars are means ± SE.

However, Ribble (1968) followed that with a discussion on the variation in the width of the facial fovea in the female and the shape of the apical lobes of the male S7. Both of those characters are generally consistent within species and are important in delineating species boundaries.

Ribble (1968) did not examine the holotype of *A. vernalis*, though he appears to have examined the two paratypes at NCSU. A note on the location of the paratypes: although the holotype of *A. vernalis* is located at MCZ and Mitchell (1960) indicated that three of the four paratypes were also deposited at MCZ, none of the paratypes were able to be located there. Two of them (from Colebrook, CT) are currently at NCSU and it's not clear where the third purported MCZ paratype (collected from Pine Island, NY) is located.

Examination of specimens reveals that in addition to the pleural depression and ridge, there are multiple other consistent characters that differentiate *A. vernalis* and *A. ziziae*, including the width of the facial fovea, sculpturing of the propodeum, length of tergal hair bands, length of transparent apical rims, length of the r-rs crossvein, relative length of the antennal segments, and the male terminalia. These characters are discussed in depth in the diagnosis for *A. vernalis*. The pleural ridge is indeed one of the more variable characters, ranging from deep with a strong carina to shallow with a weak carina in *A. vernalis*. The pleural depression and ridge are weaker in the males than the females, though it is consistently present. Some *A. ziziae* females have a weak pleural depression, but it never reaches the level seen in *A. vernalis* and no specimens were found that fully intergrade. Overall the pleural depression and ridge is a consistent character that can distinguish *A. vernalis*, but it is often partially or fully obscured by the midlegs and wings, requiring it to be viewed at a non-ideal angle if it is even visible at all. As a result, in females, the facial fovea is the clearest and most consistent defining character, though the difference is difficult or impossible to see if the foveae are matted.

The species status of *A. vernalis* is most strongly supported by the differences in male terminalia (see diagnosis for details). Six male *A. vernalis* were collected at the same collection events as females and one additional male was found at MCZ that was collected at the same collection event as the holotype but was apparently never seen by Mitchell. The males and females of *A. vernalis* are associated based on the shared pleural depression and ridge, the relatively shorter antennae in both sexes, and the relatively longer clear apical rims of the terga. Plus, the correct association between the male and female in *A. ziziae* is clear, since the lectotype of *A. ziziae* was caught in copula and pinned with the male. In addition, numerous male *A. ziziae* were collected in association with females (including two in copula) at sites where *A. vernalis* was not found. In light of these clear and consistent morphological differences in both males and females, we are reinstating *A. vernalis* as a valid species.

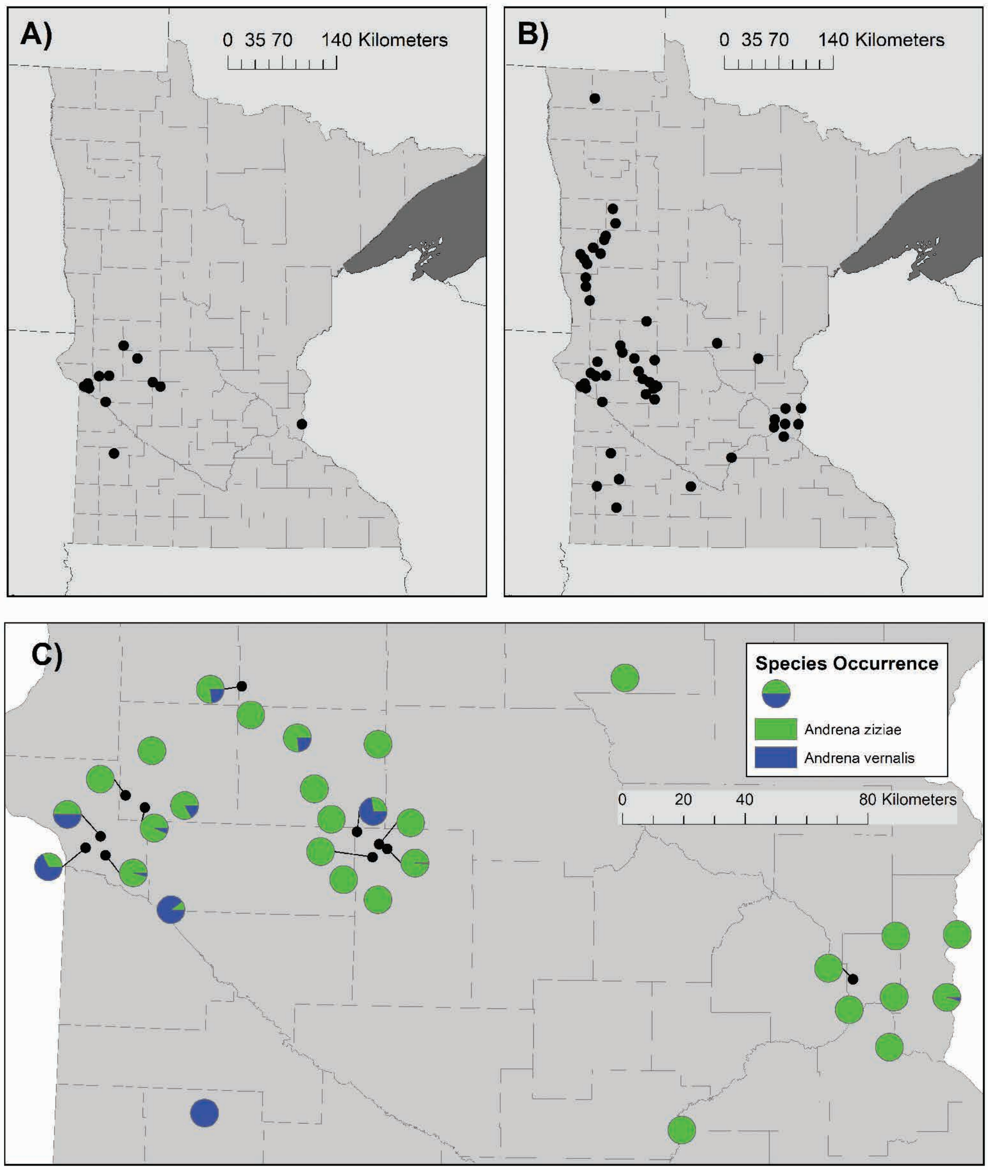

Figure 8. Distribution of *Andrena vernalis* and *A. ziziae* in Minnesota: (A) distribution of *A. vernalis*; (B) distribution of *A. ziziae*; (C) area where the range of *A. vernalis* and *A. ziziae* overlap, showing the relative proportion of each species at each site.

Examination of specimens at MCZ revealed five additional topotypical specimens of *A. vernalis* (4 ♀ and 1 ♂), with two females and the male collected from the same collection event as the type. All the specimens have a prominent pleural depression and ridge (Fig. 9). Indeed, this character seems to be enhanced because the faded integument of these aged specimens provides better contrast. In addition to the pleural depression and ridge, the male and female topotypical specimens and the holotype are a morphological match with the specimens from Minnesota. As a result, we can confidently assign the Minnesota specimens to *A. vernalis* despite the moderate geographic distance between them.

Historically, there has been a fair amount of confusion regarding the identity

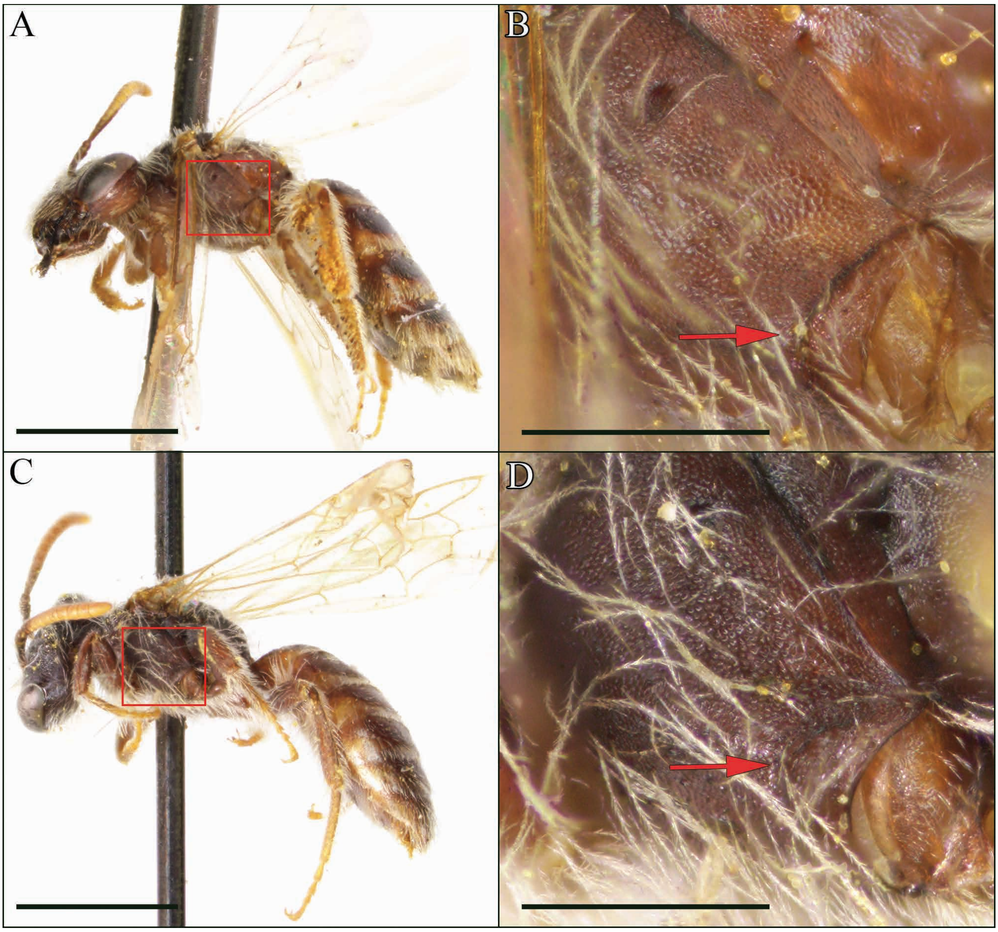

Figure 9. Topotypical specimens of *A. vernalis* with pleural depression and ridge: (A) female lateral view; (B) closeup of female pleural depression and ridge, indicated by red arrow; (C) male lateral view; (D) closeup of male pleural depression and ridge, indicated by red arrow. Scale bars: A–B = 2 mm; C–D = 500 µm.

of *A. vernalis*. Even Mitchell (1960), despite originally describing *A. vernalis*, may have confused some specimens with *A. ziziae*, since he noted that some specimens of *A. ziziae* had broader facial fovea and more broadly hyaline apical impressed areas of the abdominal terga; both of these characters are suggestive of *A. vernalis*. The terminalia illustrations by Ribble (1968) for *A. ziziae* do not match the current understanding of that species; instead, the illustrations match our current understanding of *A. vernalis*. In contrast, the terminalia illustrations of *A. ziziae* by Mitchell (1960) are consistent with our current understanding of *A. ziziae*. Finally, Ribble (1968) extensively discussed the apparent variation in *A. ziziae*, including variation in the width of the fovea, the shape of the male S7, and pleural ridge.

The *A. ziziae/vernalis* complex has sometimes been confused with other species. For example, one female *A. vernalis* was found misidentified as *A. personata* in the MCZ collection (identifier unknown) and a mix of females (6 *A. ziziae* and 1 *A. vernalis*) from Minnesota were all misidentified as *A.* (*Simandrena*) *nasonii* Robertson, 1895 by S. Droege.

***Andrena* (*Micrandrena*) *ziziae* Robertson**

Fig. 1B,D,F, 2B,D,F, 3B,D,F, 4B,D,F, 5C–D, 6D–F, 7, 8B–C

Andrena ziziae Robertson, 1891: 55, ♀♂ (in part). Lectotype ♀ (designated by Ribble 1968), USA, IL, Carlinville, 7 May 1887, C. Robertson leg., on *Zizia aurea*, INHS #179494; Robertson, 1897: 335 (redescription, separation from *A. personata*); Bruner, 1903: 242 (key); Viereck, 1916: 712, 716 (key).

Opandrena ziziae: Robertson, 1902: 193 (new generic assignment, key).

Micrandrena ziziae: Cockerell, 1909: 420 (new generic assignment).

Andrena (*Micrandrena*) *ziziae*: Cockerell, 1932: 157–158 (subgeneric assignment, key); Mitchell, 1960: 93, 99, 168–169, Fig. 31, 32 (key, redescription); Ribble, 1968, 246, 267 (key, redescription) (in part); Hurd 1979: 1810 (catalogue).

Diagnosis. See diagnosis of *A. vernalis* in order to separate these two species.

Both females and males key out correctly in Mitchell (1960); since male *A. vernalis* are not included in Mitchell (1960), see diagnosis of *A. vernalis* to separate males.

Andrena ziziae males key out to the *A. ziziae/piperi* Viereck couplet in Ribble (1968) but don't quite match the *A. ziziae* couplet since its antennal segments are longer than would be expected by the key. Females key out to the *A. ziziae/chlorogaster* Viereck couplet in Ribble (1968) but the fovea are slightly narrower than would be expected by the key (taking up slightly more than half the space between the eye and lateral ocelli). Since neither male nor female *A. vernalis* are included in Ribble (1968), see the diagnosis of *A. vernalis* to separate from *A. ziziae*.

Description of male. Body length: 6.0 mm, range 5.5–6.3 mm; ITD: 1.22 mm (n = 10).

See Mitchell (1960) for full description.

Description of female. Body length: 6.9 mm, range 6.5–7.3 mm; ITD: 1.33 mm (n = 10).

See Mitchell (1960) for full description.

Floral records. Apiaceae (58 ♂ 642 ♀): *Zizia aptera* 5 ♂ 151 ♀, *Z. aurea* 53 ♂ 491 ♀, **Asteraceae**: *Taraxacum officinale* 3 ♂ 6 ♀, **Fabaceae**: *Trifolium repens* 1 ♀. Thirty-five female *A. ziziae* collected in 2018 had their body pollen analyzed. Individuals of *A. ziziae* had on average 252 *Zizia* pollen grains on their bodies and 91.95% of the pollen carried was from *Zizia* (Fig. 7).

Phenology. Active in May and June in Minnesota.

Type material examined. Lectotype ♀, Illinois: Macoupin Co., Carlinville, 7 May 1887, C. Robertson leg., on *Z. aurea.* Robertson #3819, INHS #179,494 (INHS). 1 Paralectotype, ♂, on same pin as lectotype (INHS).

Additional material examined. Total specimens: 61 ♂ 664 ♀. **CONNECTICUT: Litchfield Co.:** Colebrook: 2 ♀ (MCZ), 8–11 Jun 1911, W.M. Wheeler leg.; 5 ♀ (MCZ), 31 May 1922, W.M. Wheeler leg. **MINNESOTA: Becker Co.:** (47.0337 –96.0814): 2 ♀, 8 Jun 2017, R. Tucker leg., *Zizia aurea*; Heliksen WPA (47.0793 –96.0579): 2 ♂, 8 Jun 2017, C. Herron-Sweet leg., *Z. aptera*; 2 ♀, 8 Jun 2017, C. Herron-Sweet leg., *Z. aurea*; 3 ♀, 27 Jun 2017, A. Waananen leg., *Z. aurea*; Lunde WMA (46.8710 –96.1321): 1 ♀, 13 Jun 2018, D. Drons leg., *Z. aurea*; Lunde WMA (46.8713 –96.1319): 3 ♀ (2 ♀ MNDNR), 13 Jun 2018, D. Drons leg., *Z. aurea*; **Big Stone Co.:** (45.3065 –96.2874): 6 ♀, 9 Jun 2017, C. Herron-Sweet leg., *Z. aurea*; 2 ♀, 1 Jun 2018, A. Ritchie leg., *Taraxacum officinale*; 4 ♀, 1 Jun 2018, A. Ritchie leg., *Z. aurea*; 5 ♀, 1 Jun 2018, I. Lane leg., *Z. aurea*; 9 ♀, 1 Jun 2018, T. Eicholz leg., *Z. aurea*; 9 ♀, 21 Jun 2018, S. Marconie leg., *Z. aurea*; 9 ♀, 18 Jun 2019, G. Pardee leg., *Z. aurea*; 22 ♀, 18 Jun 2019, I. Bur leg., *Z. aurea*; (45.3259 –96.3714): 2 ♀, 1 Jun 2018, S. Marconie leg., *Z. aptera*; 8 ♀, 10 Jun 2019, G. Pardee leg., *Z. aptera*; 5 ♀, 10 Jun 2019, I. Bur leg., *Z. aptera*; Larson Slough WPA (45.3612 –96.3119): 1 ♀, 3 Jun 2017, P. Pennarola leg., *Z. aptera*; **Brown Co.:** Joseph A. Tauer Prairie SNA (44.2009 –94.5326): 1 ♀, 18 Jun 2010, C. Kern leg.; **Clay Co.:** (46.8016 –96.4056): 1 ♂, 31 May 2017, C. Herron-Sweet leg., *Z. aurea*; 1 ♀, 22 Jun 2017, R. Tucker leg., *Z. aurea*; Bluestem SNA (46.8542 –96.4723): 1 ♀, 31 May 2017, R. Tucker leg., *Z. aurea*; 1 ♀, 22 Jun 2017, C. Herron-Sweet leg., *Z. aurea*; Clay County WMA (46.7478 –96.3535): 5 ♀, 19 Jun 2017, A. Waananen leg., *Z. aurea*; 8 ♀, 19 Jun 2017, R. Tucker leg., *Z. aurea*; Hoykens WPA (46.9368 –96.2631): 2 ♂ 8 ♀, 6 Jun 2017, R. Tucker leg., *Z. aurea*; **Dakota Co.:** Pine Bend Bluffs SNA (44.7912 –93.0320): 1 ♀, 4 Jun 2013, C. Boyd leg., *Z. aurea*; **Douglas Co.:** Miltona WMA (46.1073 –95.3218): 2 ♀, 13 Jun 2018, L. Gedlinske leg., *Z. aurea*; Staffanson Prairie (45.8161 –95.7460): 28 ♀, 5 Jun 2018, G. Pardee leg., *Z. aptera*; 15 ♀, 5 Jun 2018, I. Lane leg., *Z. aptera*; 7 ♀, 5 Jun 2018, T. Eicholz leg., *Z. aptera*; **Isanti Co.:** Dalbo WMA (45.6962 –93.4558): 1 ♀ (MNDNR), 20 Jun 2018, N. Gerjets leg., *Z. aurea*; **Kandiyohi Co.:** (45.2031 –95.1528): 1 ♂, 25 May 2017, R. Tucker leg., *Z. aurea*; (45.3273 –95.1790): 5 ♀, 2 Jun 2017, I. Lane leg., *Z. aurea*; (45.3529 –95.1192): 21 ♀, 2 Jun 2017, C. Herron-Sweet leg., *Z. aurea*; 1 ♀, 4–6 Jun 2018, J. Brokaw leg.; 12 ♀, 4 Jun 2018, I. Lane leg., *Z. aurea*; 15 ♀, 4 Jun 2018, S. Marconie leg., *Z. aurea*; 19 ♀, 4 Jun 2018, T. Eicholz leg., *Z. aurea*; 1 ♀, 27 Jun 2018, G. Pardee leg., *Z. aurea*; 2 ♂ 18 ♀, 5 Jun 2019, G. Pardee leg., *Z. aurea*; 4 ♂ 18 ♀, 5 Jun 2019, I. Bur leg., *Z. aurea*; 5 ♀, 12 Jun 2019, G. Pardee leg., *Z. aurea*; 5 ♀, 12 Jun 2019,

I. Bur leg., *Z. aurea*; (45.3658 –95.1537): 2 ♀, 18 Jun 2019, B. Bruninga-Socolar, M. Dutta, D. Harder leg.; Brenner Lake WPA (45.4006 –95.2463): 3 ♀, 4 Jun 2018, A. Ritchie leg., *Z. aptera*; 1 ♀, 12 Jun 2019, G. Pardee leg., *Z. aptera*; 2 ♀, 12 Jun 2019, I. Bur leg., *Z. aptera*; **Lyon Co.:** Glynn Prairie SNA (44.2638 –95.6962): 1 ♀, 14 May 2017, P. Pennarola leg., *Z. aptera*; **Mahnomen Co.:** Santwire WMA (47.2303 –95.8998): 1 ♀ (MNDNR), 19 Jun 2018, D. Drons leg., *Z. aurea*; Wambach WMA (47.3976 –95.9536): 1 ♀, 6 Jun 2018, D. Drons leg., *Z. aurea*; **Morrison Co.:** Rice Area Sportsmens Club WMA (45.8685 –94.1419): 2 ♀, 12 Jun 2018, L. Gedlinske leg., *Z. aurea*; **Murray Co.:** Lundblad Prairie SNA (43.9347 –95.7197): 1 ♀, 8 Jun 2015, K.J. Jokela leg., *Z. aurea*; Ruthton WMA (44.1729 –96.0463): 3 ♀, 15 Jun 2015, A. Fulton leg.; **Pope Co.:** (45.4353 –95.3556): 1 ♀, 14 Jun 2017, R. Tucker leg., *Z. aurea*; (45.5229 –95.4303): 13 ♂ 6 ♀, 31 May 2017, I. Lane leg., *Z. aurea*; (45.6707 –95.5077): 1 ♂ 5 ♀, 3 Jun 2019, G. Pardee leg., *Z. aptera*; 2 ♂ 14 ♀, 3 Jun 2019, I. Bur leg., *Z. aptera*; 17 ♀, 11 Jun 2019, G. Pardee leg., *Z. aptera*; 5 ♀, 11 Jun 2019, I. Bur leg., *Z. aptera*; 5 ♀, 11 Jun 2019, I. Bur leg., *Z. aurea*; (45.7357 –95.7054): 2 ♂ 5 ♀, 5 Jun 2018, A. Ritchie leg., *Z. aurea*; 1 ♂, 5 Jun 2018, M. Rancour leg., *Z. aurea*; 8 ♀, 5 Jun 2018, S. Marconie leg., *Z. aurea*; 2 ♀, 22 Jun 2018, T. Eicholz leg., *Z. aurea*; 3 ♂ 4 ♀, 4 Jun 2019, G. Pardee leg., *Z. aurea*; 1 ♂ 6 ♀, 4 Jun 2019, I. Bur leg., *Z. aurea*; Krantz Lake WPA (45.6590 –95.1701): 2 ♀, 20 Jun 2018, L. Gedlinske leg., *Z. aurea*; Krantz Lake WPA (45.6591 –95.1693): 1 ♀, 20 Jun 2018, L. Gedlinske leg., *Z. aurea*; Krantz Lake WPA (45.6592 –95.1691): 1 ♀, 20 Jun 2018, L. Gedlinske leg., *Z. aurea*; Krantz Lake WPA (45.6596 –95.1692): 1 ♀, 20 Jun 2018, L. Gedlinske leg., *Z. aurea*; Krantz Lake WPA (45.6650 –95.1684): 1 ♂ (MNDNR), 31 May 2018, N. Gerjets, L. Gedlinske leg., *Z. aurea*; Krantz Lake WPA (45.6651 –95.1684): 1 ♂ (MNDNR), 31 May 2018, N. Gerjets, L. Gedlinske leg., *Z. aurea*; Krantz Lake WPA (45.6653 –95.1679): 1 ♂ 1 ♀ (MNDNR), 31 May 2018, N. Gerjets, L. Gedlinske leg., *Z. aurea*; Krantz Lake WPA (45.6653 –95.1682): 1 ♂ (MNDNR), 31 May 2018, N. Gerjets, L. Gedlinske leg., *Z. aurea*; Krantz Lake WPA (45.6654 –95.1680): 1 ♀, 31 May 2018, N. Gerjets, L. Gedlinske leg., *Z. aurea*; **Ramsey Co.:** Bald Eagle-Otter Lake Regional Park (45.1171 –93.0059): 7 ♀, 5 Jun 2015, E. Evans leg., *Z. aurea*; Battle Creek Regional Park (44.9380 –93.0126): 1 ♀, 8 Jun 2016, J. Gardner leg., *Trifolium repens*; 3 ♀, 8 Jun 2016, J. Gardner leg., *Z. aurea*; Battle Creek Regional Park (44.9380 –93.0127): 4 ♂ 4 ♀, 27 May 2015, J. Gardner leg., *Z. aurea*; Battle Creek Regional Park (44.9386 –92.9914): 4 ♀, 10 Jun 2015, J. Gardner leg., *Z. aurea*; Battle Creek Regional Park (44.9394 –92.9881): 2 ♀, 8 Jun 2016, J. Gardner leg., *Z. aurea*; UMN Bee Lab Garden (44.9893 –93.1815): 2 ♂ 1 ♀, 28 May 2019, I. Bur leg., *Z. aurea*; 1 ♀, 31 May 2019, I. Bur leg., *Z. aptera*; **Roseau Co.:** Two Rivers Aspen Parkland SNA (48.6679 –96.3444): 1 ♂ (MNDNR), 30 May 2015, C. Boyd leg., *Z. aurea*; **Scott Co.:** Ney WMA (44.5445 –93.8825): 1 ♀, 14 Jun 2018, N. Gerjets leg., *Z. aurea*; Ney WMA (44.5446 –93.8825): 1 ♀, 14 Jun 2018, N. Gerjets leg., *Z. aurea*; Ney WMA (44.5447 –93.8822): 1 ♀ (MNDNR), 14 Jun 2018, N. Gerjets leg., *Z. aurea*; **Stevens Co.:** (45.4507 –96.1325): 3 ♀, 9 Jun 2017, A. Waananen leg., *Z. aurea*; 1 ♂ 28 ♀, 9 Jun 2017, I. Lane leg., *Z. aurea*; 3 ♂ 4 ♀, 22 May 2018, I. Lane leg., *T. officinale*; 1 ♂, 22 May 2018, I. Lane leg., *Z. aurea*; 2 ♂ 23 ♀, 7 Jun 2018, I. Lane leg., *Z. aurea*; 16 ♀, 7 Jun 2018, M. Rancour leg., *Z. aurea*; 3 ♂ 60 ♀, 7 Jun 2018, S. Marconie leg., *Z. aurea*; 1 ♂ 25 ♀, 7 Jun 2018, T. Eicholz leg., *Z. aurea*; 5 ♀, 18 Jun 2019, G. Pardee leg., *Z. aurea*; 7 ♀, 18 Jun 2019, I. Bur leg., *Z. aurea*; (45.4841 –96.2151): 2 ♀, 9 Jun 2017, R. Tucker leg., *Z. aurea*; Cin WMA (45.6184 –96.1130): 1 ♀, 18 Jun 2015, K.J. Jokela leg., *Z. aurea*; John Freeman WMA (45.4611 –95.9681): 1 ♀, 22 May 2018, A. Ritchie leg., *Z. aptera*; 15 ♀, 6 Jun 2019, G. Pardee leg., *Z. aptera*; 19 ♀, 6 Jun 2019, I. Bur leg., *Z. aptera*; **Swift Co.:** Bengtson WPA (45.2593 –95.2977): 3 ♀, 1 Jun 2017, P. Pennarola leg., *Z. aurea*; Chippewa Prairie (45.1545 –96.0086): 1 ♀, 31 May 2018, I. Lane leg., *Z. aptera*; **Washington Co.:** Coldwater Spring (44.9007 –93.1977): 1 ♂, 31 May 2017, K. Friedrich leg., *Z. aurea*; Arcola Bluffs (45.1210 –92.7510): 1 ♀, 7 Jun 2017, K. Friedrich leg., *Z. aurea*; Belwin Conservancy (44.9367 –92.7952): 1 ♂, 18 May 2016, J. Gardner leg., *Z. aurea*; Belwin Conservancy (44.9444 –92.8169): 2 ♀, 9 Jun 2015, E. Evans leg., *Z. aurea*; Belwin Conservancy (44.9445 –92.8169): 11 ♀, 7 Jun 2016, E. Evans leg., *Z. aurea*; Belwin Conservancy (44.9450 –92.8170): 1 ♀, 18 May 2016, J. Gardner leg.; Belwin Conservancy (44.9455 –92.8175): 3 ♀, 9 Jun 2015, E. Evans leg., *Z. aurea*; Belwin Conservancy (44.9482 –92.7853): 2 ♂, 9 Jun 2015, E. Evans leg., *Z. aurea*; **Wilkin Co.:** Foxhome Prairie Preserve TNC (46.3246 –96.2825): 2 ♀, 21 Jun 2018, L. Gedlinske leg., *Z. aurea*; Rice SNA (46.5884 –96.3680): 3 ♀, 20 Jun 2017, R. Tucker leg., *Z. aurea*; Tanberg 29-1 (46.4838 –96.3569): 1 ♀, 9 Jun 2017, P. Pennarola leg., *Z. aurea*.

Remarks. Examination of the lectotype and one of the paralectotypes reveal that *A. ziziae* match the traditional definition of that species (i.e. does not match *A. vernalis*). As noted by Ribble (1968), some male *A. ziziae* have small yellow spots on the paraocular areas. One female was found with 2 submarginal cells on one wing and the normal 3 on the other.

Note that the terminalia illustrations by Mitchell (1960, Fig. 31, 32) are correct, whereas the terminalia illustrations by Ribble (1968, Fig. 26–29) actually match *A. vernalis*. The illustration of S8 by Ribble (1968, Fig. 30) lacks key details and could potentially match either *A. ziziae* or *A. vernalis*.

Discussion

Here, we reinstated *A. vernalis*, which had been previously synonymized with *A. ziziae* by Ribble (1968). Although the taxonomic treatment of a single species in a limited range is not ideal, we believe it is warranted in this case because we are reinstating a synonym rather than describing an entirely new species. In addition, a clear species concept of *A. vernalis* is needed for upcoming pollinator studies on Minnesota prairies where *A. vernalis* features prominently. Finally, the apparently restricted habitat requirements of *A. vernalis* in Minnesota make it a potential species of conservation concern.

It is our hope that the identification resources provided here will allow other researchers to confidently separate *A. vernalis* and *A. ziziae* and flesh out the respective ranges of these two species. The frequent co-occurrence of these two similar species is particularly intriguing. In general, *A. ziziae* was more widely distributed and more abundant than *A. vernalis* across Minnesota, though there was substantial overlap between the two species (Fig. 8). Of the 50 locations in our study where *A. ziziae* was found, *A. vernalis* was also present at 12 of them (Fig. 8C). There was only a single site where *A. vernalis* was found but *A. ziziae* was not, and this was represented by a single specimen. This co-occurrence pattern may hold throughout the range of these two species, since their frequent co-occurrence was a primary reason that Ribble (1968) synonymized *A. vernalis* with *A. ziziae*, and specimens of *A. vernalis* and *A. ziziae* even co-occurred in the type locality of *A. vernalis* (Colebrook, CT).

Sites with *A. vernalis* were located exclusively in central Minnesota, where six sites had greater than seven individuals captured. Of these sites, five of them were considered high quality remnant prairie, while the sixth was an older prairie restoration (> 6 years). These six sites were all topographically complex, containing both wet lowlands and well-drained uplands. The species of *Zizia* differed somewhat between prairie remnants and restorations, with *Zizia aurea* more characteristic of restorations, and *Z. aptera* more characteristic of prairie remnants. In general, *A. vernalis* was much more commonly found on *Z. aptera* than on *Z. aurea*, though it is unclear if this constitutes a floral preference or is a function *of Z. aptera* dominating the high-quality remnants where *A. vernalis* was most commonly found.

Regardless of habitat type, *A. vernalis* and *A. ziziae* were strongly associated with *Zizia*. The vast majority of specimens were collected through hand netting from *Zizia* spp., though a small number were netted from other plant species (n = 10) or were collected through passive traps (n = 5). The goal of one study that provided 480 specimens for this work was to characterize entire bee community floral associations, meaning that netting was performed on all flowering plants in the system throughout the flowering season (Lane et al. 2020, I. Lane, unpublished data). However, despite this whole-community sampling, all *A. vernalis* were caught on *Zizia* and only nine *A. ziziae* were caught on a non-*Zizia* host (*Taraxacum*). In addition, the high fidelity of *A. vernalis* and *A. ziziae* to *Zizia* is supported by the high proportion of *Zizia* pollen found on the bodies of both species (Fig. 7). This suggests that *Zizia* is the primary nectar source as well as pollen source for both bee species. While *Zizia* are by far the dominant spring plants in most of the systems where collection took place for this study, it remains unknown to what extent these two species also use the pollen of other Apiaceae. However, in Minnesota, related species of Apiaceae typically do not share the same habitat or flowering phenology as *Zizia*.

Finally, reinstating *A. vernalis* creates some uncertainty on previous studies that recorded *A. ziziae*. For example, previous studies on the pollination of *Zizia* and *Thaspium* (Lindsey 1984, Lindsey and Bell 1985) may have a more complex system that initially supposed if *A. ziziae* and *A. vernalis* both occur in those systems. In addition, once both species are taken into account, previous work showing that *A. ziziae* is broadly oligolectic on Apiaceae may reveal that one or both of the species have even more specialized floral preferences (Robertson 1926, Ribble 1968, LaBerge 1986, Wood and Roberts 2018). In addition, faunal studies and checklists that recorded *A. ziziae* (e.g. Wolf and Ascher 2008, Smith et al. 2012, Harmon-Threatt and Hendrix 2015, Gibbs et al. 2017) should be revisited in order to determine which species are present.

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