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A new species of *Andrena* (*Labergeia*) from Texas with an unusual phenology and floral host, including a redescription of *Labergeia* (Hymenoptera: Andrenidae)

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Abstract. *Andrena* is a species-rich genus of bees with a wide distribution, predominantly in the Holarctic. Here, we describe and illustrate a previously unknown species, ***Andrena* (*Labergeia*) *cenizophila*** Neff, Bossert & Zabinski n. sp., from southwestern Texas and central Coahuila, Mexico. Phylogenomic analyses recovered the new species as most closely related to *Andrena* (*Labergeia*) *nahua* Neff, a central Mexican species that was hitherto known only from the male sex. The discovery and examination of additional specimens of *A. nahua* allows us to describe and illustrate the previously unknown female, which shares diagnostic morphological features with the female of *A. cenizophila* n. sp. Based on these insights, we expand the diagnosis of *Labergeia* Neff to accommodate both species and discuss morphological affinities with their closest relatives in the subgenus *Dactylandrena* Viereck. Fossil-informed divergence time estimates indicates that *Labergeia* originated in the late Miocene, around 8 million years ago (5.37–11.82 mya), and that all known species of the subgenus, as well as its sister lineage *Dactylandrena*, are distributed in western and/or central North American. Lastly, we discuss the unusual foraging biology of *A. cenizophila* n. sp., which, based on observations and analyses of scopal pollen loads, is an oligolege of *Leucophyllum frutescens* (Berl.), I. M. Johnst. (Scrophulariaceae), a shrub commonly known as cenizo, Texas ranger, or Texas purple sage, among others. Interestingly, cenizo has a distinct floral phenology with comparatively short-termed mass blooms of not more than a week in duration, rendering it an unexpected choice for a specialist pollen collector. To our knowledge, *A. cenizophila* n. sp., is the only New World *Andrena* species that is oligolectic on plants of the family Scrophulariaceae.

INTRODUCTION

With about 470 described species, *Andrena* Fabricius (Hymenoptera: Andrenidae) is the second largest genus of bees in North America. The first species from the continent was described in 1837 (Kirby, 1837), although the status of *Andrena impuncta* Kirby, 1837 is unclear as the fate of the type specimen is unknown. Later, Smith (1853) described a set of 12 species. This was followed by an era of great alpha-taxonomic activity around the turn of the 20th century (Fig. 1). By 1930, about half of the presently

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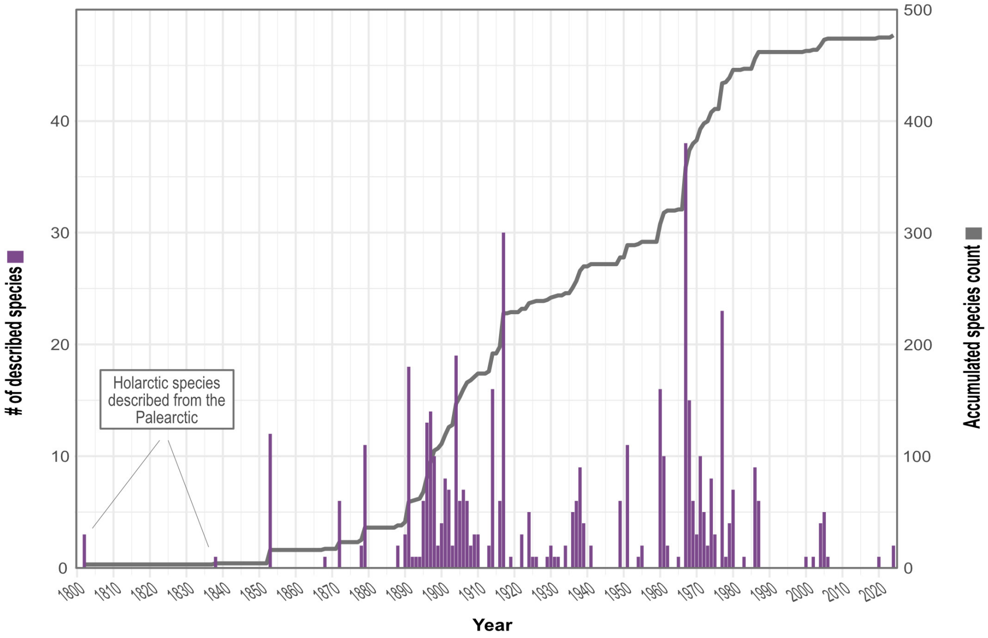


Figure 1. Accumulation of newly described *Andrena* species in the North American fauna over time, including only species that are currently recognized as valid.

accepted North American *Andrena* had been described. The second half of the 20th century saw great revisionary efforts by Wallace E. LaBerge and colleagues, who revised the North American representatives of the genus in a series of revisionary treatments of individual subgenera (Bouseman & LaBerge, 1978; LaBerge, 1967, 1969, 1971, 1973, 1977, 1980, 1985, 1986, 1989; LaBerge & Bouseman, 1970; LaBerge & Ribble, 1972, 1975; LaBerge &Thorp, 2005; Thorp & LaBerge, 2005). These works greatly facilitated taxonomic, systematic and faunistic research over the last decades and contributed to a significant number of newly described species for North America. Fewer North American species were described in the past two decades, however, ongoing fieldwork and efforts to identify *Andrena* in museum holdings continue to uncover North American *Andrena* previously unknown to science, primarily from the southern parts of the continent (Bossert *et al.*, 2024a; Larkin, 2004; Neff, 2024; Neff & Larkin, 2002; Pohl & Larkin, 2006; Sheffield, 2020; Zabinski, 2024).

Recently, our understanding of *Andrena* phylogeny has significantly improved. Pisanty *et al*. (2022) published a densely sampled phylogenomic dataset with a broad inclusion of subgenera (98 subgenera), while a simultaneous phylogenetic study of the family Andrenidae contributed additional phylogenomic data for species of *Andrena* (Bossert *et al.*, 2022), including more North American species. This phylogenomic framework facilitates new species descriptions, as it allows one to delineate subgenera more reliably than using morphology and/or single gene sequence data alone and makes it easier to place undescribed taxa into a suitable subgeneric context that reflects both evolutionary history and diagnosability based on morphology.

One such case concerns was *Andrena* (*Labergeia*) *nahua* Neff, 2024, a recently described species from Central Mexico. This species was based on three male specimens that originally had been identified as *Andrena* (*Celetandrena*) *vinnula* LaBerge & Hurd. These were borrowed by G. Pisanty for inclusion in his study of relationships within *Andrena*, but after sequencing and phylogenomic analysis, it was found that DNA from these bees did not group with that of other specimens identified as *A. vinnula*.

After examination of the three males, J. Neff found they had been misidentified and represented a new species. As it shared none of the distinctive features of its closest relatives in the *Andrena* phylogeny of Pisanty *et al.* (2022), it also was placed in a new subgenus. Unfortunately, due to COVID related problems, publication of these descriptions (Neff, 2024) was delayed until after the publication of the phylogenetic analysis (Pisanty *et al.*, 2022). Fortunately, however, the description of the male facilitated discovery of the female of *A. nahua*.

The goals of the present study are threefold. First, to describe and illustrate the previously unknown female of *A. nahua*. Second, to expand the diagnosis of *Labergeia* Neff in light of the newly studied female morphology. Lastly, to describe a new species of the subgenus, *Andrena* (*Labergeia*) *cenizophila* n. sp., using an integrated, morphological-molecular phylogenetic approach.

MATERIAL AND METHODS

Our taxonomic work considers a recently published phylogenetic hypothesis of *Andrena* (Bossert *et al.*, 2024a), which includes both *A. nahua* and a closely related species that we herein describe as new. This hypothesis is based on combined sequence data of the comprehensive phylogenomic analysis of *Andrena* (Pisanty *et al.*, 2022), the Andreninae of Bossert *et al.* (2022), and eight publicly available genomes of the genus. For details on molecular and analytical methods, see Bossert *et al.* (2024a). Briefly, this phylogeny includes 264 samples of Andrenidae and 249 species of *Andrena*, which are represented by 1,175 ultraconserved elements (UCEs). The authors analyzed a DNA alignment of 555,734 bp using maximum likelihood methods and carried out divergence time estimates using RelTime (Tamura *et al.*, 2012), informed by a set of eight secondary calibrations.

The terminology for the morphology-based work presented here follows that of LaBerge (1967) with some additions and exceptions as discussed in Neff (2024). Abbreviations used include S for sternum, T for tergum, FS for flagellar segment, pw for puncture width, ITS for intertegular span (Cane, 1987), ML for mandibular length, and IMD for intermandibular distance (the distance between the mandibular bases). Additional terms include the mandibular basoventral lamella and the distifemoral plate. The distribution of the mandibular basoventral lamella within *Callandrena* Cockerell was discussed by LaBerge (1967), although he did not define the structure. It was discussed by Dubitzky *et al.* (2010) who called the structure the condylar lamella and defined it as "a convex lamellate projection along the lower margin of the female mandible distal to the mandibular condyle". According to Dubitzky *et al.* (2010), it is unique to *Andrena*. The distifemoral plate is a plate-like structure at the apex of the hind femur, adjacent to the basitibial plate and presumably serving a similar function. It was described but not named or figured by Michener (1944) for *Protoxaea* Cockerell & Porter. We used the following museum acronyms: CTMI – Central Texas Melittological Institute, Austin, TX, USA; INHS – Illinois Natural History Survey, Champaign, IL, USA; SEMC – Snow Entomological Museum Collection; University of Kansas Biodiversity Institute, Lawrence, KS, USA; USNM – National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; UTIC – University of Texas Insect Collection, Austin, TX, USA; WSUC – Washington State University Insect Collection, Pullman, WA, USA (houses the first author's research collection).

Size measurements were made to 0.02 mm with a Wild dissecting microscope fitted with an ocular micrometer. Scopal pollen was extracted, mounted in glycerin jelly on slides and examined under a compound microscope and compared with the illustrations in Niezgoda & Tomb (1975). Where necessary, counts of pollen grain were adjusted for pollen grain volume to determine the relative composition of pollen loads (Buchmann & O'Rourke, 1991). Photographs of specimens were generated using a Macropod Pro imaging system, which is comprised of a Canon EOS 6D camera and a Stackshot 3× Cognisys device. Z-stacking was carried out using Zerene Stacker (Zerene Systems, LLC.) and the Pmax option. Distributional records were initially visualized with SimpleMappr (Shorthouse, 2010) and later modified using standard image processing software.

RESULTS

DNA Sequencing and Phylogeny

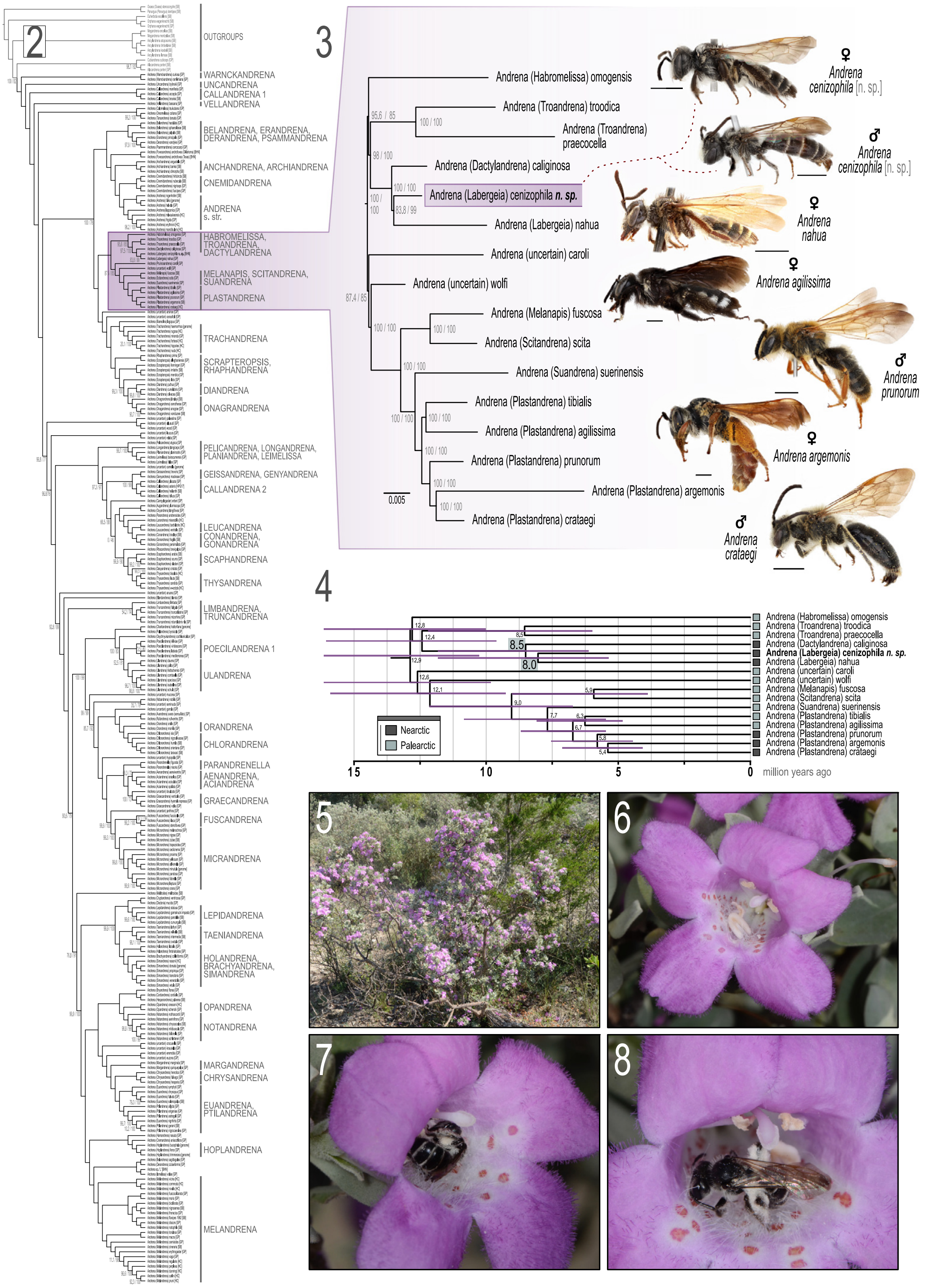
Whole genome sequencing of *A. cenizophila* n. sp., which is treated as *Andrena* sp. 'C' in Bossert *et al.* (2024a), returned 69,979,302 short illumina reads. Assembly of these short reads into contiguous sequences (contigs) using the de-novo assembler SPAdes (Prjibelski *et al.*, 2020) generated a genome assembly of 244.51 Mb length, 196,799 contigs with an average contig coverage of 23.48 × (estimated through SPAdes), and an N50 of 3,611. We carried out a BUSCO analysis (Benchmarking Universal Single-Copy Orthologs; Manni *et al.*, 2021), which scored the genome as follows: 66.32% BUSCO genes were found as complete and single-copy, 0.05% as complete and duplicated, 21.3% as fragmented, and 12.0 % as missing. Bossert *et al.* (2024a) mined this genome for ultraconserved elements of Hymenoptera using the UCE Hym-v2 probe set (Branstetter *et al.*, 2017), using comparatively strict parameters (Bossert & Danforth, 2018) and 1000 bp flanking regions, which allowed to extract 2,350 UCEs of 4,476,029 total bp length. The genome assembly and the UCE extract can be retrieved from a FigShare repository under https://doi.org/10.6084/m9.figshare.26352121.

Phylogenetic analysis of this UCE sequence data recovered *A. cenizophila* n. sp. as sister species to *A. nahua* (Figs. 2–4). Previously considered monotypic and only known from the male, this finding was not obvious based on morphology alone, however, (re-)examination of morphological features, especially that of the newfound female, revealed similarities sufficient to consider an expanded subgenus *Labergeia* with two species as the most adequate solution to associate *A. cenizophila* n. sp. with a subgenus. Statistical support values for the respective phylogenetic placement are good but not perfect; ultrafast bootstrap approximations (UFBoot2) recovered 99 (out of 100) and SH-like approximate likelihood ratio tests found 83.8 (out of 100). However, reanalysis of this and slightly altered data matrices using different parameters recovered the same relationship in every case, providing additional support for this relationship. The phylogenetic analysis further recovered *Labergeia* as most closely related to *Andrena* (*Dactylandrena*) *caliginosa* Viereck, the sole representative of *Dactylandrena* Viereck, in both the present and previous phylogenomic analysis of *Andrena* (Bossert *et al.*, 2024a; Pisanty *et al.*, 2022); this finding is congruent and maximally supported among all these studies. Fossil-informed divergence time estimates for *Labergeia* recovered a comparatively old crown age of 8.0 million years for the subgenus (Fig. 4).

Systematics
Genus *Andrena* Fabricius
Subgenus *Labergeia* Neff

TYPE SPECIES: *Andrena nahua* Neff, 2024

REVISED DIAGNOSIS: Small bees (7.3–8.5 mm); integument black to dark brown, with or without facial maculation; head broader than long; eyes subparallel, slightly converging above; ocello-occipital distance equal to or slightly more than medial ocellar diameter; gena as broad as eye or broader; galea short, shorter than clypeus, galeal length exceeded by maxillary palpal segments 4–6; labral process emarginate, malar space linear. Pronotum with distinct humeral angles and rounded dorsoventral



Figures 2–8. Phylogenetic relationships of *Andrena*. **2**. Maximum likelihood phylogeny of *Andrena* and closely related lineages, representing 249 species of *Andrena*, including *Andrena* (*Labergeia*) *cenizophila* n. sp. Support values show SH-like approximate likelihood ratio tests (SH-aLRT; left values) and ultrafast bootstrap approximations (UFBoot2; right values); if node values are omitted, then nodes received maximum support by both measures. Bracketed abbreviations after taxon names indicate the origin of the sequence data: GP – Pisanty *et al.* (2022), HC – Grab *et al.* (2019), HPG17 – Faircloth *et al.* (2015), SB — Bossert *et al.* (2022), and BHN – Bossert *et al.* (2024a). **3**. Magnified insert showing our hypothesis on the evolutionary history of *Labergeia*. Scale bar next to tree shows DNA substitutions per site and bars next to specimens correspond to 2 mm length. **4**. Divergence time estimates of the focal group in millions of years. Node bars display 95% confidence intervals. **5–8.** Habitus and flowers of *Leucophyllum frutescens* (Berl.), I. M. Johnst. (Scrophulariaceae), the only known pollen source of *A. cenizophila* n. sp. *Leucophyllum frutescens* is a mass-blooming shrub native to southern Texas and northeastern Mexico. Figures 7 and 8 show a pollen collecting female of *A. cenizophila* n. sp.

ridges; metapostnotum finely roughened. Pterostigma large, length half of marginal cell; three submarginal cells, 1st recurrent vein nearly interstitial with 2nd transverse cubital vein; vestiture sparse, T2–T4 with apical fascia.

Female: Facial maculation absent; facial fovea shallow, not constricted below, separated from lateral occellus by slightly more than one ocellar diameter and extending to level of lower margin of antennal fossae; mandibular basoventral lamella present; subgenal coronet present but weak; flagellum with length segment 1 equal length of 2 + 3; propodeal corbicula present but weak; trochanteral flocculus complete; tibial scopal hair long, simple; hind tibia and basitarsus long and narrow; tergal fascia strong.

Male: Head broader than long; gena as broad or broader than eye in lateral view; FS1 nearly twice length of FS2; mandibles slender and elongate, strongly crossing apically. Tergal fascia weak; apical margin of S6 slightly reflexed and weakly emarginate; gonocoxae with large apicodorsal processes, apices of processes narrowly separated from gonostyli.

COMMENT: Our phylogenetic analysis, as does that of Pisanty *et al.* (2022), indicates that *Labergeia* is sister to *Dactylandrena*, a small subgenus of four species in the western United States. This clade is closely related to *Troandrena* Warncke, a small Old World subgenus of five species occurring from Greece to Pakistan. This clade of three subgenera is sister to *Habromelissa* Hirashima & LaBerge, a small Asian subgenus of six species (Figs. 2–4). *Labergeia* lacks the distinctive characters of *Dactylandrena*: head longer than broad (broader than long in *Labergeia*), malar space distinct, distinct, ¼ to $1^{\times}$ basal mandibular width (linear in *Labergeia*; labral process bidentate (weakly emarginate in *Labergeia*), tergal fascia absent (present in *Labergeia*) and other characters (LaBerge, 1985). Wood (2024) characterized *Troandrena* as possessing a flattened or slightly domed clypeus with an impunctate midline and a strongly emarginate labral process, while in *Labergeia* the clypeus is rounded, lacks an impunctate midline and the labral process is weakly emarginate. *Habromelissa* is distinguished by having the third submarginal cell receiving the second recurrent vein at or near the end of the cell (Hirashima, 1964) while in *Labergeia,* like most other bees, it meets the third submarginal well before its apex.

Andrena (*Labergeia*) *nahua* Neff, 2024
(Figs. 9–11)

MATERIAL EXAMINED: ♀: MEXICO: Mexico, 5.8 mi. SE of Temascalapa, 8100′, 28 August 1962, U. Kans. Mex. Exp., identifier SM0644477, also 11 ♀♀ and 24 ♂♂, with same label data, female identifiers #SM064415, SM064417, SM06444419, SM064435, SM064473, SM064447, SM0644476, SM0644478, SM0644479, SM0644480, SM0644481, and SM0644482. SM0644476 with metasoma missing, SM0644481 and SM0644480 with head missing. 1♂, MEXICO: Puebla, 8 mi. W. Huachinango, 6450′, 21 August 1962, U. Kans. Mex. Exp., SEMC. All female specimens labeled *Andrena* (*Celetandrena*) *vinnula* Laberge and Hurd, det. W. E. Laberge, 2003, and *Andrena nahua* ♀ (or ♂ as appropriate), det. W. Zabinski and deposited in SEMC.

DIAGNOSIS: The female of *A. nahua* can be recognized by the combination of its small size, broad head, erect short, hooked hair on sides and ventral surface of the stipes, mix of sparse erect black and white hair on scutum and mesepisternum, slender hind tibia, and 1st recurrent vein nearly interstitial with 2nd transverse cubital vein.

DESCRIPTION: ♀, Measurements ($n = 10$): body length = 7.9 (7.5–8.3) mm, mesosomal width = 2.3 (2.1–2.3) mm, ITS = 1.53 (1.44–1.60), forewing length = 7.2 (7.0–7.4) mm, metasomal width = 4.2 (4.1–4.2) mm.

Figures 9–11. Female of *Andrena* (*Labergeia*) *nahua* Neff. **9.** Frontal view. **10.** Dorsal view. **11.** Lateral view. Scale bars: 1 mm.

Color: Black except mandibles with apical third reddish brown, condylar lamella with outer margin translucent yellow, dark basally; tegulae dark translucent brown; wings with yellowish tinge, veins including stigma light brown except radial vein dark brown; legs with distal tarsomeres light brown, claws clear reddish yellow with apices darkened; tibial spurs, including malus of foreleg, clear yellow-brown, apices darkened.

Structure: Head: broader than long, head width/head length = 1.29 (1.23–1.33), facial quadrangle = 1.13 (1.10–1.18). Eye length to head length ratio = 0.70 ± 0.02 (0.69–0.75, clypeal length = 0.38× head length (0.36–0.40), inner margins of eyes weakly concave in frontal view. Clypeus slightly raised with disc rounded, apex slightly depressed medially and more strongly laterally. Clypeal apex concave, protruding beyond lower eye margin by $0.16^{\times}$ eye length medially and $0.25^{\times}$ eye length laterally. Disc of clypeus shiny but lateral portions dulled by weak tessellation, disc with moderate punctures 1–3 pw apart, punctures slightly smaller and denser laterally. Parocular and supraclypeal area with sculpture similar to lateral portions of clypeus. Frons, outside facial fovea, with fine longitudinal striae reaching level of ocelli. Facial fovea shallow, near oval, slightly narrowed below, extending from upper margin of eye to lower margin of antennal sockets, outer margin closely paralleling inner eye margin but slightly diverging below, occupying approx. $0.46^{\times}$ space between eye and lateral ocellus and $0.42^{\times}$ space between eye antennal socket. Vertex behind ocelli dulled by fine tessellation with scattered obscure punctures. Lateral ocellar diameter = 0.18 mm, ocello-occipital distance = 1.11 x lateral ocellar diameter, ocello-ocular distance = $2.89^{\times}$ lateral ocellar diameter. Gena as broad as eye laterally, surface shiny with very weak tessellation and very sparse fine punctures. Antenna normal, FS1 slightly longer than combined length segments 2 + 3, segments increasing in length from FS2–FS10 with FS10 slightly shorter than FS1. Malar space linear. Mandibles with strong preapical tooth; basoventral lamella present, widest basally. Subgenal coronet present but weak, consisting of short, sparse erect hairs. Labral process trapezoidal, length $0.38^{\times}$ basal width; apical margin rounded, weakly emarginate and half as wide as basal width; surface shiny. Galea short, length = $0.20^{\times}$ head length, apex rounded, surface smooth. Glossa short, length $0.12^{\times}$ head length. Stipes with numerous erect, short, slender, apically curved hairs, length stipes $0.51^{\times}$ head length. Surface of prementum smooth, length = 0.51 head length. Maxillary palps $2.5^{\times}$ as long as galea, ratio of segment lengths 8:6:4:3:2:2, basal segments stout and cylindrical but distal segments slender. Labial palps short, $0.65^{\times}$ as long as galea, ratio of segments 5:4:2:2.

Mesosoma: Pronotum with surface dulled by fine shagreening; humeral angles present but rounded, dorso-ventral ridge rounded and bisected by distinct groove. Scutum weakly shiny, surface dulled by fine shagreening, with medium punctures 2–4 pw apart, these slightly denser laterally and in anterior fourth. Scutellum with surface shinier and punctures slightly stronger and denser. Metanotum with surface dull, punctures finer and approx. 1 pw apart. Metapostnotum with basal triangular area weakly roughened, lateral areas dulled by dense shagreening. Mesepisternum and metepisternum with surface dull, sparsely punctate with fine punctures 2–4 pw apart. Tegulae shiny except densely punctate in apical fourth. Wing with three submarginal cells; second submarginal cell short, approx. 0.41 as long as third on posterior margin; first recurrent vein nearly interstitial with second transverse cubital vein.

Legs slender, hind tibia only slightly expanded, $0.12^{\times}$ as wide as long; distifemoral plate narrowly triangular, slightly smaller than basitibial plate; basitibial plate ovate, relatively small $0.20^{\times}$ as long as hind tibia. Tarsal claws with inner teeth well developed. Tibial spurs normal.

Metasoma: T1 with anterior surface shiny with very fine punctures approx. 1–2 pw apart, punctures becoming slightly larger on dorsal surface and surface distinctly duller on apical half of dorsal surface, T2–T5 with surface as in apical half of T1. Pygidial plate usually hidden by hair, triangular with rounded apex, surface dull. Sterna with surfaces dull, very finely punctate.

Vestiture: Head: Hair sparse, nowhere obscuring surface except on facial foveae; hair entirely white except scattered black hair on upper half gena and hair of facial fovea dark gray. Scape with short, inconspicuous hair. Labral process bare, margin of labrum with row of very short, curved, orange hair; disc of labrum beyond process with longer erect, curved hairs. Stipital comb weak; stipes with sparse, short, simple, erect yellow hair on lateral and ventral surfaces.

Mesosoma: Hair sparse, mainly white, but mix of erect black and white hair on scutum, scutellum, and mesepisternum. Propodeal corbicula incomplete, poorly defined posteriorly and anterior row missing, interior with numerous erect simple hairs. Hair of foreleg white except mainly black on tibia; hair of midleg similar. Hair of hindleg white except distifemoral tuft, hair on surface of basitibial plate and strip of scopal hair running medial length of tibia dark brown to black; trochanteral flocculus complete; scopal hairs of hind tibia relatively sparse, appearing simple (with sparse short branches under high magnification), and strongly arched, particularly on basal half.

Metasoma: Hair of T1 sparse, short, white, not obscuring surface; T2–T4 with complete apical fascia of off-white hair, discs with very short dark hair not obscuring surface; T5 with apical half covered with appressed long hair, this dark medially but lighter on sides; T6 with long appressed dark hair. S1–S5 with weak apical fascia of white hair with short branches, hair longest laterally, with short sparse, semi-appressed hair basally; hair of S6 semi-appressed, dark with very short branches.

Comment: The localities and collection dates of these specimens fall within the previously known range and flight period of *A. nahua* in the Central Mexican highlands (Neff, 2024).

Andrena* (*Labergeia*) *cenizophila Neff, Bossert & Zabinski, new species

ZooBank: urn:lsid:zoobank.org:act:168A174A-ED6E-4D91-B0A2-534F3AAB8D88
(Figs. 12–20)

Diagnosis: Both sexes of *A. cenizophila* n. sp., can be distinguished from *A. nahua*, the only other *Labergeia* by their shinier terga and denser scutal punctation. The male of *A. cenizophila* differs by its maculate clypeus, and the gena being no wider than the eye. The female of *A. cenizophila* differs from that of *A. nahua* in its darker tibial spurs, more extensive black scutal pubescence, and the scopal hair of the hind tibia being shorter, denser, not strongly arched, and mainly black.

Description: Holotype, ♀. Measurements (n = 10 paratypes): Body length = 7.9 ± 0.4 mm (7.3–8.5 mm); head width = 2.6 ± 0.1 mm (2.4–2.8 mm); wing length = 7.1 ± 0.2 mm (6.8–7.5 mm); mesosomal width = 2.5 ± 0.2 mm (2.1–2.8 mm); ITS = 1.7 ± 0.1 mm (1.6–1.9 mm); metasomal width = 2.5 ± 0.1 mm (2.2–2.7 mm).

Color: Black, except as follows: pedicel dark reddish brown, flagellum grading from black basally to dark reddish, brown distally; apical third of mandible dark reddish brown; tegulae translucent, dark brown; wings translucent, with slight yellowish tinge, apices lightly darker due to denser microtrichia, veins translucent reddish brown basally, stigma and distal veins pale yellow, prestigma and marginal vein darker; claws and distal tarsomeres reddish brown; fore tibial spur with malus mainly brown, velum colorless, mid- and hind tibial spurs dark brown.

Structure: Head broad, width = 1.32× length; facial quadrangle = 1.0; eye length = 0.78× head length: clypeal length = 0.37× head length; genal width = 1.33× lateral eye width; eyes subparallel, upper interocular distance = 0.96× lower interocular distance; ocello-occipital distance = ocellar diameter; ocello-ocular distance= 2.78× ocellar diameter. Facial fovea large and shallow, extending from upper margin of eye to lower margin of antennal insertion, occupying near all of space between eye and lateral ocellus above but narrowed below, outer margin near eye but widely separated from antennae, occupying less than half space between eye margin and antenna. Clypeus slightly produced and rounded, disc flattened, apical margin strongly depressed, depressed area broadest above lateral margins of labrum. Disc of clypeus smooth and shiny, punctures moderate, deep, and well separated (2–3 pw apart); lateral and upper surfaces slightly dulled by weak shagreening and punctures becoming smaller and denser (1–1.5 pw apart). Paraocular and subantennal areas similar to lateral part of clypeus. Supraclypeal area roughened, with indistinct punctures. Supraclypeal line slightly widened in upper third, appearing as narrow smooth area with fine longitudinal striae. Vertex dull, densely tessellate with indistinct punctures, except

Figures 12–15. Paratype female of *Andrena* (*Labergeia*) *cenizophila* n. sp. **12.** Lateral view. **13.** Dorsal view. **14.** Frontal view. **15.** Metapostnotum, rotated dorsal view. Scale bars: 1 mm.

area above upper margin of eyes narrowly shiny with distinct punctures. Genae weakly shiny, with fine punctures 1.5–2 pw apart. Galea short, length 0.27× head length, apex narrowly rounded, surface dulled by fine tessellation, lateral margin with row of sparse, short (approx. 0.2 mm) hair. Glossa short, 0.71× length galea. Stipes shiny, length 0.49× head length. Stipital brush weak, consisting of approx. 20 pale erect hairs. Maxillary palps 1.85× galea length, ratio of length of segments 10:7:7:6:5:5. Labial palps 0.92× as long as galea, ratio of segments 10:6:4:5; basal segment arcuate, 4th segment very narrow. Antennae with F1 1.50× its apical width, F2 and F3 shorter than

Figures 16–20. Paratype male of *Andrena* (*Labergeia*) *cenizophila* n. sp. **16.** Lateral view. **17.** Dorsal view. **18.** Frontal view. **19.** Metapostnotum, rotated dorsal view. **20.** Genital capsule, dorsal view. Scale bars: 1 mm.

wide and F2 + F3 = 0.87× F1, F10 = 1.6× its basal width. Malar space linear. Mandible with subapical tooth well developed, mandibular length = 0.63 intra-mandibular span, subgenal coronet reduced to few thickened, branched hairs; basoventral flange reduced, not evident in lateral view. Labral process trapezoidal, basal width 1.7× apical width, length 0.6× basal width, apical margin weakly emarginate.

Mesosoma: Pronotum with well-defined humeral angle but margins rounded, not carinate; lateral ridge absent, medial area weakly impressed by transverse line. Mesosoma, except scutum, scutellum, metanotum and metapostnotum, dulled by dense shagreening, largely obscuring fine punctation. Scutum with anterior margin dull and nearly impunctate, becoming weakly shiny over most of disc, punctation distinct, densest laterally and sparsest postero-medially. Scutellum mainly smooth and shiny, with strong, well separated punctures, these 2–3 pw apart medially. Metanotum dulled by fine, shallow, subcontiguous punctures. Metapostnotum finely roughened, weakly contrasting with dull, lateral propodeal surfaces. Wings with three submarginal cells, submarginal 2 much shorter than submarginal 3, length submarginal 2 = 0.4× length submarginal 3. Submarginal 2 receiving first recurrent vein very near insertion of 2nd submarginal crossvein. Stigma large, length 0.7× length marginal cell. Hind tibia relatively slender, 0.19× as wide as long, 1.1× as wide as hind basitarsus. Tibial spurs unmodified. Distifemoral plate small, bare; basitibial plate ovoid, apex broadly flattened, surface obscured by short appressed pubescence. Claws with inner claw well developed. Metasoma: T1–T4 smooth and shiny; T1 with punctures very fine, sparse and widely separated on anterior half, becoming denser distally. T2–T4 with punctures stronger and denser, 1–1.5 pw apart, punctures of postgradular area finer and denser. T5 with surface dulled by strong shagreening. Pygidial plate triangular, apex rounded, surface dull. Sterna weakly shiny, slightly dulled by weak shagreening, punctation as in T2 and T3, apices of S1–S4 with narrow impunctate areas.

Vestiture: Hair white except as follows: long simple hairs arising from apical clypeal fovea translucent brown; hair of posterior 2/3 of scutum and anterior ¾ of scutellum black to dark brown; short, erect hairs of wings translucent golden brown; distifemoral tuft, short appressed hair on surface of basitibial plate hair of outer face of tibia 1 and 2, scopal hairs on posterior 2/3 of tibia 3 (long and white on anterior third), and all tarsi dark brown to black; simple hairs of discs of T1–T4 and long appressed hair of T5 and T6 (except on extreme sides) dark brown to black; appressed hair of S6 dark brown. Hair of head mainly sparse and erect, disc of clypeus bare; densest in area between antennae and fovea, hair of vertex short and erect; hair of genae sparse and erect, longest below. Hair of mesosoma mainly sparse and erect to semi-erect; hair short, erect and dense on sides of posterior 2/3 of scutum; disc of scutellum bare, hair of margins erect but sparse. Propodeal corbicula weak, upper and posterior margins delimited by relatively sparse row of long, erect, sparsely branched hairs; anterior row absent; inner surface with erect long hairs with very short branches. Trochanteral flocculus complete. Scopal hairs dense, simple, except series of branched hair on posterior margin. Discs of T1–T4 with very sparse, short, simple, inconspicuous hairs; T1 without apical fascia (weakly indicated in a few specimens); T2–T4 with complete apical fascia of appressed hair, T5 and T6 with semi-appressed, longer hair, obscuring surface. S1–S5 with long, relatively sparse, S6 with denser, long, appressed hair largely obscuring surface.

Male. Measurements ($n = 10$): Body length = 7.0 ± 0.6 mm (5.7–8.1 mm); head width = 2.4 ± 0.2 mm (1.9–2.6 mm); wind length = 6.4 ± 0.6 mm (5.1–7.1 mm); mesosomal width = 2.1 ± 0.2 mm (1.6–2.3 mm); ITS = 1.4 ± 0.1 mm (1.2–1.6 mm).

Color: As in female except clypeus white with usual mesolateral dark spots and apical margin narrowly black; antennae with scape, pedicel and FS1 black, distal segments dark reddish-brown; tibial spurs translucent light yellow brown including malus of foreleg; all tarsi and hind tibia dark reddish brown.

Structure: Head 0.73× as long as wide; facial quadrangle with length = 0.93× width; eye length = 0.81× head length; gena broad, width = 1.45× lateral eye width; eyes subparallel with upper intraocular distance = 1.05× lower intraocular distance; ocello-occipital distance = ocellar diameter, ocello-ocular distance = 2.88 ocellar diameter. Clypeus similar to female but surface smooth and shiny throughout, with very sparse, shallow punctures; paraocular areas similar to female except lateral part of frons dulled with fine shagreening and fine punctures. Sculpture of genae similar to female but shiny area along eye narrower. Galea short, length $0.33^{\times}$ head length, surface dulled by fine tessellation. Glossa short, length $0.18^{\times}$ head length. Stipes with length $0.53^{\times}$ head length. Combined length maxillary palps $1.20^{\times}$ as long as galea, ratio of length of segments 8:7:6:6:5:4. Labial palps $0.67^{\times}$ as long as galea, ratio of segments 8:4:4:4; basal segment arcuate. Antennae moderately long, extending in repose past posterior margin of tegulae; length scape = 0.33 head length; length F1= $1.18^{\times}$ its apical width; F2 shorter than wide (l = 0.55 width) and F3 slightly shorter than long (l = $0.82^{\times}$ width); length F2 + F3 = $1.15^{\times}$ length F1; length F11 = $1.3^{\times}$ basal width. Mandible moderately elongate, ML = $0.83^{\times}$ IMD. Labral process trapezoidal, basal width $1.60^{\times}$ apical width, length $0.63^{\times}$ basal width, apical margin weakly emarginate but strongly so if viewed from below, surface smooth, shiny. Mesosoma as in female but humeral angle weaker, more rounded. Distifemoral plate small; basitibial plate deltoid, apex narrowly rounded, margins raised, surface shiny and densely punctate basally. Pygidial plate absent. Wings as in female. Metasoma with tergal sculpture similar to female but punctures slightly more separated on T1–T4, discs of T5 and T6 shiny and punctate as in preceding terga. Pygidial plate absent. Exposed sterna (except S6) as in female; S6 slightly reflexed, apex broadly emarginate. S7 with medial process short, bidentate, S8 with medial process densely hairy, apex capitate and weakly emarginate. Dorsal gonocoxal lobes triangular, apices rounded; gonostyli narrow basally, distal portion expanded, subtriangular, surface concave. Penis valves slender, apices bluntly rounded.

Vestiture: Hair entirely white except translucent golden brown on inner surfaces of tarsi, apical tuft of hind femur brown, discs of T1–T4 with bands of sparse, inconspicuous dark hair; apical brush of T6 with mix of pale and golden-brown hair; hairs of S6 light brown. Hair of head sparse and erect, nowhere obscuring surface, densest laterad of antennae. Hair of mesosoma as in female except sparser on metanotum and usual sex-related differences. Hair of legs entirely pale. T1–T6 with apical fascia of appressed hair, these very weak on T1 and often interrupted medially on T1 and T2; T2 and T3 with depressed basal areas with bands of sparse erect hair (best seen in lateral view); T6 with brush of long, branched hairs. S2–S5 with apical fascia of long semi-erect hair, fascia incomplete laterally on S2 but complete on S3–S5, hair longest laterally, lateral hair curving toward midline; S6 with appressed moderate hair.

Holotype: ♀, USA: Texas, Kimble Co., Junction, 3 mi., 30.475° S, 99.781° W, 13 September 2013, leg. J. L. Neff, on flowers of *Leucophyllum frutescens*, identifier 36624. Deposited USNM.

Paratypes: 1♂, same data as holotype except identifier 36619. Deposited USNM.

11♀♀, USA: Texas, Kimble Co., Junction, 3 mi. S, 11 September 2001, leg. J. L. Neff, on *Leucophyllum frutescens*, identifiers #22492, 22493, 22494, 22495, 22496, 22497, 22498, 22499, 22501, 22502, 22503, CTMI; 5♀♀, Kimble Co., Junction, 1 mi. SE, 11 September 2001, leg. J. L. Neff, on *Leucophyllum frutescens*, identifiers #22505-22509, CTMI; 2♂♂, Kimble Co., Junction, 1 mi. SE, 11 September 2001, leg. J. L. Neff, on *Leucophyllum frutescens*, identifiers #22510-22511, CTMI; 12♀♀, USA: Texas, Kimble Co., Junction, 3 mi. S, 13 September 2013, leg. J. L. Neff, on *Leucophyllum frutescens*, identifiers #36621-36623,36625-36633, CTMI; 1♂, USA: Texas, Kimble Co., Junction, 3 mi. S, 13 September 2013, leg. J. L. Neff, on *Leucophyllum frutescens*, identifier #36620, CTMI; 1♀, Kimble Co., Junction, 1 mi. SE, 25 September 2013, leg. J. L. Neff, on *Leucophyllum frutescens*, identifier #36704, CTMI; 1♀, Kimble Co., Junction, 1 mi. SE, 4 September 2014, leg. J. L. Neff, on *Leucophyllum frutescens*, identifier #37587, CTMI; 4♂♂, Uvalde Co., Garner State Park, 1 October 2006, leg. J. L. Neff, on *Leucophyllum frutescens*, CTMI; 1♂, Val Verde Co., Dolan Falls Preserve, 15 October 1994, leg. P. Carrell, UTIC; 4♀♀, MEXICO: Coahuila, La Gloria, S. of Monclova, 24 August 1947, leg. C. D. Michener (D. Rockefeller Exp.), INH insect identifiers #836,006-836,009, INHS; 2♂♂, USA: Texas, Starr Co., Falcon State Park, 26 May 2021, leg. P. Sharp, on *Leucophyllum frutescens*, identifiers

#39766-39975, CTMI; 1♂, USA: Texas, Starr Co., Falcon State Park, 26 May 2021, leg. P. Sharp, on *Leucophyllum frutescens*, identifier 39767, WSUC; 7♀♀, USA: Texas, Starr Co., Falcon State Park, 26 May 2021, leg. P. Sharp, on *Leucophyllum frutescens*, identifiers #39765, 39768-39773, CTMI; 1♀, USA: Texas, Starr Co., Falcon State Park, 26 May 2021, leg. P. Sharp, on *Leucophyllum frutescens*, identifier #39774 and DNA extraction voucher code AV1, WSUC; 3♀♀, USA: Texas, Starr Co., Falcon State Park, 29 May 2021, leg. P. Sharp, on *Leucophyllum frutescens*, identifiers #39776-39778, CTMI; 1♀, USA: Texas, Brewster Co., Big Bend N. P., 5 km. E. of Panther Jct., 4 August 1992, leg. R. L. Minckley, on *Leucophyllum frutescens*, identifier #SM0295838, SEMC; 2♂♂, USA: Texas, Brewster Co., Big Bend N. P., 5 km. E. of Panther Jct., 4 August 1992, leg. R. L. Minckley, on *Leucophyllum frutescens*, identifiers #SM0295836-SM0295837, SEMC.

ETYMOLOGY: The name for this small, handsome bee refers to its close association with cenizo, *Leucophyllum frutescens* (Berl.), I. M. Johnst. (Scrophulariaceae), a shrub native to southwest Texas and adjacent Mexico.

DISCUSSION

Phylogeny of *Labergeia*

Phylogenomic analysis of 1,175 UCE loci using maximum likelihood recovered the newly described *A. cenizophila* as most closely related to *A. nahua* (Figs. 2–4; Bossert *et al.*, 2024a). This finding is supported by morphological similarities between the two species in the female sex, as well as different data permutations of the original sequence matrix. However, the support values for the node involving *A. cenizophila* and *A. nahua* reflect strong but not maximum support— 83.8 and 99 for SH-like approximate likelihood ratio tests and ultrafast bootstrap approximations, respectively. While the bootstrap support can be considered very strong, the more conservative SH-like likelihood ratio test indicates some degree of conflicting signal in the underlying genomic data. Possible reasons for this finding are challenging to establish because they could include true topological discordance among the underlying gene loci (Bossert *et al.*, 2017; Degnan & Salter, 2005; Maddison, 1997) or methodological shortfalls (*e.g.*, Kolaczkowski & Thornton, 2004; Roure & Philippe, 2011). Further, limited sequencing success can lead to uncertain estimates using concatenated UCE sequence data and increase gene tree estimation error (Bossert *et al.*, 2021). UCE extraction of the whole genome assembly of *A. cenizophila* recovered 2,321 out of the targeted 2,545 UCE loci (~91.2%) and can thus be considered good. Conversely, the UCE capture success was lower for *A. nahua* at 1,171 UCEs (~46%), indicating that the sequence representation for this species is lower in the final matrix, potentially weakening phylogenetic signal. Despite this, a close relationship of *A. nahua* to the subgenus *Dactylandrena* is maximally supported here and in previous work that included these samples (Pisanty *et al.*, 2022), and can thus be considered very certain. Similarly, we deem it very likely that *A. cenizophila* is indeed most closely related to *A. nahua* and that improved sequence data for *A. nahua* may resolve statistical uncertainty in the future. Considering this, we deemed it most appropriate to broaden the diagnosis for the subgenus *Labergeia* to accommodate both species, *A. nahua* and *A. cenizophila*.

Andrena cenizophila is part of a lineage of mining bees with restricted distributions in western North America and Central America. All known records of the putative sister species *A. nahua* are restricted to central Mexico, and *A. cenizophila* is known from south-central Texas and Northern Mexico (Fig. 21). All four species of the closely related *Dactylandrena*, as currently circumscribed, are species of western North America and thus occur in relatively close spatial proximity. An interesting biogeographic pattern emerges when considering the sister lineage to *Dactylandrena* + *Labergeia* which is the Middle Eastern endemic subgenus *Troandrena*, with all three species known to occur only in the Middle East and adjacent countries. These two lineages are biogeographically disjunct, yet occur in climatically similar habitats characterized by xeric, seasonally hot and dry environments. Highly similar biogeographic patterns are known from other lineages of bees, such as for the Nearctic *Dieunomia* Cockerell and the Middle Eastern *Clavinomia* Warncke (Bossert, 2017; Bossert *et al.*, 2024b), yet mechanisms, dispersal routes or extinction patterns that could explain this pattern are unclear.

Figure 21. Presently known localities of the two species of *Andrena* subgenus *Labergeia*.

Andrena cenizophila as an oligolege of *Leucophyllum frutescens*

Andrena cenizophila is currently known from only a few sites on the southwestern edge of the Edwards Plateau of south-central Texas, along the Colorado River from the Big Bend region to the western edge of the Lower Valley, and one locality in central Coahuila, Mexico (Fig. 21). All these regions are characterized by semi-arid scrub vegetation. Interestingly, all available floral record suggests *A. cenizophila* is oligolectic on *Leucophyllum frutescens* (Berl.), I. M. Johnst. (Scrophulariaceae), a shrub known as cenizo, purple sage, Texas ranger, Texas sage or barometer bush (Hendrickson & Flyr, 1985). It is one of the official state shrubs of Texas (Texas House Concurrent Resolution No. 71, 2005). This plant species is often abundant on limestone soils in the southern half of Texas, sometimes forming large monospecific stands, and is widespread in the drier areas of northeast Mexico (Hendrickson & Flyr, 1985), so *A. cenizophila* is expected to be found at more sites across the range of *L. frutescens*. *Leucophyllum* currently consists of 17 species, occurring in arid and semi-arid habitats from the southwest US to Oaxaca (Hendrickson & Flyr, 1985; POWO, 2025). The range of *A. cenizophila* in Mexico may be considerably more extensive than currently known. Beyond its native range, *L. frutescens* is widely planted as an ornamental.

Our analysis of 12 scopal pollen loads of *A. cenizophila* found that all consisted of 100% *Leucophyllum* pollen. Loads from Texas specimens consisted only of *L. frutescens* pollen as that was the only *Leucophyllum* species occurring at those sites but two loads from Mexico could be from another species such as *L. minus* A. Gray in Torr., which co-occurs with *L. frutescens* in Coahuila and has very similar pollen (Hendrickson & Flyr, 1985; Niezgoda & Tomb, 1975). This strongly suggests that *A. cenizophila* is the only North American *Andrena* oligolectic on a member of the Scrophulariaceae as currently circumscribed. *Andrena cenizophila* has been collected only on flowers of *L. frutescens* but it is not known if it collects pollen from any other *Leucophyllum* species. Dietary restriction to the Scrophulariaceae is rare within *Andrena*. In the Old World, the only *Andrena* Scrophulariaceae specialist is the unrelated *Andrena* (*Euandrena*) *scrophulariae* Wood, 2020, a Middle Eastern species and apparent oligolege of *Scrophularia* (Wood *et al*., 2020).

Despite its abundance, cenizo is at first glance an odd host for an oligolectic bee because of its distinctive floral phenology. *Leucophyllum frutescens* is a mass bloomer, with plants commonly covered with hundreds of lavender-colored flowers about 10–14 days after significant warm season rains. This typically happens after late summer or fall rains but under certain conditions may occur in May or earlier (Hendrickson & Flyr, 1985). Predictability of bloom is a good trait for the host of an oligolectic bee but as the mass bloom usually lasts only four to five days, it appears exceedingly short to sustain significant populations of oligolectic bees, particularly given the low cell provisioning rates typical of *Andrena*, which can be less than one cell per day (Giovanetti & Lasso, 2005). *Andrena cenizophila* may be a faster provisioner, however, we have no observational information on this. Low level flowering may continue among scattered individuals for several weeks after the initial massive bloom that may be sufficient to sustain populations of *A. cenizophila* if it proves to be strictly oligolectic. Alternatively, since cenizo may have multiple short periods of mass bloom in any given year, female *A. cenizophila* may be able to wait out the down periods and just exploit the periods of peak bloom, although to date there is no direct evidence of such behavior.

The interior dimensions of the rose-lavender to rose-pink colored, solitary, five-lobed, zygomorphic, campanulate corollas of *Leucophyllum frutescens* are approximately 8 mm wide at the mouth, narrowing to 5 mm at the base, and are 12 mm long. Female *A. cenizophila* can easily fit within the corolla tube while they lap nectar or harvest pollen from the four nototribic, dorsifixed anthers (Figs. 6–8). The stigma of an *L. frutescens* flower is slightly exserted, so smaller bees like *A. cenizophila* do not consistently contact it when entering or exiting the flower. This may render *A. cenizophila* a less than perfect pollinator on a per-visit basis, but its local abundance, frequency of visitation, and floral constancy probably still bring *A. cenizophila* to carry out a significant amount of cenizo pollination when present. Besides *A. cenizophila, L. frutescens* flowers are visited, and presumably pollinated, by a variety of generalist bees such as *Agapostemon texanus* Cresson, *Apis mellifera* Linnaeus, *Bombus sonorus* Say, *Exomalopsis solani* Cockerell, *Megachile sidalceae* Cockerell, and *Melissodes tristis* Cockerell (JLN, pers. obs.).

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