



Navarretia crystallina and *N. miwukensis* (Polemoniaceae): new species endemic to California with affinity for soils derived from pyroclastic deposits

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Abstract

Two species endemic to California in the western United States, *Navarretia crystallina* and *N. miwukensis*, are here described. Both species occur on soils derived from pyroclastic flows. *N. crystallina* is distributed more widely, generally at higher elevations, and occurs predominantly to the north and east of *N. miwukensis*. Though similar in habit to *N. divaricata* and *N. prolifera*, *N. crystallina* and *N. miwukensis* can be distinguished consistently from both of these species by inflorescence structure, bract lobing, and flower size, and from each other by bract and calyx lobe shape, inflorescence indumentum, and stamen insertion. The species are also distinguishable by DNA sequences.

Key words: edaphic endemism, identification key, taxonomy

Introduction

Narrow endemism and habitat specialization is a repeated theme in *Navarretia* Ruiz & Pavón (1794: 20), with some species showing strong preferences for sandy soils, others to serpentine, and still others to varying degrees of seasonal inundation ranging from moist depressions to vernal pools. Though less well characterized, the distribution of a few *Navarretia* coincide with soils that are volcanic in origin or dominated by volcanic landforms. Here, we describe two new species of *Navarretia* collected on soils derived from pyroclastic flows.

At a site in the northern sub-region of the Sierra Nevada California Floristic province, we collected material assignable to *Navarretia divaricata* Greene (1887: 136) subsp. *divaricata*, *N. divaricata* subsp. *vividior* (Jepson & V.L. Bailey in Jepson 1943: 156) Mason (1951: 449), and a third taxon similar to *Navarretia divaricata* that, with direct comparison in the field, was readily distinguished from both recognized subspecies (*Johnson 13-216*, *13-218*, *13-219*, BRY). In examining these plants, we ascertained that this new material matched a collection made several years earlier from the central Sierra Nevada subregion that had been determined provisionally as *Navarretia divaricata* (*Gowen 739*, JEPS). En route to revisit this site, a second novel entity was collected (*Gowen 1230*, BRY, JEPS). Following our approach to species delimitation under the unified species concept (de Queiroz 1998, 2007), we initiated additional field work, perusal of herbarium specimens, and both morphological and molecular characterization of sampled material to circumscribe evolutionary independent metapopulation lineages. Based on our study, we here recognize two new species, *N. crystallina* and *N. miwukensis*. With divaricate branching, these species share the general habit of *N. divaricata*, *N. prolifera* Greene (1887: 135) and, to a lesser extent, *N. filicaulis* (Torr. ex Gray 1870: 270) Greene (1887: 134), but are readily distinguished from these species, and each other, morphologically and via comparative DNA sequencing.

Materials and methods

Focusing our study on species delimitation rather than phylogenetic reconstruction, we compared DNA sequences and morphology between and among the putative new species with the described species they would most likely be

confused with, as determined from our experience with the genus and annotations on herbarium specimens assignable to the putative new species.

Using field collected material, we analyzed DNA sequence data from multiple populations representing the geographic ranges of *Navarretia divaricata*, *N. filicaulis*, *N. prolifera*, and the putative new species. We isolated DNA and PCR amplified the nuclear ribosomal ITS1, 5.8s, and ITS2 region (White *et al.* 1990, Porter 1996), the plastid 5' *trnK* intron and 5' portion of *matK* (Johnson & Solits 1995, Johnson & Johnson 2006), *trnL-trnL-trnF* intergenic spacer and intron (Taberlet *et al.* 1991), *trnS-trnG* intergenic spacer (Hamilton 1999), and *rpl16* regions (Small *et al.* 1998). Our methods for amplification and sequencing follow Johnson *et al.* (2008), and we deposited the DNA sequences in Genbank (accession numbers KX017843–KX017976; HQ116860, HQ116865, HQ116961, HQ116966, HQ117005, HQ117011, HQ117046, HQ117051, HQ117085, HQ117090). We aligned sequences by eye using AliView (Larsson 2014) and coded indels as present or absent using simple indel coding (Simmons & Ochoterena 2000) as implemented in SeqState (Muller 2005). We conducted unweighted parsimony analyses using PAUP* 4.0b10 (Swofford 2003) with 10,000 random addition replications, collapsing branches with minimum length of zero, and assessing support with 100,000 bootstrap replications using full heuristic searches and simple stepwise addition. We examined unrooted trees in the context of exclusivity (Brower 1999), where all members of a species form a contiguous group on an unrooted network separated from other groups by a single branch along which fixed character-state changes can be inferred.

We examined morphology under the framework of population aggregate analysis/specimen aggregate analysis (Davis & Nixon 1992, Snow *et al.* 2003) using specimens from field work and herbarium sheets from the following herbaria: AHUC, BRY, CAS, CHSC, JEPS, RSA, and UC. We made qualitative and quantitative comparisons from a minimum of two, to often over 10 individuals per population from five to 18 populations per species. We used digital calipers for larger features and measured smaller features from digital images taken with an Olympus SZX-12 dissecting microscope using MicroSuite Five Basic Edition software (Olympus Soft Imaging Solutions Corp.).

Results

The aligned ITS sequence matrix consisted of 630 nucleotide and seven coded indel characters, of which 39 were parsimony informative. Parsimony analysis of this matrix recovered a single topology of 54 steps (Fig. 1A; CI = 0.93; RI = 0.98). The concatenated cpDNA matrix consisted of 4379 nucleotide and 19 coded indel characters, of which 72 are parsimony informative. Parsimony analysis of this matrix recovered four topologies of 108 steps (CI = 0.95; RI = 0.98). With both datasets, *Navarretia crystallina* and *N. miwukensis* are reciprocally exclusive, and are united by a branch exclusive of the other taxa. Disagreement among topologies in the cpDNA dataset concerns relationships among populations of *N. filicaulis*, and the placement of *N. divaricata* subsp. *vividior* either in sharing an exclusive branch with *N. crystallina* and *N. miwukensis*, or an exclusive branch with *N. filicaulis*. *N. divaricata* subsp. *vividior* does not form an exclusive group with *N. divaricata* subsp. *divaricata* in the topologies recovered from either data set.

Examination of plant specimens revealed several features useful for identification and species delimitation that separate the new species from each other and from other *Navarretia*. We elaborate these features in the discussion, taxonomic treatment, and identification key presented below.

Discussion

Nuclear rDNA and ITS sequences individually provide unequivocal support for the recognition of *Navarretia crystallina* and *N. miwukensis* as distinct species. Analyses of these data with a broader sampling of species, and preliminary analyses with several nuclear DNA introns, not presented here, indicate these taxa are sister to each other, but with as yet imprecise sister relationship to other species. The distinctiveness of these taxa is well supported by character reconstructions on their exclusive branches relative to the other recognized taxa included in these analyses, and by bootstrap support of these data. The apparent non-monophyly of *N. divaricata* is being examined in depth and is not discussed further here.

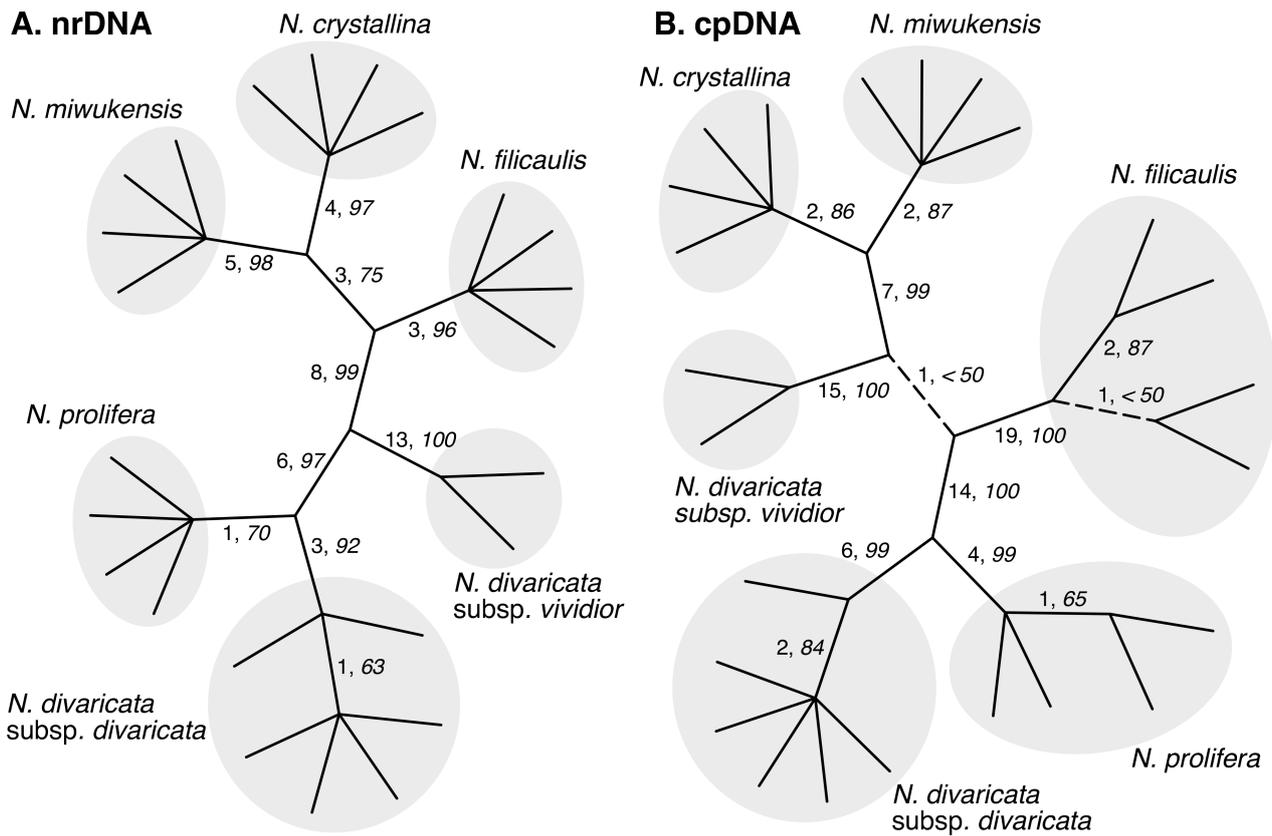


FIGURE 1. Representative most parsimonious, unrooted trees inferred from analysis of DNA sequence data. Total character change (base substitutions and indels) are reconstructed along interior branches, followed by bootstrap support values in italics. A. Single topology inferred from nrDNA ITS sequences. B. One of four topologies inferred from concatenated cpDNA sequences. Branches not found in all four topologies are represented by dashed lines.

TABLE 1. Comparison of key morphological features among *Navarretia crystallina*, *N. miwukensis*, *N. divaricata*, and *N. prolifera*.

	<i>N. crystallina</i>	<i>N. miwukensis</i>	<i>N. divaricata</i>	<i>N. prolifera</i>
Anther presentation (longest)	± at orifice,	± at orifice	± at orifice	Long exserted
Stigma presentation	Included in throat	Included in throat	Included in throat	Long exserted
Inflorescence indumentum	Abaxial bract rachis densely hairy; sinuses of calyx and bract lobes obscured	Abaxial bract rachis somewhat hairy and prominently viscid glandular; sinuses of calyx and bract lobes not obscured	Abaxial bract rachis somewhat hairy to glandular; sinuses of calyx and bract lobes not obscured	Abaxial bract rachis densely hairy; sinuses of calyx and bract lobes obscured or not
Inflorescence substructure	Internal branching absent, bracts and calyces ± on common receptacle	Internal branching absent, bracts and calyces ± on common receptacle	Internal branching present, bracts and calyces aggregated into sub-clusters	Internal branching present, bracts and calyces aggregated into sub-clusters
Bract and calyx lobe shape	Acute	Acuminate	Linear to acute	Acute
Short, abaxially diverging lobes flanking the central bract lobe	Uncommon	Not observed	Common	Common

Morphologically, *N. crystallina* and *N. miwukensis* are readily distinguished from other species in side-by-side comparisons (Table 1), yet have escaped prior species recognition even though their distinctive features have either been noted or puzzled over in the process of specimen determination. Considering flowers are small (5–7 mm long), general habit, and available taxonomic keys, both species have been understandably mistaken for *N. divaricata*, while at the same time, the densely hairy and spherical heads of *N. crystallina*, in absence of flowers, is markedly like *N. prolifera*. With higher density of stipitate glands on the bracts and calyces of *N. miwukensis*, combined with the broad base and acuminate tips of its bract and calyx lobes, mistaking *N. miwukensis* for *N. filicaulis* is also understandable if someone was unfamiliar with the latter taxon and intent on applying an available name.

The earliest collection of *N. crystallina* we viewed was from Placer County, by Nordstrom in 1934 as *N. divaricata* and later annotated to ‘approaching *N. prolifera*’ (all specimens mentioned here are detailed in the Representative Specimens sections below). Other early records of *N. crystallina* include Quick’s collections from Tuolumne County in 1938 and 1942, which were similarly determined as *N. divaricata* and then later annotated to *N. prolifera*. Eastwood and Howell’s collection from Calaveras County in 1940 was determined as *N. prolifera* and later annotated to *N. divaricata* subsp. *vividior*. Mason’s 1941 collection from Tuolumne County was simply labeled *Navarretia*; though later annotated to *N. divaricata* (by Crampton), it is reasonably likely that Mason recognized the distinctiveness of his collection given that he also collected plants he determined as *Navarretia divaricata* subsp. *divaricata* and *N. divaricata* subsp. *vividior* nearby a month later. Robbins also made an early collection of this taxon, in 1944, from El Dorado County that he determined as *N. divaricata*, though he noted on the label ‘woolly bracts not typical’.

The earliest collection of *N. miwukensis* we viewed was collected by Davy on the hills of Calaveras County in 1895, and determined as *N. divaricata*. Collections from Tuolumne County in 1940 by Hoover and in 1944 by Alexander and Kellogg were likewise determined as *N. divaricata*, whereas one collection from the same area by Wiggins in 1971 was determined initially as *N. filicaulis* (later annotated to *N. divaricata*) and a second, made three days later, was determined as *N. divaricata* but later annotated to *N. prolifera* subsp. *prolifera*.

Early in our comparative study, we noticed that *Navarretia divaricata* and *N. prolifera* often have abaxially diverging lobes flanking one or both sides of the central lobe of the inflorescence bracts that are shorter than the next pair of in-plane lobes (see Figs. 3992 and 3993 in Mason 1951), whereas such out-of-plane lobes are lacking in *N. filicaulis* (Fig. 3996 in Mason 1951), *N. miwukensis*, and usually lacking, but not always, in *N. crystallina*. The frequency of such out of plane lobes is low in *N. crystallina*, particularly in the northern portion of its range. Inflorescence heads of *N. divaricata* and *N. prolifera* can also generally be dissected into two or more smaller bracteate flower clusters united by short peduncles, whereas the heads of *N. miwukensis*, *N. crystallina*, and *N. filicaulis* cannot be so readily separated; instead, bracts are removed one-by-one, with one or two flowers per bract, all sharing a more-or-less common receptacle.

Within their inflorescence heads, *Navarretia crystallina* and *N. miwukensis* both have short stipitate glands as well as much longer uniserrate hairs. In the densely hairy heads of *N. crystallina*, the glands are smaller and more obscure. In contrast, the glands are larger and more prominent in *N. miwukensis*, and the longer hairs comparatively less dense; it is not uncommon for the sinuses between bract and calyx lobes to be obscured by the dense hairs in *N. crystallina*, yet visible in *N. miwukensis*. Stamens in *N. miwukensis* are usually inserted more strongly unequal, with the difference between the lowest and highest insertion points within a single flower ranging from ca. 0.6–1.0 mm, compared to 0.11–0.5 mm in *N. crystallina*. Insertion distance from the sinus is also greater in *N. miwukensis*, ranging from 0.35–1.8 mm compared to 0.3–0.8 in *N. crystallina*. Calyx and bract lobes also vary between these species, with the lobes long acute in *N. crystallina* versus acuminate with a broad base in *N. miwukensis*. In both cases, these lobes are relatively broad (and broader in *N. miwukensis*) compared to *N. divaricata* (Table 1).

No mixed populations of *N. crystallina* with *N. miwukensis* have yet been identified, though the two species grow within 1.5 miles of each other near Lyons Dam Reservoir off highway 108 in Tuolumne County. We have not observed *N. miwukensis* further east along this highway, or *N. crystallina* further west. Though their elevation ranges overlap, *N. crystallina* prefers higher elevations than *N. miwukensis*. *Navarretia divaricata* frequently occurs with *N. crystallina*, and *N. prolifera* also co-occurs in some populations. We have also found *N. divaricata* growing in the vicinity of *N. miwukensis*. Sequencing of several individuals from syntopic populations and populations near the interface between *N. crystallina* and *N. miwukensis* reveals no evidence of interbreeding among any of these congeners.

Both *N. crystallina* and *N. miwukensis* occur on rubble derived from pyroclastic mud flows (Fig. 2), particularly when the deposits are open, sparsely vegetated, and having a south-facing aspect to them. Labeled ‘Tv^p’ on the 2010 Geologic Map of California (<http://www.quake.ca.gov/gmaps/GMC/stategeologicmap.html>), these deposits are common in the Sierra Nevada mountains and we used the location of such deposits to successfully find new populations of these species. Nevertheless, further study is needed to better understand the relationship between these species, pyroclastic deposits, and other abiotic factors that may influence distribution. For example, pyroclastic flows are

common north of Interstate 80, yet we did not find any previous collections from our survey of herbarium specimens or populations in our field collecting north of Interstate 80 despite finding other species that co-occurred with the new species further to the south.

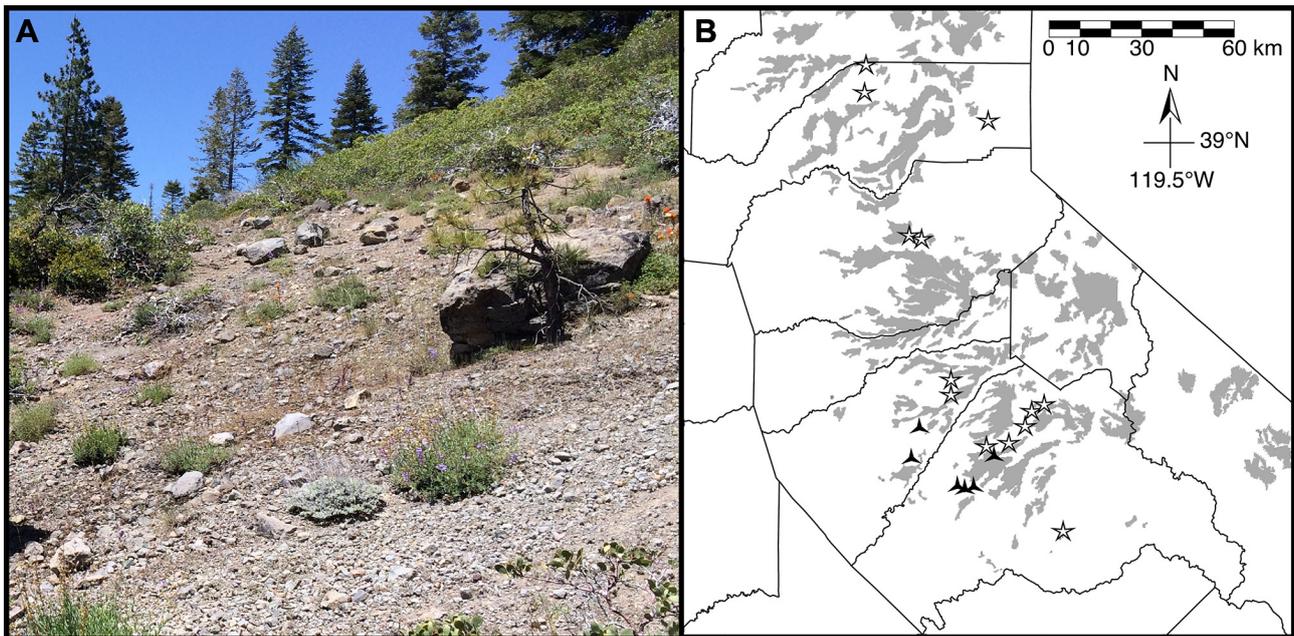


FIGURE 2. A. Pyroclastic rubble on a south facing slope in Placer County, California, where *N. crystallina* was collected in 2014 (Johnson *et al.* 14-030, BRY; photograph by L. A. Johnson). B. Map of a portion of California, U.S.A., with county borders, showing the distribution of *Navarretia crystallina* (white stars with five points) and *N. miwukensis* (black stars with three points). Tertiary pyroclastic deposits are shaded gray (derived from 2010 Geologic Map of California; <http://www.quake.ca.gov/gmaps/GMC/stategeologicmap.html>).

Systematic treatment

Navarretia crystallina L.A.Johnson & D.Gowen, *sp. nov.* (Fig. 3)

A species similar to *Navarretia divaricata* and *N. prolifera* in habit and branching; from *N. prolifera*, it differs by having smaller flowers with anthers near the orifice and style included; from *N. divaricata* it differs by the inflorescence being densely long hairy, somewhat larger corollas with longer filaments, and usually having the veins in the lobes and throat colored pink to red; from both species it differs in having tight, spherical, inflorescence heads not readily disarticulated into smaller cymose flower clusters.

TYPE:—U.S.A. California: Calaveras County, Along Hwy 4 at 5000 ft elevation marker and marquee for east end of Big Trees State Park; north side of road, 38.28769° N 120.30037° W, 4 June 2014, L. A. Johnson, R. L. Johnson, Brabazon, & Goates 14-063 (holotype BRY!; isotypes JEPS! RSA!).

Taprooted annuals commonly 3–12(–18) cm tall and 2–15(–30) cm wide. Primary stem erect, generally exceeded in length by secondary stems, with tertiary, and quaternary stems occasionally present; branches ascending to spreading and ± leafless, except for leaves subtending higher order branches; primary stem (terminating in a head) (0)2–5(8) cm, secondary stems (branches) 1–10 in number, 0.1–6.5 cm, tertiary branches 0.1–4.5 cm, quaternary branches 0.1–2 cm; tertiary and quaternary branches usually arising directly below or within 1 cm of an inflorescence head; stem and branches reddish-brown, sparsely minutely stipitate-glandular puberulent, the trichomes generally less than 0.25 mm long. Cotyledons two, linear, entire, united at base. Leaves stipitate-glandular puberulent with trichome density and length greatest on the proximal, adaxial surface; leaves at the lowermost 1–2(–3) nodes opposite, linear-filiform, and widened at the point of stem attachment, the proximal nodes often congested with overlapping leaf bases. More distal leaves alternate, entire, or more commonly with 1–3 pairs of linear lobes 1–5(–7) mm long attached along the proximal 3(–5) mm of the leaf, with an elongated, linear terminal segment 1–3 cm long (leaves with lobes along the proximal 1.2 cm of the leaf uncommon; these with lobes alternating, rather than oppositely paired). Inflorescences densely white hairy, obscurely glandular, not viscid. Inflorescence bracts: outermost 1–2 similar to upper leaves; bracts grade centripetally

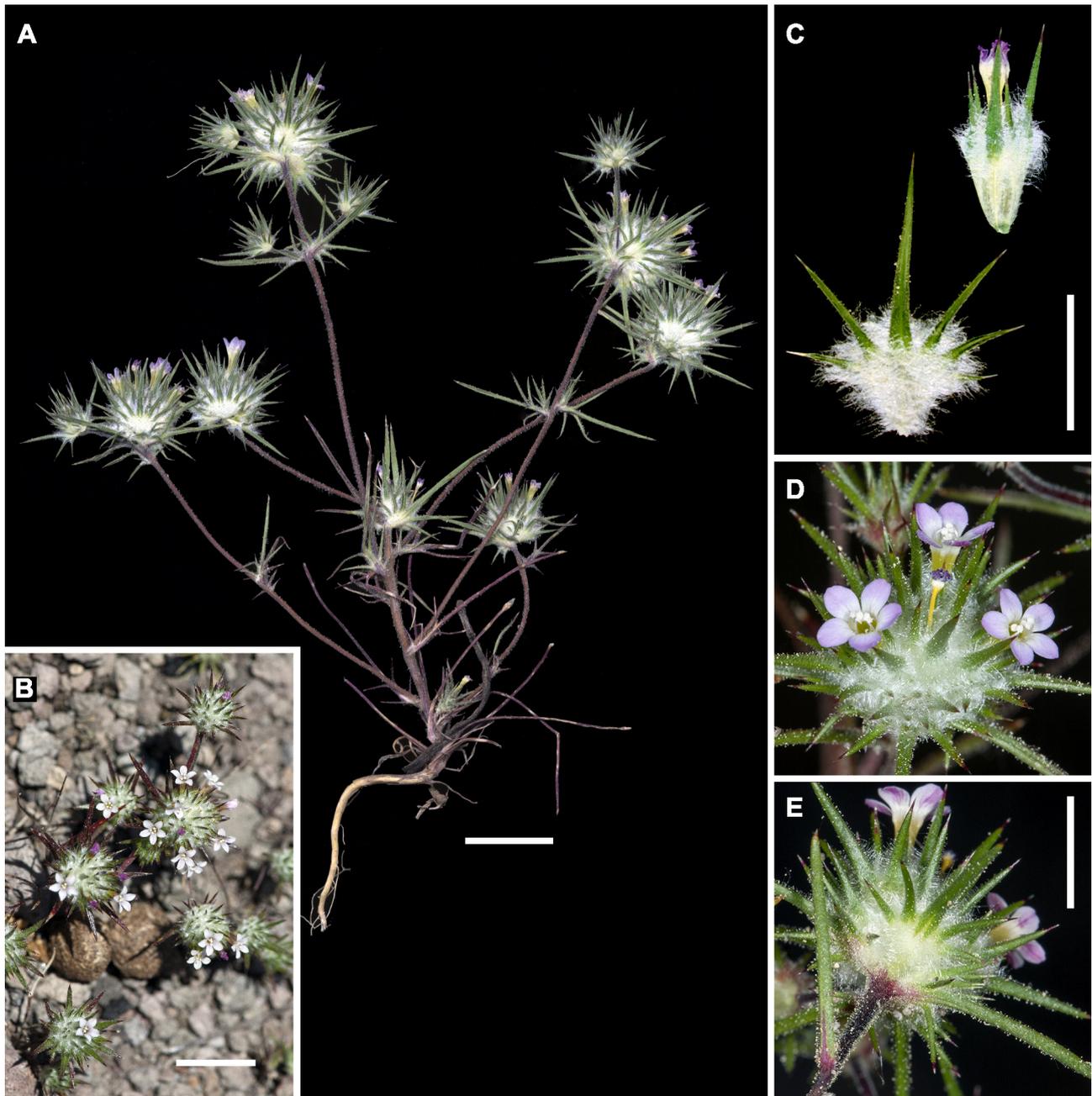


FIGURE 3. *Navarretia crystallina*. A. Pressed specimen showing plant habit, scale bar = 1 cm (Johnson *et al.* 14-100, BRY). B. Flowering individual in the field, scale bar = 1 cm (Johnson *et al.* 14-030, BRY). C. Pressed flower and inflorescence bract showing trichomes and lobe shape, scale bar = 5 mm (Johnson *et al.* 14-098, BRY). D–E. Inflorescence heads showing fresh flowers, anther presentation, and bracts, scale bar = 5 mm (Johnson *et al.* 14-102, BRY). All photographs by L. A. Johnson.

to having a wide, convex-clasping achlorophyllous and membranous-margined rachis, densely long-shaggy pubescent along the margin, adaxial surface of the bract lobes near their attachment with the rachis, and somewhat on the abaxial rachis base; bracts bear ~ 3 pairs of chlorophyllous lateral lobes co-planer with the central, elongate terminal lobe (short, abaxially diverging lobes on either side of the terminal lobe occasionally present); lobes entire, sparsely short-stipitate glandular to almost glabrous; inner bract gradation continues with the rachis widening further, the abaxial rachis surface densely covered in shaggy trichomes, and the lateral bract lobes, reduced to 2 pairs or even 1 pair, departing from the distal rachis edge; bract lobes long tapering acute, commonly becoming reddish brown with age and may gently recurve. Inflorescences, 1–18(–50) in number, head like, ± spherical, (5–)10(–13) mm in diameter exclusive of bract tips; cymes, composed of a bract and 1 or 2 flowers, subsessile and tightly packed in heads; flowers generally fewer than 20 per head. Flowers: calyces mostly 5.5–8.75 mm long, tube ~ 3mm, costae strongly to somewhat unequal with typically two lobes longer than the other three, lobes entire, long tapering acute, costae narrowing proximally, narrower at base than

the intercostal membrane which is v-shaped at sinus, obscured by dense shaggy hairs on the abaxial calyx tube and adaxial lobes at the tube-lobe junction; corolla narrowly funnel form, glabrous, 5.0–7.0 mm long, lobes 0.9–1.2(–1.4) mm long × 0.6–1.0 mm wide, tube and lower throat yellow, upper throat and lobes pink to white, veins in throat often darkened, tube base expanding and adhering to the fruit apex. Stamen filaments 0.4–0.95(–1.3) mm long, inserted unequally to subequally 0.3–0.8(–1.1) mm below corolla sinuses, included in throat to exerted less than half the length of the corolla lobes; pollen white, apertures pantoporate, acolpate; sexine seimitectate, reticulate, heterobrochate. Ovary three-chambered, style 3–4.1 mm long, stigmatic lobes ~ 0.3 mm long, included in corolla throat. Capsule ~ 2.5 mm long, dehiscing circumcissally around the base with valves splitting upward, leaving capsule base attached to receptacle inside calyx. Seeds generally 2–4 per locule, medium brown (hue 5YR, value 3, chroma 3), ovoid-angular, ca. 1.1–1.35 mm long × 0.6–0.8 mm wide, mucilaginous when wet.

Habitat, Distribution, and Phenology:—*Navarretia crystallina* occurs in open, sparsely vegetated pyroclastic derived soils often with a gently sloping terrain. This taxon is presently known from Placer, El Dorado, Calaveras, and Tuolumne counties, California at elevations from 1350–2200 meters, and blooms primarily in June (late May–early July).

Etymology:—This specific epithet, referring in Latin to ice or rock-crystal, references the first collection of this plant by the primary author along Ice House Canyon road, located some 20 km to the west of the Crystal Range of the Sierra Nevada mountains.

Additional specimens examined:—U.S.A. California: Calaveras County, near Big Trees, 19 June 1940, *Eastwood & Howell 8586* (CAS!); 3.5 miles west of Camp Connell on Summit Level Road, 1585 m, 8 June 1987, *Breedlove, Bourell, & Patterson 66147* (CAS!); El Dorado County, 2–3 miles northeast of Riverton, along Ice House Road, 4000 ft, 11 June 1944, *Robbins 1672* (Jeps! UC!); Along abandoned road heading west and upslope from Ice House Road, 6.4 miles from junction with Hwy 50, just north of Peavine Ridge Road, 38.79754°N, 124.0287°W, 1596 m, 30 May 2013, *Johnson 13-216* (BRY!, JEPS!, RSA!); Ridgetop and south-facing slope overlooking Peavine Ridge Road at northwest corner of junction between Icehouse Road and Peavine Ridge Road, 6.4 miles along Icehouse Road from junction with Hwy 50, 38.79726°N, 120.40299°W, 1596 m, 26 June 2013 *Johnson, Johnson, & Yankee 13-246* (BRY!, JEPS!, RSA!); 0.3–0.4 miles from Icehouse road along a dirt 4WD road located southeast of Icehouse Road, 0.3 miles northeast of junction with Peavine Ridge Road, 38.79545°N, 120.39105°W, 1584 m, 26 June 2013, *Johnson, Johnson, & Yankee 13-252* (BRY!); North side of Granite Springs Road on exposed volcanic gravelly ridge, about 0.5–0.6 miles from Icehouse Road, 38.80076°N, 120.38674°W, 1670 m, 26 June 2013, *Johnson, Johnson, & Yankee 13-264* (BRY!); Northeast of Riverton and Hwy 50 on Peavine Ridge Road, about 0.5 mile west from its junction with Ice House Road, 38°47.693'N, 120°24.713'W, 5266 ft, 20 June 2013, *Gowen 1215* (BRY! JEPS!); Northeast of Riverton and Hwy 50 on Peavine Ridge Road about 2.7 miles from its junction with Ice House Road, 38°48.165'N, 120°26.63'W, 5162 ft, 21 June 2013, *Gowen 1227* (BRY! JEPS!); Placer County, 0.4 miles west northwest of Mammoth Springs, Tahoe Natl. Forest, Colfax Quad., 5600 ft, 21 June 1934, *Nordstrom 150* (LA, JEPS! UC!); 1.5 miles east of Emigrant Gap, along U.S. Highway 40, on slopes above road cut, 5400 ft, 21 July 1953, *Crampton 1516* (BRY! AHUC! mixed collection with *N. divaricata*); Martis Valley, ca. 5 miles southeast of Truckee, west of 267, 39.2873°N, 120.1068°W, 6200 ft, 12 June 2005, *Matson 1271* (JEPS!); South facing slope of pyroclastic flow overlooking the North Fork of the American River, just off Sawtooth Ridge Road ca. 1.1 mile west of Dawson Spring, 39.21789°N, 120.62223°W, 1671 m, 3 June 2014, *Johnson et al. 14-030* (BRY! JEPS! RSA!); Tuolumne County, East end of North Mountain, Yosemite National Park, North mountain ridge mud flow, 10 Jun 1941, *Mason 12484* (UC!); West of Strawberry growing in open area near trailer dump station, 29 May 2007, *Gowen 739* (JEPS!); Along Hwy 108 just west of Strawberry in a large open area east of the road to the trailer dump station, 38°11.094'N, 120°0.708'W, 28 June 2013, *Gowen 1232* (BRY!, JEPS!); Strawberry Ridge, 26 June 1938, *Quick s.n.* (CAS 280487!); Along Hwy 108 between Cold Springs and Longbarn, near FS road at BM 5565, 38°8.864'N, 120°4.876'W, 28 June 2013, *Gowen 1234* (BRY! JEPS!); North side of Hwy 108 at junction with road 3N39 on lava cap, 38.14766°N, 120.0816°W, 1672 m, 5 June 2014, *Johnson et al. 14-100* (BRY! JEPS! RSA!); Just south of Hwy 108 at junction with forest service road 4N12, in vicinity of forest service signage, 38.20996°N, 120.01438°W, 1788 m, 5 June 2014, *Johnson et al. 14-102* (BRY!); East of the Punch Bowl, north side of road 4N12 ca. 5.4 miles east northeast from junction with Hwy 108, 38.23862°N, 119.9496°W, 2178 m, 5 June 2014, *Johnson et al. 14-107* (BRY! JEPS!); Lava cap southwest of Bert Reed's Meadow, 27 June 1942, *Quick 42-26* (CAS!); Along road 4N39, 0.3 km northeast of Strawberry Peak and 1.3 km southwest of its junction with Hwy 108, 38°11'56"N, 120°01'43"W, 1806 m, 27 June 2010, *Janeway & Castro 10053* (CHSC!); Just below the west-facing top of the ridge on southeast side of the head of Sugarpine Creek (Stoddard Sprint) 200 meters southeast of Hwy 108, 38°07'46"N, 120°05'57"W, 1649 m, 28 June 2010, *Janeway & Castro 10069* (CHSC!); East of Long Barn and Hwy 108, on 3N07 about 1.8 miles south of its junction with 3N01, 38.05885°N, 120.11033°W, 5471 ft, 3 June 2014, *Gowen 1261* (BRY! JEPS!); North of Hwy 108 about 1.5 miles down Lyons Dam Road, 38.09145°N, 120.1619°W,

4572 ft, 4 June 2014, *Gowen 1265* (BRY! JEPS!); Same location as *Gowen 1265*, 5 June 2014, *Johnson et al. 14-098* (BRY!); Northeastern border of Calaveras Big Trees State Park, along Forest road 5N78 near junction with Forest Road 5N03, 38.26798°N, 120.24987°W, 4900 ft, 22 June 2005, *Taylor 19538* (CHSC!).

Notes:—Fresh plants of *Navarretia crystallina* are faintly skunky in odor, with the scent more pronounced when concentrated, for example, by placing plants in a plastic bag. *N. divaricata* subsp. *divaricata*, in contrast, has no such odor. The pollen sexine sculpturing in *N. crystallina* is shared with *N. miwukensis* and many other species, including *N. divaricata* and *N. prolifera* subsp. *prolifera*.

Navarretia miwukensis D.Gowen & L.A.Johnson, *sp. nov.* (Fig. 4)

A species similar to *Navarretia crystallina*, but distinguished by being less dense with respect to inflorescence trichomes but bearing more conspicuous viscid, short-stipitate glands in the inflorescence, in having bract and calyx lobes with wide, convex bases that taper concavely (i.e., acuminate) versus evenly tapered, long-acute lobes in *N. crystallina*, and in having greater inequality in the insertion of stamens.

TYPE:—U.S.A. California: Tuolumne County, On pyroclastic rubble and soil above road cut on north side of Hwy 108 just west of hairpin in Lava Drive, 38.02665°N, 120.23697°W, 1159 m, 5 June 2014, *L. A. Johnson, R. L. Johnson, Brabazon, & Goates 14-075* (holotype BRY!; isotypes JEPS! RSA! and to be distributed).

Taprooted annuals commonly 3–12(–18) cm tall and 2–15(–30) cm wide. Primary stem erect, generally exceeded in length by secondary stems, with tertiary, and quaternary stems occasionally present; branches ascending to spreading and ± leafless, except for leaves subtending higher order branches; primary stem (terminating in a head) (0)2–5(8) cm, secondary stems (branches) 1–10 in number, 0.1–10 cm, tertiary branches 0.1–8 cm, quaternary branches 0.1–4 cm; tertiary and quaternary branches usually arising directly below or within 1 cm of an inflorescence head; stem and branches reddish-brown, sparsely minutely stipitate-glandular puberulent, the trichomes generally less than 0.25 mm long. Cotyledons two, linear, entire, united at base. Leaves stipitate-glandular puberulent with trichome density and length greatest on the proximal, adaxial surface; leaves at the lowermost 1–2(–3) nodes opposite, linear-filiform, and widened at the point of stem attachment, the proximal nodes often congested with overlapping leaf bases. More distal leaves alternate, entire, or more commonly with 1–3 pairs of linear lobes 1–5(–7) mm long attached along the proximal 3(–5) mm of the leaf, with an elongated, linear terminal segment 1–3 cm long (leaves with lobes along the proximal 1.2 cm of the leaf uncommon; these with lobes alternating, rather than oppositely paired). Inflorescences sparsely to moderately white hairy, prominently glandular, viscid. Inflorescence bracts: outermost 1–2 similar to upper leaves; bracts grade centripetally to having a wide, convex-clasping rachis membranous-margined and achlorophyllous proximally and chlorophyllous distally, shaggy pubescent along the margin, somewhat on the adaxial surface of the bract lobes near their attachment with the rachis, and sparsely on the abaxial rachis base with short glandular trichomes abundant; bracts bear ~ 3 pairs of chlorophyllous lateral lobes co-planer with the central, elongate terminal lobe (short, abaxially diverging lobes on either side of the terminal lobe not observed); lobes entire, short-stipitate glandular; inner bract gradation continues with the rachis widening further, the abaxial rachis surface densely covered in short stipitate glands, and the lateral bract lobes reduced to 2 pairs or even 1 pair, departing from the distal rachis edge; bract lobes acuminate from a broad base, commonly becoming reddish brown with age and may gently recurve. Inflorescences, 1–18(–50) in number, head like, ± spherical, (5–)10(–13) mm in diameter exclusive of bract tips; cymes, composed of a bract and 1 or 2 flowers, subsessile and tightly packed in heads; flowers generally fewer than 20 per head. Flowers: calyces mostly 5.0–10 mm long, tube ~ 3.2–3.7 mm, costae strongly to somewhat unequal with typically two lobes longer than the other three, lobes entire, acuminate, costae narrowing proximally, narrower at base than the intercostal membrane which is v-shaped at sinus, shaggy hairy on the abaxial calyx tube and adaxial lobes at the tube-lobe junction; corolla narrowly funnel form, glabrous, 5.5–7.0 mm long, lobes 0.9–1.2(–1.4) mm long × 0.4–1.0 mm wide, tube and lower throat yellow, upper throat and lobes pink to white, veins in throat often darkened, tube base expanding and adhering to the fruit apex. Stamen filaments 0.45–1.0 mm long, inserted unequally 0.35–1.4(–1.8) mm below corolla sinuses, included in throat to exerted less than half the length of the corolla lobes; pollen white, apertures pantoporate, acolpate; sexine seimitectate, reticulate, heterobrochate. Ovary three-chambered, style 2–3.4 mm long, stigmatic lobes ~ 0.3 mm long, included in corolla throat. Capsule ~ 2.5 mm long, dehiscent circumcissally around the base with valves splitting upward, leaving capsule base attached to receptacle inside calyx. Seeds (2)–3–8 per locule, medium brown (hue 5YR, value 3, chroma 3), ovoid-angular, ca. 1.0–1.45 mm long × 0.5–0.7 mm wide, mucilaginous when wet.

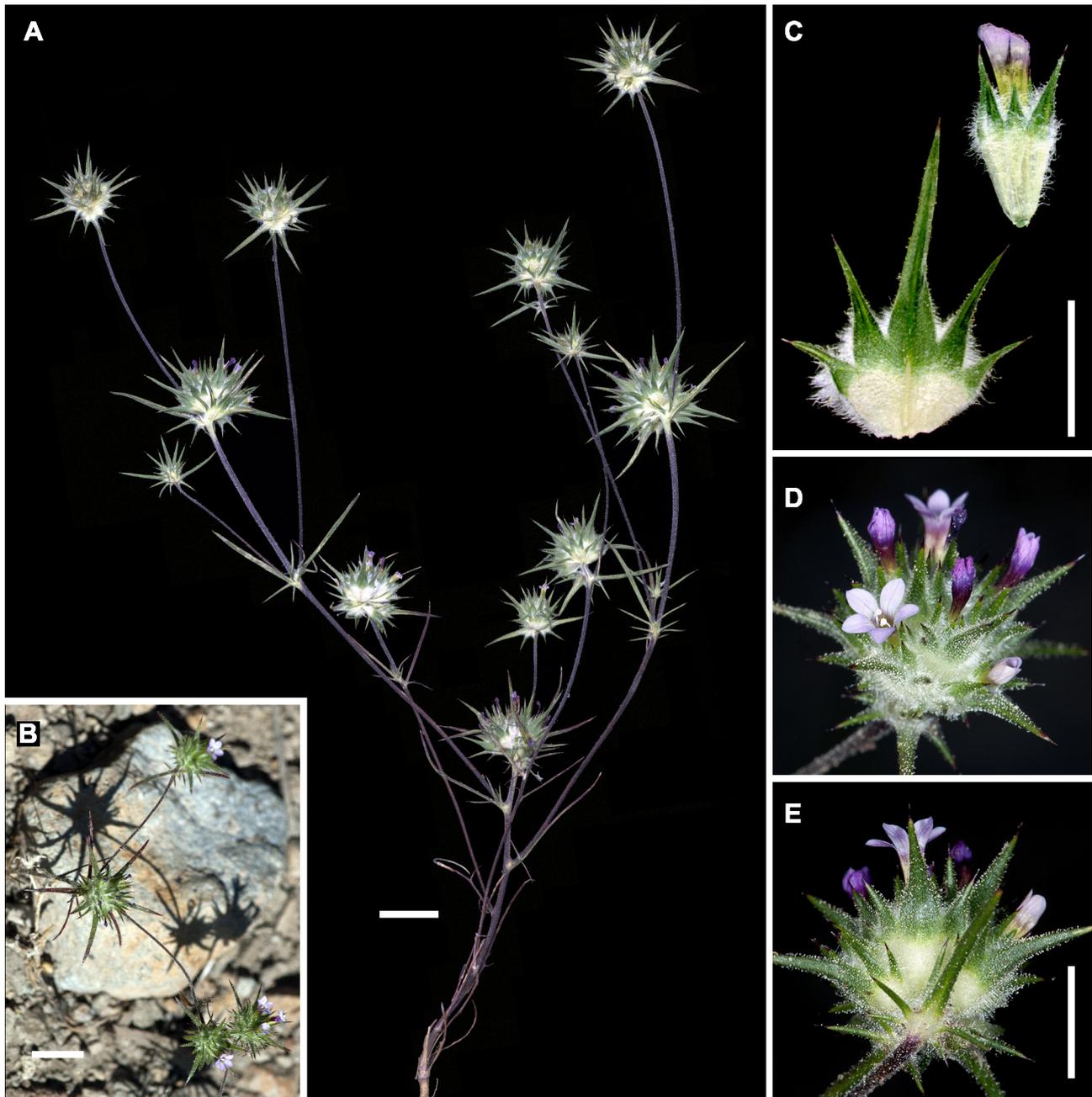


FIGURE 4. *Navarretia miwukensis* (all *Johnson et al. 14-080*, BRY). A. Pressed specimen showing plant habit, scale bar = 1 cm. B. Flowering individual in the field, scale bar = 1 cm. C. Pressed flower and inflorescence bract showing trichomes and lobe shape, scale bar = 5 mm. D–E. Inflorescence heads showing fresh flowers, anther presentation, and bracts, scale bar = 5 mm. All photographs by L. A. Johnson.

Habitat, Distribution, and Phenology:—*Navarretia miwukensis* occurs in open, sparsely vegetated pyroclastic derived soils often on gently sloping terrain. This taxon is presently known only from Calaveras and Tuolumne counties, California at elevations from 800–1480 meters, and blooms primarily May–June (July).

Etymology:—The specific epithet, literally ‘from Miwuk’, refers to Mi Wuk village, a community within the range of the species nestled among historic gold-rush settlements and named to honor the Me-Wuk Indians that have inhabited this region for centuries.

Additional specimens examined:—U.S.A. California: Calaveras County, Dry hillsides, 18–30 May 1895, *Davy 1623* (UC!); West of Avery at the end of a short forest service road off of Avery Sheep Ranch road, 38.19488°N, 120.39969°W, 3695 ft, 17 June 2015, *Gowen 1304* (BRY! JEPS!); Avery sheep Ranch Road about 1.8 miles west of Avery, 38.19841°N, 120.39886°W, 3567 ft, 3 Jun 2014, *Gowen 1258* (BRY!, JEPS!); North side of Avery-Sheep Ranch Road, across from forest service road 4N41Y, 38.19697°N, 120.40027°W, 1098 m, 4 June 2014, *Johnson et*

al. 14-067 (BRY!); Table Mountain, ca. 3 air miles ESA of Murphys, on flat volcanic surface west from Ponderosa Way and reached via Camp Nine road. 2700 ft, 20 May 1999, *Taylor 17162* (JEPS!); Tuolumne County, 1 mile south of Confidence, 1 June 1940, *Hoover 4411* (UC!); Confidence road, about 1.8 miles south of the Confidence store on Hwy 108, 38.02497°N, 120.21114°W, 3929 ft, 19 May 2014, *Gowen 1254* (BRY! JEPS!); South side of Hwy 108 just east of Sierra Village at Lyons Dam road, 38°4.692'N, 120°9.864'W, 4843 ft, 28 June 2013, *Gowen 1230* (BRY! JEPS!); South side of Hwy 108 just west of road to Lyons Reservoir, 38.07798°N, 120.16479°W, 1476 m, 5 June 2014, *Johnson et al. 14-080* (BRY!); South side of Hwy 108 just south of Twain Harte, 4 June 2014, *Gowen 1266* (BRY! JEPS!); Southwesterly open slope 1.2 miles from Highway 108, along Cedar Springs Road en route to Cherokee and Tuolumne City, 3480 ft. elevation, 22 May 1971, *Wiggins 21151* (CAS!); Corner of Twain Harte Drive and Ponderosa Drive, ca. 1 mile west of center of Twain Harte Village, 3620 ft., 25 May 1971, *Wiggins 21251* (CAS!); Twain Harte Post Office, Sierra Nevada, 4000 ft., 3 June 1944, *Alexander & Kellogg 3622* (UC!).

Notes:—Fresh plants of *N. miwukensis* are noticeably skunky in odor, and more so than *N. crystallina*. In addition to a smaller range, more populations of this species are likely at risk to future development than *N. crystallina*.

Key distinguishing *Navarretia crystallina* and *N. miwukensis* from morphologically similar *Navarretia* species

This short key replaces couplet 33 in the treatment of *Navarretia* in California (Johnson 2013), with the exception that subspecies are not treated and the first lead in couplet one below is not elaborated to species

1. Leaves, at least the upper, with lateral lobes extended along rachis for more than 3 mm (\pm pinnate) and the terminal segment less than 2.5 \times the laterally lobed portion of the leaf; cauline leaves as conspicuous as the stems and inflorescences.....
.....*N. atractyloides*, *N. breweri*, *N. hamata*, *N. heterodoxa*, *N. mellita*, *N. peninsularis*, *N. rosulata*, *N. squarrosa*, *N. viscidula*.
- Leaves, at least the upper, with lateral lobes confined to the proximal 3 mm (palmate or nearly so) and an elongated terminal segment 3–10 \times longer than the laterally lobed portion of the leaf; cauline leaves inconspicuous compared to stems and inflorescences2
2. Inflorescence bract lobes all in the same plane; lateral lobes diminishing in length basipetally (if bracts as below, then heads long white hairy and flowers less than 7 mm long); heads tight, not separable into multi-flowered clusters, flowers subsessile3
- Inflorescence bract lobes, at least some, diverging in two planes—the terminal lobe flanked on one or both sides by an abaxially diverging lobe shorter than the distal-most pair of lateral lobes that are co-planar with the terminal lobe; heads loose, separable into multi-flowered clusters, flowers short petiolate / penduculate.....5
3. Trichomes more or less uniform, minute-stipitate glandular throughout; stigma and anthers exerted well beyond corolla lobe tips*N. filicaulis*
- Trichomes variable: many of those on the proximal portion of upper leaves and bracts much longer stalked and either eglandular or less obviously glandular than those on the stems and distal portions of leaves or bracts; stigma included, anthers included or slightly exerted but not beyond corolla lobe tips4
4. Inflorescence heads densely long hairy and only obscurely glandular, not viscid; bract and calyx lobes long acute, sinuses between lobes obscured by hairs*N. crystallina*
- Inflorescence heads sparsely to moderately hairy and prominently glandular, viscid; bract and calyx lobe acuminate, sinuses between lobes not fully obscured by hairs*N. miwukensis*
5. Inflorescence heads densely long hairy; corolla 8–12mm; most or all stamens and style well exerted beyond corolla throat.....
.....*N. prolifera*
- Inflorescence heads sparsely to moderately glandular, hairy, or glandular-hairy; corolla 4–7(–8) mm; stamens and style included or presented at orifice of corolla throat*N. divaricata*

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Appendix I. Specimens used in DNA sequence analyses, all deposited at BRY

Navarretia crystallina. California, Calaveras County, *Johnson et al. 14-063*. El Dorado County, *Johnson 13-216*. Placer County, *Johnson et al. 14-030*. Tuolumne County, *Johnson et al. 14-098*.

Navarretia divaricata subsp. *divaricata*. California, El Dorado County, *Johnson 13-219*. Lassen County, *Johnson 11-029*. Tehama County, *Johnson 04-140*. Tulare County, *Johnson 94-065*. Idaho, Boise County, *Porter & Machen 13772*. Washington, Asotin County, *Johnson & Johnson 94-049*.

Navarretia divaricata subsp. *vividior*. California, Napa County, *Johnson & Gowen 09-049*. Trinity County, *Gowen 452*.

Navarretia filicaulis. California, Butte County, *Johnson 04-068*; *Ahart 12140*; *Ahart 12151*. Tuolumne County, *Johnson et al. 14-074*.

Navarretia miwukensis. California, Calaveras County, *Johnson et al. 14-067*. Tuolumne County, *Johnson et al. 14-075*; *Johnson et al. 14-080*; *Gowen 1254*.

Navarretia prolifera subsp. *lutea*. California, El Dorado County, *Johnson, Gowen, & Mort 09-044*; *Johnson 04-078*.

Navarretia prolifera subsp. *prolifera*. California, El Dorado County, *Johnson 09-055*; *Johnson 09-065*.