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Navarretia panochensis (Polemoniaceae), a new species from the Panoche Hills and Panoche Valley of the San Joaquin Desert, California

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Abstract

A new species narrowly endemic to the extremely arid western portion of the San Joaquin Desert, California, *Navarretia panochensis,* is here described. This species belongs to the *N. pubescens* group of *Navarretia* section *Mitracarpium*, sharing several features including the presence of three cotyledons. It is distinguished from these near relatives by having entire rather than forked cotyledons, generally lavender corolla lobes, and like some populations of *N. pubescens*, lacking a widened distal rachis of its upper leaves and bracts. A key distinguishing *N. panochensis* from other species of the *N. pubescens* group is provided.

Key words: Badlands, narrow endemic, section *Mitracarpium*, pincushion plant

Introduction

California is the center of diversity for the genus *Navarretia* Ruiz & Pavon (1794: 20), with 91.4% of the recognized taxa occurring within the state, and 56.9% endemic to the state. With 46 species currently recognized, *Navarretia* has greatly increased in number from the 28 that were recognized in the first edition of The Jepson Manual (Day 1993). Four species were added as the result of molecular work, placing these former members of *Gilia* Ruiz & Pavon (1794: 25) within *Navarretia* along with resurrecting a cryptic species long lost in synonymy (Porter & Johnson 2000; Johnson & Cairns-Heath 2010). Twelve additional species have been described as new (Spencer & Spencer 2003; Johnson 2007; Johnson *et al.* 2012, 2013, 2016; Johnson & Gowen 2017), one subspecies was returned to species status (Johnson *et al.* 2012), another elevated to species status (Johnson & Gowen 2017), and two new taxa have been described at the subspecies level (Day 1995; Björk 2002). Some of the taxonomic novelties enumerated above are geographically widespread while others are narrowly distributed; some are edaphic specialists while others are more generalists. Most, however, are at least somewhat superficially similar to previously recognized species such that their taxonomic recognition has been previously overlooked. Here, we describe a new, narrowly-distributed species adapted to the extremely arid western edge of the San Joaquin Desert.

This new species has clear affinities to *Navarretia* section *Mitracarpium* Brand (1907: 152). This section is named for its characteristic fruiting capsule that dehisces circumscissiley at the base and then partially upwards to form four or eight incompletely separated valves (Fig. 1A). These species also share a characteristic calyx morphology with all costae being ± linear proximally rather than tapering (Fig 1B), have conspicuously glandular external corolla tubes (Fig. 1C; rare elsewhere in *Navarretia*), and have two, rather than three, stigmatic lobes—a feature otherwise restricted to *N. filicaulis* (Torr. ex Gray 1870: 270) Greene (1887: 134), most species in section *Navarretia,* and in an intermediate form in *N. divaricata* Greene (1887: 136), which has two of its three stigmatic lobes nearly entirely fused. Section *Mitracarpium* has been informally divided into two groups (Day 1993; Johnson 2007). The separation of these two groups centers primarily on whether the rachis of the upper leaves and outer bracts expand above the middle or not (Fig. 1D). Johnson (2007) referred to the expanded rachis group as the *N. pubescens* (Bentham 1833) Hooker & Arnott (1839: 368) complex, although he noted that *N. pubescens* sometimes has a linear rather than expanded rachis. In addition to the expanded rachis, members of the *N. pubescens* complex generally have three cotyledons (though some

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individuals may only have two), whereas the other members of sect. *Mitracarpium*, as well as all other *Navarretia*, have only two. Furthermore, each of the three cotyledons is linear and forks equally into two linear segments at approximately mid-length (Fig. 1E).

In early 2008, the first author noticed two collections, *Yadon s.n.*, recently accessioned into UC/JEPS (JEPS 98210, JEPS 98219). Although labeled *N. nigelliformis* Greene (1887: 132) and despite the absence of flowers, these plants varied in important ways from that taxon. Suspecting they might be related to the recently described *N. gowenii* Johnson (2007: 455), the first author searched for the plants in 2008 after confirming their general location with the original collector. On the first visit while the plants were very immature, the plants appeared possibly to be *N. mitracarpa* Greene (1887: 135), but on a subsequent visit when the plants were blooming, it was clear that these plants differed from any described species. Following additional observation and fieldwork, we here describe this material as a new species and provide a revised key to aid in distinguishing it from the other members of the *N. pubescens* complex.

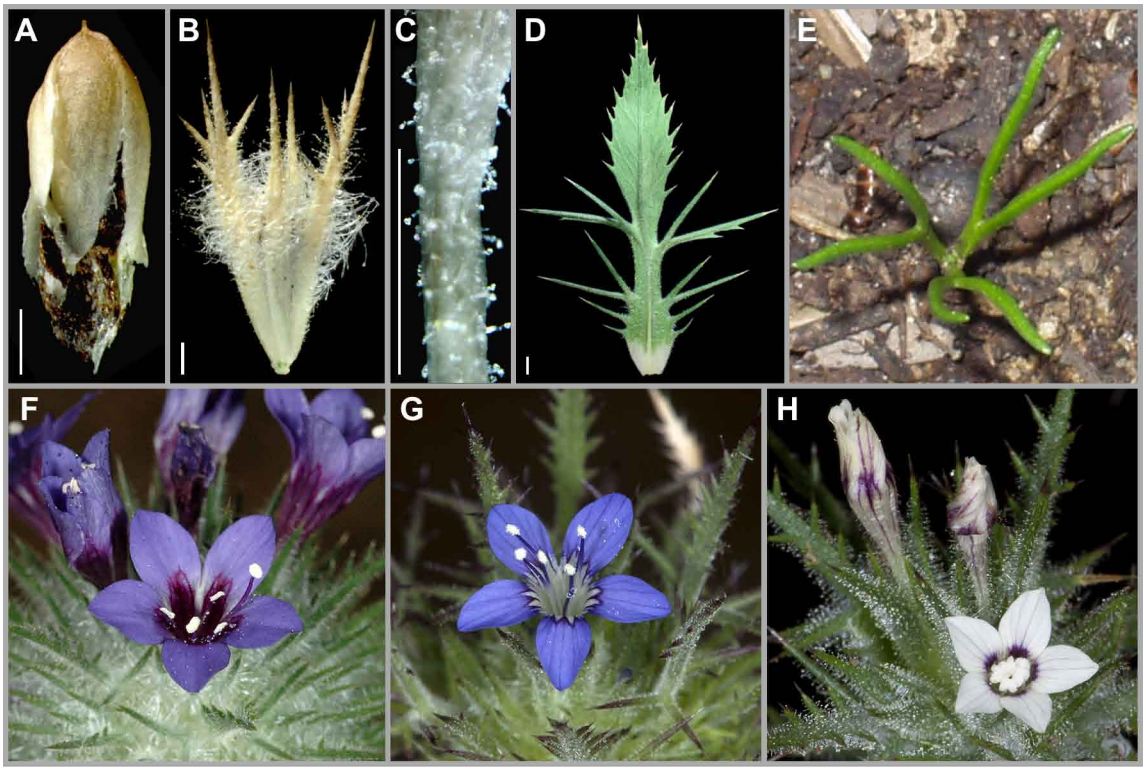

FIGURE 1. Morphological features of the *Navarretia pubescens* group of *Navarretia* section *Mitracarpium*; scale bars (A–D only) = 1 mm). A, B. *Navarretia pubescens* (*Johnson 15-041*, BRY). A. Mature, dehisced fruit with seeds extending from base. B. Calyx with broad, strap like costae joined by narrow membrane forming tube. C, D. *Navarretia setiloba* (*Johnson & Zhang 05-117*, BRY). C. External corolla tube with glands. D. Outer bract with expanded distal rachis. E. *Navarretia pubescens*, seedling with three, forked cotyledons (*Gowen s.n.,* from Lime Ridge Open Space, Contra Costa County, JEPS). F. *Navarretia pubescens* (*Johnson 05-056*, BRY). G. *Navarretia setiloba* (*Johnson & Gowen 10-087*, BRY) H. *Navarretia gowenii* (*Johnson et al. 09-046*, BRY). All photographs by L. Johnson except E by D. Gowen.

Taxonomy

Navarretia panochensis D.Gowen & L.A.Johnson, *sp. nov*. (Fig. 2)

A species similar to *Navarretia pubescens* but differing by having a yellowish-white corolla throat and lavender lobes vs. purple throat and lobes in *N. pubescens*; from *N. mitracarpa* it differs by having bracts with a linear rachis and a generally upright rather than low, spreading habit; from both it differs by having cotyledons unlobed (rarely rudimentary lobed) and narrowly elliptic vs. equally forked into two linear lobes.

Type:—U.S.A. California: Fresno County, North of the BLM road east of Mercy Hot Springs, 36.7188°N, 120.8530°W, 1388 ft. elev., 8 May 2016, *Gowen 1329* (holotype: JEPS; isotype: BRY).

Taprooted annuals generally under 16 cm tall and wide, branched or unbranched; central axis erect, to 13 cm and secondary axes, if present, spreading to ascending, to 8 cm; all axes terminating in a head-like inflorescence. *Stems* tawny yellow to greenish suffused with purple or strongly anthocyanic, densely villous with eglandular and uniseriate stipitate-glandular trichomes. *Cotyledons* usually 3, connate proximally, narrowly elliptic, entire or occasionally with a rudimentary lobe. *Leaves*: lowermost connate proximally, opposite or whorled in 3's, becoming alternate, withering with age, pinnate to bipinnate with a filiform rachis and lobes, the rachis of the terminal segment sometimes slightly wider than the proximal rachis; any widening of the terminal leaf segment's rachis diminishes higher on the plant toward the inflorescence such that the rachis of more distal leaves and inflorescence bracts taper proximally to distally without widening; leaves at mid-plant and distally, including those subtending branches or heads, persistent, ± bipinnate proximally with a distal, pinnately lobed or toothed segment, the proximal lobes forked (V- or Y-shaped) or pinnately lobed in a plane rotated ± 90° from the leaf's primary plane; leaves densely villous and glandular similar to stems with trichomes somewhat longer along the proximal rachis of the distal leaves. *Inflorescences* head-like with ca. 8–24 flowers, ca. 15–20 mm diameter exclusive of projecting bract tips, to 40 mm inclusive of bract tips; outer inflorescence bracts like upper leaves, the bracts becoming somewhat shorter centripetally while at the same time diminishing in number and size of proximal lobes and the bract base (achlorophyllous region above which lobes depart) elongating and widening somewhat; bracts immediately subtending flowers may exceed or be exceeded by calyces in length; bracts villous and stipitate glandular similar to leaves and stems, with the longest trichomes of the plant body occurring along bract bases. *Calyx* 9.5–16 mm, costae unequal, the shortest entire and the longest two or three with 1–4 pairs of acerose lobes; costae chartaceous and ± linear proximally, connate into a 2–4 mm tube via an intercostal membrane that is shallowly U-shaped at the distal sinus, the costae becoming green in the distal tube and remaining green except at their acerose tips; calyx glandular externally throughout, internally only along the free portion of the costae, the glands short-stipitate proximally and distally, becoming longer (± 1mm) near mouth of calyx tube. *Corolla* 9–11 mm, exceeded by or exceeding the calyx, lobes 2–2.75 mm long × 1.4–2.2 mm wide with tip pointed to apiculate; tube white to cream, throat yellowish white, lobes lavender (occasionally whitish cream) with the vasculature darker and prominently magenta in the region of the anastomoses and the veins extending above and below the anastomoses at the throat-lobe junction; stipitate-glandular externally along the tube, less densely on the throat and lobes, glabrous internally. *Stamens* attached equally to subequally ca. 2.3–3 mm below the sinus, filaments unequal to subequal in length, 3–5.2 mm, exserted to about 1/2 to ± equal to the length of the corolla lobes; anthers ca. 0.75–1 mm, pollen white. *Ovary* situated on a nectary disk; style ± 5.8–8.2 mm, included in corolla throat to exserted, stigma bilobed, each lobe ca. 0.4 mm. *Capsules* ca. 3.2–3.8 mm with an apicular beak (ca. 0.18 mm); often purple-blotched apically; not exceeding calyx prior to dehiscence; chartaceous in distal 5/6 and membranous in proximal 1/6, dehiscing unevenly, circumscissiley, about the base, and then splitting in 4 lines incompletely toward the apex; locules 1. *Seeds* 1 or 2 per fruit, ca. 2.2–2.5 mm, tan or light brown, producing spiricles when wetted. *Diploidy* inferred from amplification and direct sequencing of low copy nuclear gene regions.

Distribution, habitat, and conservation assessment:—*Navarretia panochensis* is presently known from a few locations in the Panoche Hills and Panoche Valley of the San Joaquin Desert (Germano *et al.* 2011) in Fresno and San Benito Counties, California at ± 400–650 meters elevation (Fig. 3). Where *N. panochensis* occurs, the hills are mapped as the Tulare Formation, of Plio-Pleistocene age. It consists largely of pebble gravel/conglomerate, including cobbles, of detritus of Franciscan rocks, sandstone, and shale in clay matrix. On the valley floor, *N. panochensis* occurs on surficial sediments of alluvial deposits of sand, clay, and pebbles of sandstone, shale, and serpentinite; these sediments are Holocene in origin (Dibblee & Minch 2007).

The Panoche vicinity receives little annual precipitation (177–203 mm; https://wrcc.dri.edu/summary/Climsmcca.html), which comes primarily in the months of November through April. The low average annual rainfall and low aridity index of 0.15 (arid) qualifies the Panoche area climatically as a cold desert (BWk) under Köppen climate system (CDFW 2003: 15; Peterson 2016; R. O'Dell, California BLM Central Coast Field Office, pers. comm.). The dominant vegetation types are desert scrub and desert annual forbland that has been extensively invaded such as to appear as an annual grassland (Sawyer *et al.* 2009; Buck-Diaz & Evens 2011; Stout *et al.* 2013).

Though the precise geographic range of *N. panochensis* has yet to be determined (Fig. 2), we estimate that its range is roughly 16 km long × 12 km wide with some occurrences numbering in the 1000's on a year with sufficient rainfall. A preliminary conservation assessment places this taxon in Red List Category EN (Endangered; IUCN 2012) based on its limited area of occupancy, a limited number of known locations, and extreme fluctuations in the number of mature individuals from year to year. Coupled with industrialization and potential industrialization in a portion of its range, further study is warranted.

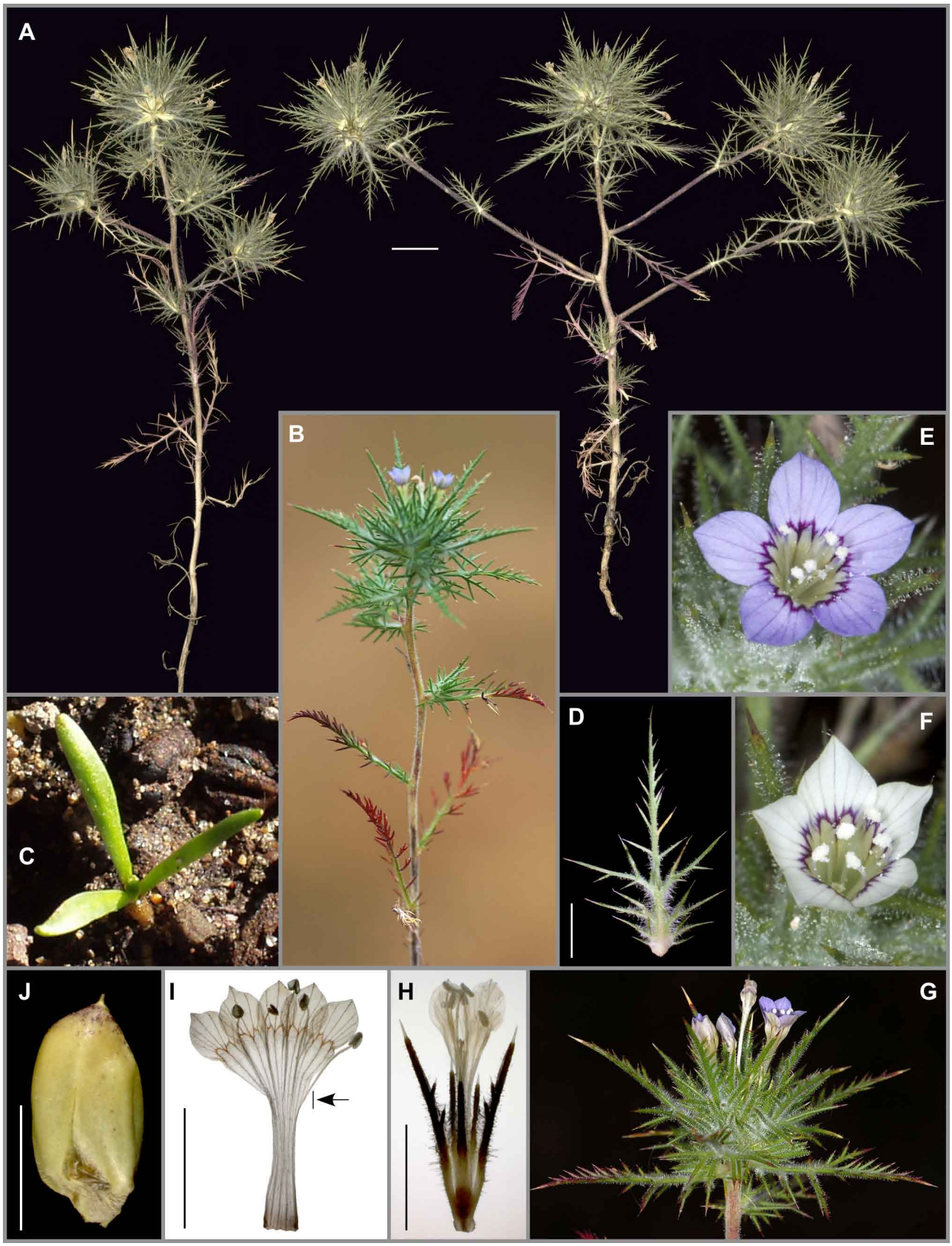

FIGURE 2. *Navarretia panochensis*. A. Pressed specimens showing plant habit, scale bar = 1 cm (*Gowen 1329*, BRY). B. Flowering individual in the field (*Johnson & Gowen 10-073*, BRY). C. Cotyledons from seedling germinated in cultivation (seed collected from type locality). D. Outer bract, scale bar = 5 mm (*Johnson & Gowen 10-073*, BRY). E–G. Close up of flowers and inflorescence heads in the field with typical (E, G) and less common (F) corolla coloration (*Johnson & Gowen 10-073*, BRY). H–I. Rehydrated flower (H) and dissected corolla (I), with arrow pointing to region of stamen insertion, scale bars = 5 mm (*Johnson & Gowen 10-073*, BRY). J. Mature fruit, scale bar = 2 mm (*Gowen 1329*; BRY). All photographs by L. Johnson except C by D. Gowen.

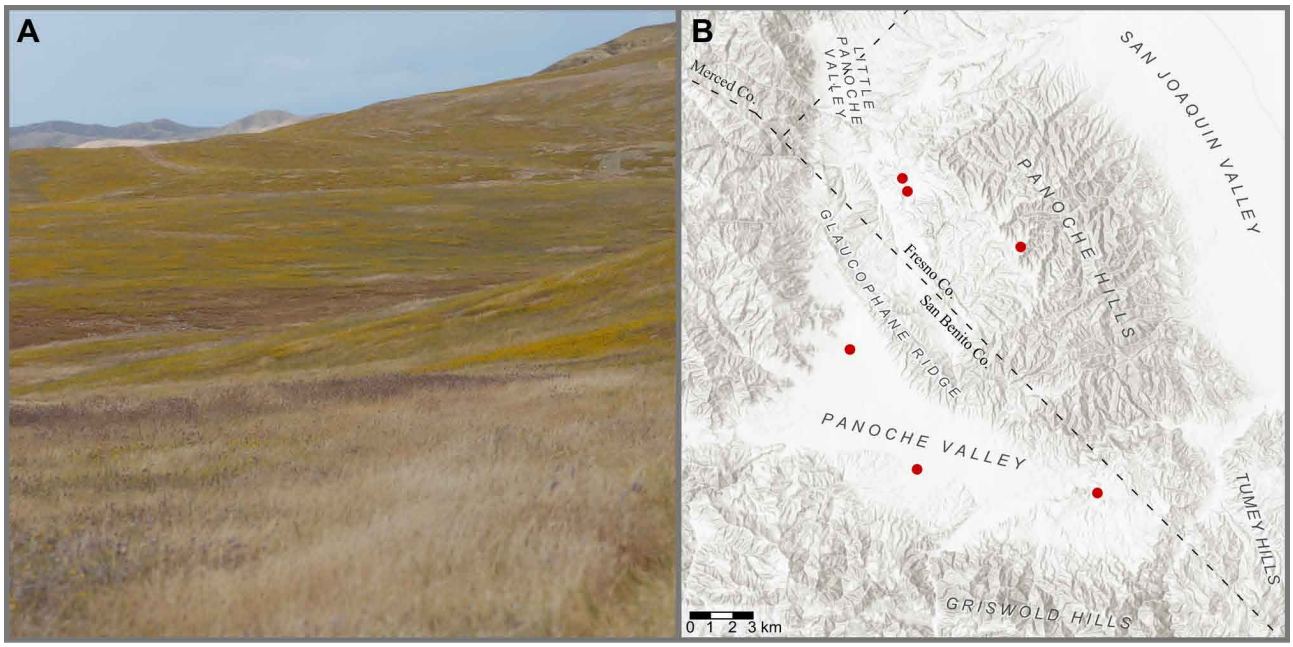

FIGURE 3. A. View of the Panoche Hills in May 2010 from the type locality, Fresno County, California; photograph by L. Johnson. B. Map of the Panoche Hills and Panoche Valley with county borders indicated showing the distribution of known occurrences of *Navarretia panochensis* (red dots).

Etymology:—The specific epithet refers to the Panoche Hills and Panoche Valley in western Fresno and eastern San Benito counties where this species occurs.

Paratypes:—U.S.A. California: Fresno County, Northeast of Mercy Hot Springs on BLM road (dirt), ca. 1.25 miles east of Little Panoche Road, 29 April 2008, *Gowen 875* (BRY, JEPS); Same area, 27 May 2008, *Gowen 927* (JEPS); Same area, 3 May 2010, *Gowen 1094* (JEPS); Same area, 9 May 2010, *Gowen & Johnson 1102* (JEPS), *Johnson & Gowen 10-073* (BRY, RSA); Near Mercy Hot Springs, Panoche Hills, 12 April 1989, *Yadon s.n.* (JEPS); On dirt road 1 mile east from Mercy Hot Springs, off little Panoche Road, Panoche Hills, 20 April 1989, *Yadon s.n.* (JEPS); Hills 3 miles east of Mercy Hot Springs on the USBLM road, 12 June 1967, *Twisselmann 13363* (CAS). San Benito County, East end of Panoche Valley near Panoche Road, on the west side of Panoche Pass near 36.5881° N, 120.7490° W, 915 ft. elev., 23 April 2016, *Gowen 1318* (BRY, JEPS); Southeast end of Panoche Valley near 36.5881° N, 120.7490° W, 1093 ft. elev., 8 May 2016, *Gowen 1328* (BRY, JEPS).

Notes and discussion:—Measurements of overall plant size used in the description are derived from ca. 50 individuals collected on various years mostly from the type locality, with floral measurements taken from rehydrated flowers from ca. 10 individuals following the same methodology used by Johnson & Gowen (2017).

Navarretia panochensis, with its three cotyledons, clearly fits within the *N. pubescens* complex. Cotyledon shape and number has been discussed previously (Brand 1907; Jepson 1925, 1943; Spencer & Porter 1997; Johnson 2007) and additional observations of seedlings in the *N. pubescens* complex indicate that they are three in number and forked into two linear lobes (Fig. 1E). The generally entire cotyledons (with an occasional rudimentary lobe) of *N. panochensis* clearly set this taxon apart (Fig. 2C). The somewhat widened, rather than narrowly linear cotyledons of *N. panochensis* are suggestive of the spatulate cotyledons of several other members of sect. *Mitracarpium* (*N. eriocephala* Mason (1946: 196)*, N. heterandra* (Mason (1946: 197)*,* and *N. nigelliformis*), though these taxa have only two cotyledons.

DNA sequences from the nuclear ITS region (Spencer & Porter 1997) recover the *N. pubescens* group as understood at that time (i.e., *N. pubescens*, *N. jaredii* Eastwood (1900: 89) = *N. mitracarpa*, and *N. setiloba* (1893: 153)) as a monophyletic group sister to the other members of section *Mitracarpium.* In exploratory work, we added additional ITS sequences from multiple populations of these species plus those since described (*N. ojaiensis* Elvin, J.M.Porter & L.A.Johnson in Johnson (2007: 458) and *N. gowenii*) including *N. panochensis*, and continue to recover a monophyletic group that has little structure among species (results not shown). Similarly, we sequenced several chloroplast loci that have been useful in species delimitation in other groups of *Navarretia* (e.g., Johnson *et al.* 2013; Johnson *et al.* 2016; Johnson & Gowen 2017), and again recover a monophyletic *N. pubescens* group with little variation among species or structure within the group (results not shown). These data suggest that, relative to other *Navarretia*, and similar to

the *N. prostrata* Greene (1887: 130)–*N. leucocephala* Bentham (1849: 324 in Bentham 1839–1857) group of section *Navarretia* (Spencer & Porter 1997), the *N. pubescens* group has radiated relatively recently and rapidly, perhaps in response to fluctuating climate regimes associated with episodic Quaternary glaciations. Other genetic markers such as microsatellites, or the use of coalescent methods with multiple nuclear regions may be useful for assessing species relationships and testing species boundaries in this complex.

Within the *N. pubescens* complex, *N. panochensis* is most similar to *N. pubescens*, which has many populations with bracts that also lack an expanded rachis. Corollas of *N. pubescens* are distinct from the other members of the *N. pubescens* complex by having a purple throat (Fig. 1F). All other members, including *N. panochensis*, have a yellowish to white throat. In addition, corolla lobes of *N. panochensis* are pale lavender (rarely white; Fig. 2E, F), whereas the other members have lobes generally blue or purple (e.g. Fig. 1F, G) or white (e.g. Fig. 1H). The exception is a form of *N. setiloba*, which also has lavender lobes. The pointed to apiculate lobes of *N. panochensis* (Fig. 2I) approach the more pronounced acute to apiculate lobes of *N. ojaiensis*.

Of the five members of the *N. pubescens* complex, only two are very wide ranging. *Navarretia pubescens* occurs in the northern half of California in the Coast Ranges, as well as the western edge of the Sierra Nevada and into southern Oregon. *Navarretia mitracarpa* occurs in the southern half of California, primarily in the south Coast Ranges and the western end of the Transverse Range. *Navarretia panochensis* occurs at the junction of these two ranges. This may explain its unique suite of characters, which individually have similarities to either *N. pubescens* or *N. mitracarpa*, though these latter two species tend to grow in oak woodland or associated grassland habitats that contrast with the desert badland habitat occupied by *N. panochensis*. An example of the flora reflecting the desert climate inhabited by *N. panochensis* is the co-occurrence of *Chorizanthe spinosa* Watson (1880: 481), a disjunct species from the western Mojave Desert.

Key distinguishing *Navarretia panochensis* from other species of the *N. pubescens* complex

All species with typically colored corolla lobes may occasionally produce white-lobed individuals.

1. Corolla tube, throat, and lobes blue-purple with reddish-purple veins near anastomoses ..... *N. pubescens*
- Corolla tube and throat white or yellowish white, lobes white to cream, lavender, or blue-purple, generally with reddish-purple veins or spots near anastomoses 2
2. Upper leaves and bracts with linear rachis to the tip ..... *N. panochensis*
- Upper leaves and at least outer bracts with widened, more or less elliptic rachis distally 3
3. Plants generally taller than broad with a dominant, erect central axis; secondary branches shorter than, and typically not exceeding, the primary axis in absolute length or the terminal inflorescence of the primary stem in overall height 4
- Plants generally as broad as tall, branching from near the base, secondary branches often equaling or exceeding the primary axis in absolute length and the terminal inflorescence of the primary stem in overall height 5
4. Corolla lobes purple to lavender, anthers exserted well beyond middle of corolla lobes; stigma exserted ..... *N. setiloba*
- Corolla lobes white with darker markings at anastomoses, anthers included to exserted below middle of corolla lobes; stigma included ..... *N. gowenii*
5. Upper stems and inflorescence heads densely white villous to glandular; corolla lobes rounded to blunt pointed, blue to violet (uncommonly white) with reddish-purple veins near anastomoses ..... *N. mitracarpa*
- Upper stems and inflorescence heads stipitate-glandular; corolla lobes apiculate, white (some populations mixed with blue-lobed individuals in the Santa Monica Mtns), purple spotted at point of corolla anastomoses ..... *N. ojaiensis*

TABLE 1. Comparison of key morphological features among *Navarretia panochensis, N. pubescens, N. gowenii*, *N. setiloba, N. mitracarpa,* and *N. ojaiensis*. All species with colored corolla lobes may occasionally have individuals or mixed populations with whitish lobes.

	N. panochensis	*N. pubescens*	*N. gowenii*	*N. setiloba*	*N. mitracarpa*	*N. ojaiensis*
Plant habit	Erect, branches if present mostly from upper nodes	Erect, branches if present mostly from upper nodes	Erect, branches if present mostly from upper nodes	Erect, branches if present mostly from upper nodes	Spreading, many branches from base	Spreading, many branches from base
Cotyledon shape	Entire, linear to narrowly elliptic	Forked, linear lobes	Forked, linear lobes	Forked, linear lobes	Forked, linear lobes	Forked, linear lobes
Upper leaf and outer bract distal rachis shape	Linear	Linear to elliptic	Elliptic	Elliptic	Elliptic	Elliptic
Stigma presentation	Included to exserted	Exserted	Included	Exserted	Exserted	Exserted
Corolla lobe color	Lavender	Blue-purple	Whitish	Purple, lavender	Blue-purple	Whitish (also blue in Santa Monica Mtns.)
Corolla lobe apex shape	Pointed to apiculate	Rounded to blunt pointed	Rounded to blunt pointed	Rounded to blunt pointed	Rounded to blunt pointed	Pointed to apiculate

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