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# *Navarretia furnissii* (Polemoniaceae), a new diploid species from the intermountain western United States distinguished from tetraploid *Navarretia saximontana*

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## Abstract

Morphological and DNA-based characters distinguish a new diploid species centered in the Intermountain Region of the western United States, *Navarretia furnissii*, from *N. saximontana*, which is tetraploid. The two species are reciprocally monophyletic in analyses of chloroplast DNA sequences and nrDNA ITS sequences. *Navarretia furnissii*, presently known from Utah, Idaho, Wyoming, Montana, and Colorado, is distinguished morphologically from *N. saximontana* by a smaller corolla, greater frequency of pronged calyx lobes, and fewer seeds. A key to *Navarretia* of the Intermountain Region is presented.

**Key words**: cryptic species, polyploidy, *Pistillata*, species delimitation, taxonomy, unified species concept

## Introduction

*Navarretia,* with ca. 35 species, is one of the larger genera of Polemoniaceae. *Navarretia* are annual herbs with the majority of species possessing spinescent leaves, accrescent calyces with unequal, pungent lobes, and a base chromosome number of *x* = 9. *Navarretia* section *Navarretia* forms a monophyletic group in the genus that includes species tightly associated with seasonal pools (*e.g. N. fossalis* Moran (1977: 155) and *N. leucocephala* Bentham (1849: 324)) and species that often occur in shallow and seasonally moist depressions, but not necessarily vernal or seasonal pool habitats (*e.g. N. tagetina* Greene (1887: 137) and *N. subuligera* Greene (1887: 137). The widest ranging and most commonly encountered species in this section include *N. intertexta* (Bentham 1833: 1622) Hooker (1838: 74) and *N. propinqua* Suksdorf (1906: 26). The latter species was reduced to a variety of the former by Brand (1907: 163; see also Cronquist 1984) and treated as a subspecies by Day (1993: 336). Comparative DNA sequencing and laboratory work indicates *N. intertexta* is a diploid whereas *N. propinqua* is an allotetraploid with *N. intertexta* or its ancestor putatively identified as one of the parental species (Johnson *et al.* 2008). Neither polyploidy nor hybridization has been emphasized previously as important factors for speciation in *Navarretia* (but see Johnson *et al.* in press). Nevertheless, because the tetraploid genome of *N. propinqua* provides an intrinsic barrier to gene exchange with the diploid *N. intertexta*, we treat these two taxa as distinct at the species level.

*Navarretia intertexta* ranges along the western portion of North America from Baja California to British Columbia and eastward into Idaho and Nevada, while *N. propinqua* ranges from California to British Columbia and east to Arizona, Utah, and Idaho. Spencer recognized that material being referred either to *N. intertexta/N. propinqua* or *N. leucocephala* subsp. *minima* (Nuttall 1848: 13) Day (1993: 337) along the western flanks of the Rocky Mountains eastward is distinguishable by morphology and nrDNA ITS sequences from anything previously described (Spencer & Spencer 2003). This new species, *N. saximontana* Spencer (in Spencer & Spencer 2003: 198)*,* ranges from Arizona north to southeastern Alberta and eastward to central

Saskatchewan, North Dakota, Wyoming, and Colorado. It is a remarkable species in that it is one of the few *Navarretia* with a present day distribution entirely outside of California (which counts 92% of *Navarretia* species as native), and the only species before the present study with a distribution entirely east of the Great Basin.

Comparative DNA sequencing in our lab implicated the second parent of *N. propinqua* as a taxon close to *N. saximontana*. In pursuing this hypothesis, we sampled *N. saximontana* widely, from Arizona to Canada from herbarium material (from BRY) and from Arizona, Idaho, Utah, and Wyoming with multiple individuals from newly collected populations. This work led to the unanticipated discovery of yet additional cryptic diversity involving polyploidy in *Navarretia* that is centered on *N. saximontana*. Specimens cited as paratypes for *N. saximontana* (Spencer & Spencer 2003) represent populations composed either of diploid or tetraploid entities. Both diploid and tetraploid populations share the shorter stamen lengths that distinguish this material from *N. propinqua,* and the bright yellow pollen and well-divided stigma that distinguish them from *N. leucocephala*. They are also distinguishable from each other by a combination of features outlined below. We determined that plants from the type locality of *N. saximontana* are tetraploid and, therefore, here recognize the diploid entity as a new species, *Navarretia furnissii*, putatively reproductively isolated from *N. saximontana* via the difference in ploidy level and, as yet, no known syntopy of populations. We accordingly emend the description of *N. saximontana* to restrict the circumscription of this speciesto include only tetraploid plants, and list from among the paratypes for this species only those specimens representing this species as defined herein.


## Materials and methods

Our working concept for species follows the general lineage concept (de Queiroz 1998, 2007) and we use evidence of non-homogenizing gene flow from both morphological and molecular data as criteria for distinguishing the evolutionary independence of the metapopulation lineages we here delimit as species (e.g. Johnson & Johnson 2006, Johnson & Cairns-Heath 2010).

We performed comparative DNA sequence analyses on data obtained from individuals representing 25 populations as follows: two populations of *Navarretia intertexta*, seven populations of *N. propinqua*, eight populations of *N. saximontana*, and eight populations of *N. furnissii*. For one population each of *N. saximontana* and *N. furnissii*, we sequenced eight individuals and two or three individuals from several of the other populations to examine within population variation, but individuals did not vary in more than one or two nucleotides across all sampled regions. We therefore used single individuals to represent populations in our sequence analyses. We isolated DNA and PCR amplified selected regions using standard conditions as described in Johnson *et al*. (in press). We sequenced four chloroplast regions *(trnH–psbA* intron, *rpl16* intron, *trnS–trnG* intergenic spacer and the adjacent *trnG–trnG* intergenic spacer; primers as described in Shaw *et al*. 2005) and the nuclear ribosomal ITS1, 5.8s, and ITS2 region (White *et al*. 1990, Porter 1996). For a subsampling of populations (two *N. intertexta*, two *N. propinqua*, four *N. furnissii*, and three *N. saximontana*), we also sequenced a portion from the 5' end of the nuclear *Pistillata* region as described in Johnson *et al*. (in press). All sequences are available from GenBank (accession numbers JQ478875–JQ479002).

We aligned sequences by eye in Se-Al (Rambaut 1996) and coded indels not associated with poly-n repeats as present or absent using simple indel coding (Simmons & Ochoterena 2000). We conducted unweighted parimony analyses to produce unrooted networks using PAUP* 4.0b10 (Swofford 2002). Following Brower (1999), all members of a species should form a contiguous group on an unrooted network separated from other groups by a single branch along which fixed character-state changes (e.g. nucleotide substitutions or indels) can be inferred. For presentation purposes, we rooted trees with *N. intertexta* as outgroup.

We first inferred relative ploidy level by the presence of two homeologs in the low copy nuclear gene *Pistillata* in *N. saximontana* (and *N. propinqua*) compared to a single homeolog in *N. furnissii* and *N.*

*intertexta* (Johnson *et al*. in press, see below). We subsequently used flow cytometry of fresh leaf material following methodology outlined in Broderick (2010) to compare nuclear 2C content from the type locality of *N. saximontana* with two populations of *N. furnissii*, two populations of *N. intertexta* and two populations of *N. propinqua*.

We compared 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 visits to, or loans from, the following herbaria: ASU, BRY, CAS, IDS, UTC, UT, RSA, RICKS, RM, and US. We examined two to five individuals per population from a minimum of ten populations per species. We measured several vegetative and reproductive features using digital calipers for larger features and, for smaller features, made measurements from digital images taken with an Olympus SZX-12 dissecting microscopy using MicroSuite Five Basic Edition software (Olympus Soft Imaging Solutions Corp.). We assessed variation in measured features using Aabel 3.0.3 (Gigawiz Ltd. Co.).

## Results

Parsimony analyses recovered two trees of 27 steps from the concatenated cpDNA matrix (CI = 0.96; RI = 0.99), four trees of 51 steps from the ITS matrix (CI = 0.86; RI = 0.98), and two trees of 86 steps from the *Pistillata* matrix (CI = 0.97; RI = 0.99). In the cpDNA trees, *N. furnissii*, *N. saximontana*, and *N. propinqua* are each recovered as monophyletic groups (Fig. 1A). With ITS sequences, we observed a single repeat type in direct sequencing of *N. saximontana* that is distinct from *N. furnissii*, but recovered two repeats from *N. propinqua*. One of the *N. propinqua* repeats clusters with or near *N. furnissii*, while the other clusters near *N. intertexta* (Fig. 1B). With *Pistillata*, both *N. saximontana* and *N. propinqua* had two homeologs. The pattern of clustering of these homeologs for *N. propinqua* is the same as with ITS sequences, while for *N. saximontana*, one homeolog clusters tightly with *N. furnissii* while the other is sister to, but divergent in sequence from, *N. furnissii* and the homeologs of *N. propinqua* and *N. saximontana* that cluster with it (Fig. 1C).

We measured nuclear DNA content in picograms as follows: *Navarretia intertexta*: 2C = 7.69; *N. propinqua*, 2C = 12.54; *N. furnissii*, 2C = 5.85; and *N. saximontana*, 2C = 11.09. Qualitative morphological differences between *N. furnissii* and *N. saximontana* are wanting, while quantitative differences show some overlap in most measured characters (Fig. 2). Whereas *N. saximontana* flowers vary from white to white suffused with pink or blue, we have only observed white flowers in *N. furnissii*. Seed number, frequency of pronged calyx lobes (Table 1), and corolla length show the greatest utility in distinguishing these species.

**TABLE 1**. Percent of calyces observed with given patterns of pronged calyx lobes. Only patterns observed are included in the table, with the exception of a single observation of a 4-pronged lobe in *N. furnissii*, which is not recorded. Overall = percentage over all observations within each species; low and high = observations from individual populations within each species. "n:n: <5" shows values for calyces with any lobes bearing prongs.

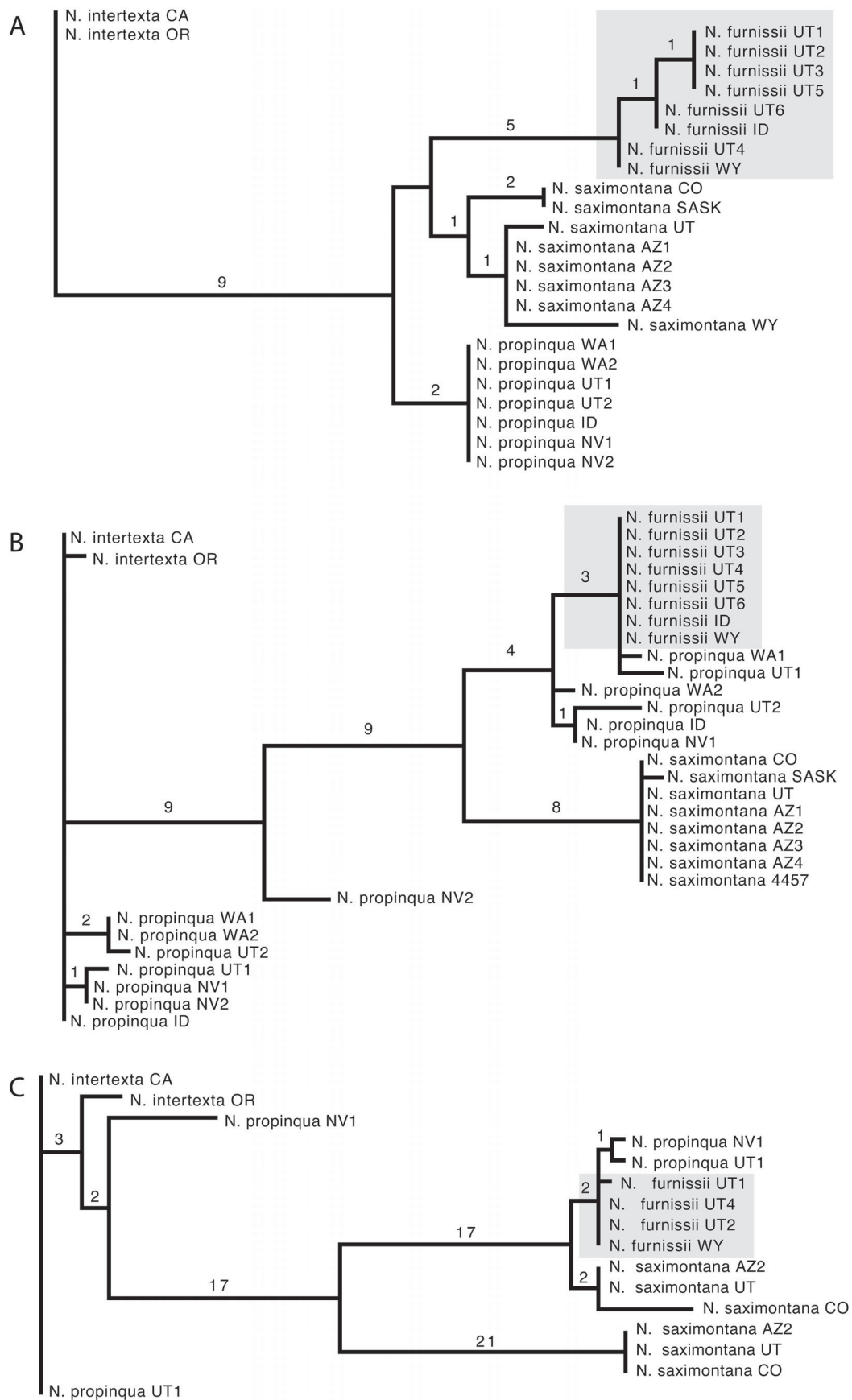| | Calyx lobes with three:two:no prongs (no prongs = entire lobes) | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 0:0:5 | 1:0:4 | 2:0:3 | 3:0:2 | 0:1:4 | 0:2:3 | 1:1:3 | 2:1:2 | n:n: < 5 |
| *N. furnissii* | | | | | | | | | |
| Overall | 16.2 | 12.1 | 35.4 | 1.0 | 6.1 | 13.1 | 14.1 | 2.0 | 83.8 |
| Low | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 47.1 |
| High | 52.9 | 20.0 | 84.6 | 12.5 | 16.6 | 40 | 30 | 12.5 | 100 |
| *N. saximontana* | | | | | | | | | |
| Overall | 91.2 | 5.3 | 0.0 | 0.0 | 1.8 | 0.9 | 0.9 | 0.0 | 8.8 |
| Low | 75.9 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| High | 100 | 10.3 | 0.0 | 0.0 | 6.9 | 3.4 | 3.4 | 0.0 | 24.1 |

**FIGURE 1.** Most parsimonious phylograms reconstructed from Parsimony analyses. Acronymns following species names are correlated to specimens in Appendix A. Total character change (base substitutions and indels) are reconstructed above interior branches (terminal values can be inferred by branch length). Branches not found in all shortest trees are indicated by arrows.
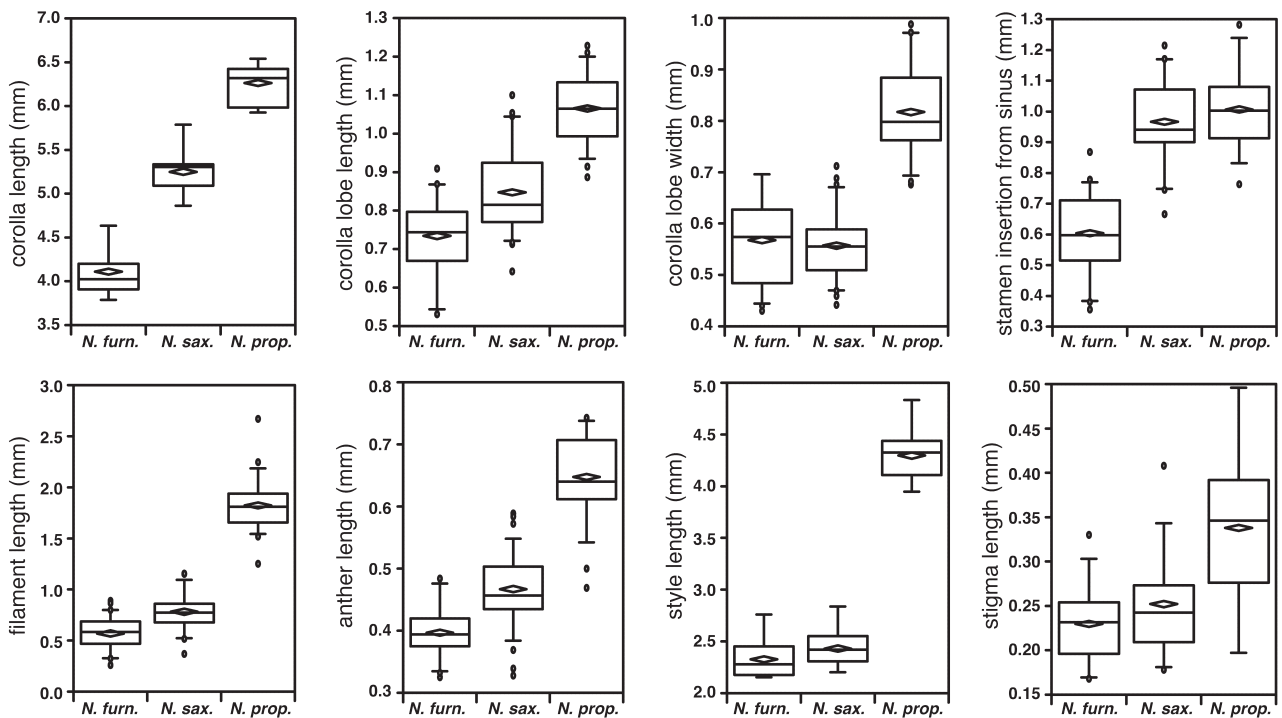
**FIGURE 2**. Box plots of variation in floral features among *N. furnissii*, *N. saximontana*, and *N. propinqua*. Boxes bound the 25 and 75 percentiles; horizontal line marks the 50 percentile, wiskers extend to the 5 and 95 percentiles with outliers shown as dots. The diamond demarks the mean (horizontal vertices) and standard deviation vertical vertices.

## Discussion

*Navarretia* section *Navarretia* is a well-supported monophyletic group of rather recent origin (Spencer & Porter 1997), with many species showing little molecular differentiation in the ITS region relative to between-species variation in some other *Navarretia* species complexes. *Navarretia saximontana* and *N. furnissii* (as "sp. nov. 3 UT") were included in comparative DNA sequencing analyses of *Navarretia* section *Navarretia* using cpDNA, nuclear ITS, and nuclear PI sequences (Johnson *et al.* in press). Chloroplast DNA placed *N. furnissii* in a trichotomy with *N. saximontana* and a clade composed of *N. propinqua* and *N. willamettensis*. ITS sequences placed *N. furnissii* strongly as sister to one of the homeologs of *N. propinqua*, with this pair sometimes sister to a clade composed of *N. saximontana* and *N. fossalis*. *Pistillata* sequences placed *N. furnissii* as sister to one homeolog of *N. propinqua*, with this clade forming a trichotomy with one homeolog of *N. saximontana* and one homeolog of *N. willametensis*. Additional sequencing in the present study was conducted to assess the consistency in variation observed in chloroplast, ITS, and *Pistillata* sequences between populations identified as *N. saximontana* and *N. furnissii* based on morphology. These analyses identify minor, but consistent differences between these species in chloroplast DNA, ITS, and *Pistillata* sequences, and comparative sequencing of these regions provide a reliable assay for species identification (Fig. 1), as well as some insights into the origins and relationships of the tetraploid taxa.

DNA data not only support delimiting *Navarretia furnissii* apart from the other sampled species, but also implicate it as one of the progenitors or a derivative/close relative of one of the progenitors of *N. propinqua*, with *N. intertexta*, or its close relative/ancestor the second progenitor. *Navarretia furnissii* also appears to have played a role in the formation of *N. saximontana*. The single ITS repeat in *N. saximonta* could be the result of homogenization of one of its two parental genomes to reflect the other parent (as documented in other species; e.g. Dierschke *et al.* 2009, Johnson *et al*. in press), or reflect an autopolyploid origin. *Pistillata* sequences show fixed differences in the two homeologs for *N. saximontana* across a broad geographic range, which may evidence an allopolyploid origin from two closely related species, or divergence in one homeolog following autopolyploidization but before this taxon became widely distributed.

Nuclear DNA content supports the inference of polyploidy in *N. propinqua* and *N. saximontana* relative to diploidy in *N. intertexta* and *N. furnissii*. The 2C value for *N. propinqua* (12.54 pg ) is very close to the additive 2C values of *N. intertexta* and *N. furnisii* (7.69 and 5.85 pg, respectively), while the 2C values for *N. saximontana* (11.09 pg) is close to twice that for *N. furnissii*. This is consistent with an autopolyploid origin for *N. saximontana*, although it does not rule out the possibility of an allopolyploid origin with an as yet undocumented diploid species, close to *N. furnissii*, acting as the second parent.

*Navarretia furnissii* and *N. saximontana* are very similar morphologically. Both species show variation in calyx morphology within a single plant and even within a single head of flowers. However, whereas calyces in *N. furnissii* populations typically have at least one calyx lobe two or three pronged (and often two lobes), calyces in *N. saximontana* populations usually lack any lobing whatsoever (Table 1). We have observed infrequent populations within both species with either fewer or more lobing than expected based on summary results for the species as a whole, but in each case the populations are consistent as expected for each species for corolla size and seed number. At the whole plant level, *N. furnissii* has the appearance of being a slightly smaller version of *N. saximontana* (Fig. 3). Given the small stature of both species, however, measurable differences are not great in magnitude. Corolla length consistently differs (Fig. 2), but pollen grains of the two species are indistinguishable in size and sculpture. In both taxa, the sexine is semitectate, reticulate, heterobrocate, with muri that are wide, flat, cross-etched and with pyrameidal micoechinations (Fig. 3). We did not survey more than six seeds in any fruit of *N. furnissii*, but *N. saximontanta* frequently has up to twice this many.

## Systematic Treatment

### *Navarretia furnissii* L.A.Johnson & L.M.Chan, *spec. nov.* (Fig. 3A, D–H).

Species with affinity to *N. saximontana* S.C.Spencer, but distinguished by being diploid (rather than tetraploid); in having a majority of calyces with one or two lobes 2–3 pronged (rather than most calyces with all lobes entire and only occasionally one or two lobes 2–3 pronged); having corollas less than 4.7 mm (rather than greater than 4.8 mm); and ovules 6 or fewer (rather than 6–12).

Type:—U.S.A. Utah: Summit County, in open, disturbed spaces in a sagebrush framed meadow between Hwy 150 and the Beaver Creek picnic area, ca. 0.2 miles east of mile marker 8, 40.62242° N, 111.14703° W, 2187 m; 7 July 2005, *L. A. Johnson & C. L. Johnson 05-197* (holotype BRY!, isotypes NY!, RM!, RSA!, UC!).

Annual plants, 1.0–6.5(–9.0) cm tall and wide, the primary head caulescent, generally with 1–10(–20+) secondary or tertiary heads at the tips of spreading or ascending lateral branches. Stem and branches yellowish green to reddish brown, puberulent to glandular-puberulent with the largest trichomes retrorse, uniseriate multicellular. Cotyledons linear. Lower leaves opposite or alternate with linear segments, glabrous to puberulent, 8–17(–30) mm long, with up to 6 entire or 2–3 pronged lobes on each side of the rachis. Upper leaves alternate, acerose, 5–15 mm long; the rachis glabrous to puberulent or glandular-puberulent and 2–6 mm long, the primary lobes 3–5 on each side of the rachis, glabrous, the lowermost often simple, the remainder generally 2–4 pronged. Outer bracts similar to upper leaves but 5–10 mm long; the widened rachis at the base 1.5–4.0 mm long, the primary lobes ca. 3 per side, generally 2–4 pronged, the apex 3-pronged. Inner bracts smaller, with an expanded, clasping, ciliate membranous-margined base (membrane narrower than the rachis). Flowering heads mostly 6–10 mm long, of 1–several cymules of ± 3 subsessile flowers. Calyx (4.7–)5.5–6.8(–7.5) mm long; the tube membranous, puberulent and obscurely glandular between ribs, 2.1–3.1 mm long, with 3–4 celled unbranched trichomes at orifice and on the adaxial rib surface at the membrane rib junction; the lobes 5, glabrous, acerose, the two longest lobes 3–5 mm, one or both usually 2–3 pronged, the three shorter lobes 1.5–3.2 mm and simple. Corolla funnelform, white, (3.7–)3.9–4.5(–4.7) mm long, not exceeding the longest calyx lobes; lobes oblong, (0.5–)0.6–0.8(–0.9) mm long and 0.4–0.7 mm wide, each with a single, generally unbranched vein. Stamen filaments (0.25–)0.40–0.70(–0.80) mm long and inserted (0.3–)0.4–0.7(–0.9) mm below sinuses; anthers positioned at throat orifice or slightly exserted, but

not to tips of corolla lobes; pollen deep yellow. Ovary oblong, 2 celled; the style (2.0–)2.2–2.5(–2.8) mm long; the stigma 2-lobed. Capsule 1.7–2.3 mm long, short apiculate, membranous, indehiscent at maturity. Seeds (2–)4–6, medium to dark brown, ovid-angular, 1.1–1.6 mm long, reticulate-pitted, mucilaginous when wet. Diploid.
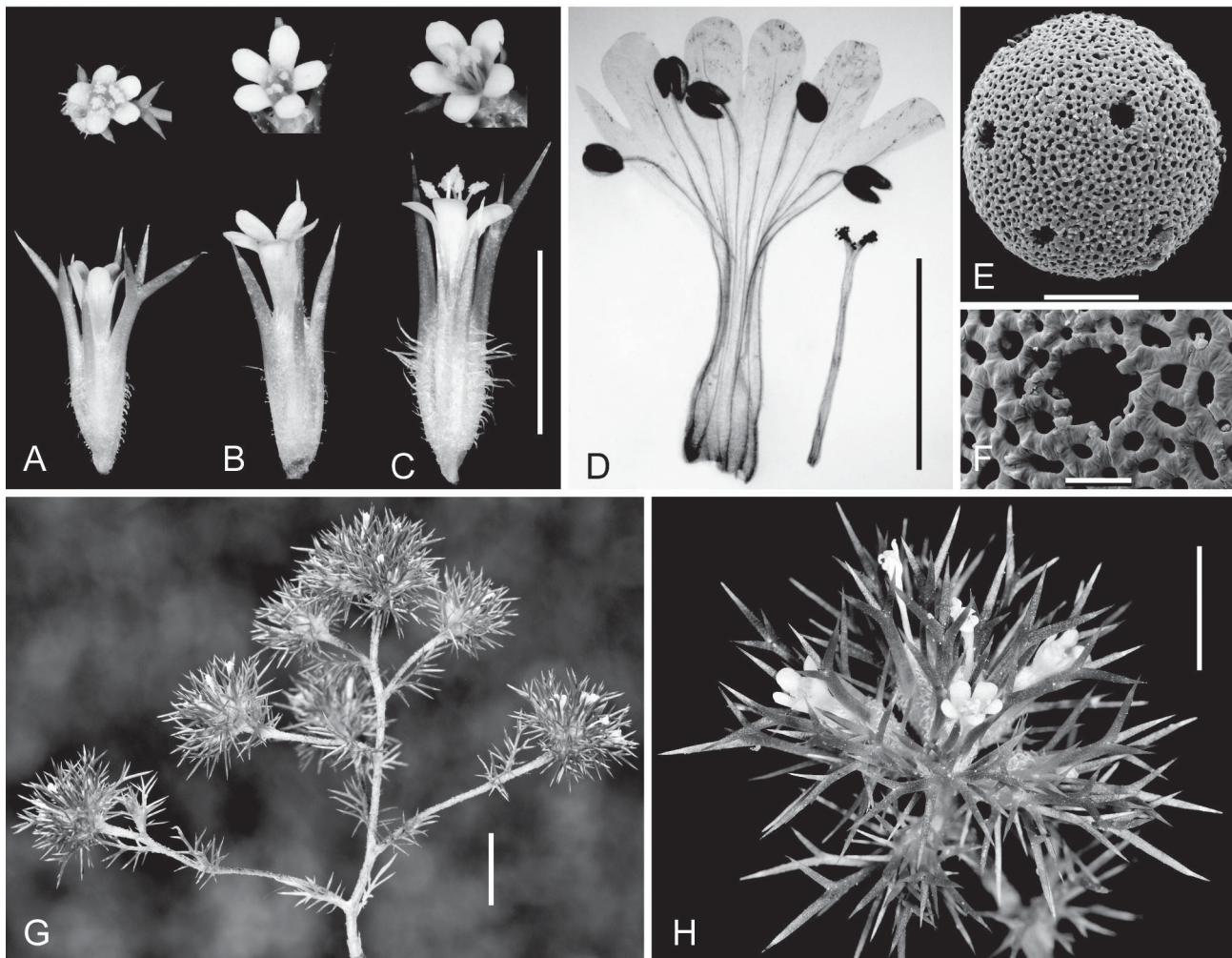


**FIGURE 3**. A–C Flowers of *Navarretia furnissii* and related species, top and side views, scale bar = 5 mm. A. *N. furnissii Johnson & Johnson 11-080*. B. *N. saximontana Johnson & Johnson 11-075*. C. *N. propinqua Johnson & Johnson 11-077*. D–H. *N. furnissii*. D. corolla split open, and style/stigma, scale bar = 2 mm; *Johnson & Johnson 05-197*. E, F. Pollen grain, *Johnson 07-069*. E. scale bar = 10 µm. F. scale bar = 4µm. G–H. *Johnson 09-073*. G. scale bar = 1 cm. H. scale bar = 5 mm.

**Habitat, distribution, and phenology**:—*Navarretia furnissii* occurs in seasonally moist pockets, vernal depressions, margins of pools, and open areas among grasses, forbs, and sagebrush in aspen communities in the Rocky Mountain floristic area (McLaughlin 1989). Presently known populations are concentrated in the Wasatch and Caribou Mountain Ranges of Utah and Idaho and consist of hundreds or thousands of individuals each. Range and population sizes suggest this species is not of conservation concern.

 Flowering occurs primarily in July (June–August), with mature capsules retained within calyces after plants have senesced. Similar to *N. saximontana* as reported by Spencer & Spencer (2003), the capsule is ruptured by seeds swelling from autumn rains within intact, or shattered, flowering heads. Seed germination proceeds following a short period of moist chilling (1–3 weeks at 4°C in a laboratory setting).

**Etymology**:—*Navarretia furnissii* is named to honor Blaine Furniss, retired professor of Botany at Brigham Young University. Professor Furniss was the primary author's first botanical mentor and is

responsible for instilling an appreciation for botany and a sense of wonder in countless students in subjects ranging from field botany to plant diversity, anatomy, morphology, classification, and evolution through his many years of service as an instructor at BYU.

**Notes**:—The earliest observed collection of this species is from Dry Lake, Cache County, Utah on 16 August 1897, *J. H. Linford s.n.* (US 960549; mounted on sheet with several collections of *N. intertexta*). No herbarium sheets were observed or populations visited by the authors that indicate co-occurrence with *N. saximontana*; however, based on herbarium data, the two species occur a maximum of 32 and 56 kilometers apart in Idaho and Colorado, respectively. *Navarretia furnissii* grows interspersed with *N. intertexta* and *N. breweri* at some locations in Utah, and *N. leucocephala* subsp. *leucocephala* has been collected in the vicinity of *N. furnissii* at Dry Lake in northern Utah.

**Additional specimens examined (paratypes)**:—U.S.A. Colorado: Routt County, Elkhead Mountains, N of Dry Fork Elkhead Creek, ca 1 airmile SW of Elkhead, grassy bottom of draw, elev. 6920–7040 ft, 29 June 2000, *Nelson 50147* (RM). Idaho: Bear Lake County, Georgetown Canyon, 16 August 1932, *Ray J. Davis 183-32* (IDS). Bingham County, NW end of Sheep Mt., 38 air mi N of Soda Springs, open areas of grassy meadow, elev. 6700 ft, 15 July 1971, *Holmgren & Martala 5433* (CAS, US, UTC). Bonneville County, Grays Lake vicinity, West Side Road, margins of small roadside marsh, elev. 1955 m, 13 July 2009, *Johnson 09-075* (BRY, UC, RSA); Grays Lake vicinity, Homer Valley, S of junction of Grays Lake Road and Long Valley Road, roadside clay soils, elev. 1946 m, 13 July 2009, *Johnson 09-077* (BRY, UC, RSA, IDS); Caribou National Forest, Caribou Basin, at junction of McCoy Creek Road and NF-164, dried mud, elev. 1946 m, 13 July 2009, *Johnson 09-078* (BRY). Caribou County, Blackfoot River Wildlife Management Area, sage habitat, late July 1997, *Maroney 268* (IDS). Clark County, Targhee National Forest, Centennial Mountains, Cottonwood Creek area, ca 6.5 miles N of Kilgore, moist meadow, elev. 6700 ft, 4 July 1992, *Markow 8608* (RM). Fremont County, Targhee National Forest, W slope Teton range, Cart Hollow, about 3 air miles NE of Lamont, Lodge pole pine forests with scattered meadows and wet areas, elev. 6200–6300 ft, 24 July 1991, *Hartman & Molina 30299* (RM). Teton County, Targhee National Forest, W slope Teton range, McRenolds Reservoir, ca 8 air miles E of Lamont, openings adjacent to river, elev. 7000 ft, 28 July 1991, *Hartman & Molina 30851* (RM). Utah: Cache County, Shore of Dry Lake, 8 July 1942, *Maguire 21596* (BRY); Summit, Jardine Canyon, on bare trampled clay in *Artemisia* community, 30 July 1935, *Maguire 12562* (BRY); Dry Lake, W side of Hwy 89 between Mantua and Wellsville, disturbed soils, elev. 1714 m, 13 July 2009, *Johnson 09-073* (BRY, RSA, UC). Summit County, 7.6 mi along Hwy 150 E of Kamas, dry ground next to a meadow, elev. 2210 m, 7 July 1984, *Goodrich 20811* (BRY, UTC); Edge of dry pond E of Mill Creek, near Bear River, elev. 8200 ft, 19 August 1927, *Goodman 316* (RM). Wasatch County, 15.5 mi E (79°) of Heber City, Little So. Fork Provo River, roadway in aspen-sagebrush, elev. 7500 ft, 11 Aug 1981, *Goodrich 16902* (BRY); By little South Fork Provo River, meadow sagebrush flat, elev. 7850 ft, 1 July 2004, *Corbin & Page 1132* (BRY); In drainages of sagebrush slopes adjacent to Hwy 32 from Heber to Kamas, ca 0.7 miles from mile marker 4, 19 July 2007, *Johnson 07-069* (BRY); Lodgepole Campground, Foreman Hollow, along trail and adjacent open areas among sagebrush, elev. 2449 m, 13 July 2007, *Johnson 07-035* (BRY); Telephone Hollow, S of Daniels Summit, dried drainage adjacent to restroom facility, 19 July 2007, *Johnson 07-073* (BRY). Wyoming: Lincoln County, W slope Grayback Ridge near McCain Guard Station, Bridger Natl. Forest, elev 6880 ft, open meadow, spring edge and drying shore, 19 July 1979, *Shultz & Shultz 3568* (RSA, USFS, UTC); Bridger National Forest, Grays River vicinity, disturbed side of Grays River Road ca 1.5 miles W of Bull Hollow Road, elev. 1959 m, 14 July 2009, *Johnson 09-080* (BRY); Bridger National Forest, along abandoned road NE of Grays River Road ca. 4 miles S of Bull Hollow Road, elev. 2036 m, 14 July 2009, *Johnson 09-081* (BRY).

*Navarretia saximontana* S.C.Spencer (2003: 198), *sp. emend*.

Plants as per the original description, with the longest two calyx lobes mostly entire, infrequently 2–3 pronged. Corolla 4.8–6.2 mm long, lobes 0.4–0.8 mm wide, 0.6–1.1 mm long. Stamen filaments 0.4–1.2 mm long, inserted 0.6–1.2 mm below the sinuses. Tetraploid.

Although widely distributed, our surveys indicate that type locality is the only known population within the state of Utah—with all other putitive populations representing *N. furnissii*. Of the paratypes listed in the original description of *Navarretia saximontana*, the following specimens agree with the circumscription of this species as defined here. CANADA. Saskatchewan: Crane Lake, Assiniboia, 20 June 1894, *Macoun 5545* (SASK, US!). U.S.A. Arizona: Coconino Co.: Ashurst Lake, ponderosa zone, near lake, 27 June 1980, *Lehto 24676* (RSA!); Schultz Spring, San Francisco Mts Forest Reserve, elev. 2500 m., 18 August 1901, *Leiberg 5861* (US!). Navajo Co.: 1 mi east of Pinetop, elev. 7300 ft, over-grazed meadow in Pinus ponderosa forest, 25 July 1946, *Parker 6071* (RSA!, ARIZ). Colorado, Jackson Co.: 8 mi W of Hebron in North Park, low meadow, elev. 9000 ft, 15 August 1898, *Shear & Bessey 3923, 3924* (RM!, US!, UTC!). Montana, Cascade Co.: Sand Goulee, 28 July 1887, *Anderson, s.n.* (OSC, RM!); Glacier Co.: vicinity of Glacier Park Station, dried up pool, 16 August 1919, *Standley 17730* (US!); Powell Co.: 10 mi NE of Helmville, edge of pothole in sagebrush flat, 1 July 1948, *Hitchcock 17896* (COLO, POM!, RM, RSA!, US!, UTC!). North Dakota, Hettinger Co.: Mott, low places in prairie, 20 July 1937, *Meisener s.n.* (US!). Mountrail Co.: Powers Lake, rather dry roadside ditch by moist prairie, 30 June 1946, *Stevens 872* (US!). Ramsey Co.: E of Devil's Lake, dry swamp in the open prairie, August 1839, *Geyer s.n.* (US!) Wyoming, Crook Co.: Between Alva and Aladdin, elev. 4400 ft, drying margin of small cattail swamp, clayey, 12 July 1960, *Porter & Porter 8346* (RSA!).

## Key to spiny navarretias of the intermountain western United States

1. Stem trichomes translucent, ± perpendicular to stem, typically glandular; corolla with 3 veins entering each lobe; stigma 3 parted; capsule hard, ovate, dehiscing regularly from the top into 3 valves at maturity (dry)......................2
- Evident stem trichomes opaque, ± appressed downward, eglandular, may be interspersed with obscure, minute glandular trichomes; corolla with 1 vein entering each lobe; stigma 2 parted or cleft; capsule membranous, indehiscent and conforming to seeds, eventually irregularly dehiscent when wet or ruptured by germinating seeds ...................4

2. Stems hairy, many trichomes approaching 1 mm or more in length; corollas white to light blue, pink, or lavender, eglandular externally...............................................................................................................................3
- Stems puberulent, trichomes glandular, less than 0.25 mm in length; corolla yellow, minutely glandular externally .. .................................................................................................................................. *Navarretia breweri*

3. Bracts ± palmately lobed, corollas 3.5–5.0 mm long, represented in region from Idaho................................................ ..........................................................................................*Navarretia divaricata* subsp. *divaricata*
- Bracts evidently pinnate, corollas 6–9 mm long, known in region from a single disjunct collection from the Arizona Strip (otherwise found in Southern California and Baja California) ........................................*Navarretia peninsularis*

4. Base of inner bracts concave expanded, the rachis much wider than a thin, membraneous margin; pollen deep yellow .......................................................................................................................................................5
- Base of inner bracts not concave expanded, the rachis equal or narrower than the broad, membranous margin; pollen white to cream.......................................................................................................................................8

5. Trichomes of calyx tube evidently overlapping, tangled, longer than the spacing between trichomes; stamens exerted beyond mid corolla lobe typically to the lobe tips or beyond.......................................................................6
- Trichomes of calyx tube (excepting fringe of trichomes along sinus margin) sparse, seldom overlapping, generally equal or shorter than the spacing between trichomes; stamens exerted to or just exceeding the sinus of the corolla lobes ............................................................................................................................................7

6. Plants generally mounding with multiple heads in close proximity; corolla (4.5–)5.0–6.5 mm long; stamens exerted ± to corolla tips .................................................................................................*Navarretia propinqua*
- Plants generally upright, or much branched with multiple heads separated along stems; corolla 6.0–8.0(–12.5) mm long; stamens exerted well beyond tips of the corolla lobes.................................................. *Navarretia intertexta*

7. Most calyces with one or two lobes 2–3 pronged; corollas less than 4.7 mm long; seeds 4–6...... *Navarretia furnissii*
- Most calyxes with all lobes entire, or infrequently with one lobe (rarely two) 2–3 pronged; corollas greater than 4.8 mm long; seeds 6–12 ................................................................................................ *Navarretia saximontana*

8. Several calyx lobes per flower 2–3-pronged, rarely all entire; corolla included in calyx at anthesis, corolla throat 1–2 mm wide.................................................................................................... *Navarretia leucocephala* subsp. *minima*
- All calyx lobes per flower entire, rarely one or two 2–3 pronged; corolla exserted from calyx at anthesis, throat 2–3 mm wide.............................................................................................*Navarretia leucocephala* subsp. *leucocephala*

## Acknowledgements

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## Appendix I. Voucher specimens used in DNA sequencing studies.

Presented with acronym label used in Fig. 1 followed by the collector and collector number. All specimens are deposited at BRY, available online at http://lib.byu.edu/sites/scholarsarchive/life-sciences/s-l-welsh-herbarium-bry/.

*Navarretia furnissii*: UT1: *Johnson 98-016*. UT2: *Johnson & Johnson 05-197*. UT3: *Johnson 07-068*. UT4: *Johnson 07-069*. UT5: *Johnson 07-071*. UT6: *Johnson 09-073*. ID: *Johnson 09-077*. WY: *Johnson 09-081*.

*Navarretia saximontana*: CO: *Zhang & Zhang 4008*. SASK: *Ledingham & Hooper 10711*. UT: *Johnson 07-036*. AZ1: *Johnson 07-037*. AZ2: *Johnson* 07-044. AZ3: *Johnson 07-055*. AZ4: *Johnson 07-061*. WY: *Dueholm 4457*.

*Navarretia propinqua*: WA1: *Johnson & Johnson 94-048*. WA2: *Johnson & Johnson 95-032*. ID: *Holmgren 6158*. UT1= *Johnson 04-163*. UT2 = *Johnson et al. 09-067*. NV1 = *Howell s.n.* (BRY 614915). *Howell s.n.* (BRY 614917)

*Navarretia intertexta*. CA: *Johnson 93-088*. OR: *Johnson & Halse 05-206*.