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Decrypting Cryptic Species: Morphological and Molecular Evidence for Recognizing *Navarretia linearifolia* as Distinct from *N. sinistra* (Polemoniaceae)

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Abstract—The unified species concept and a criterion of limited homogenizing gene flow as evidenced by genetic and morphological markers were applied to species delimitation within *Navarretia sinistra*. Concordant patterns of variation diagnose two morphologically cryptic species. As a consequence, the basionym *Gilia linearifolia* is here lectotypified and re-established for this long neglected epithet. ***Navarretia linearifolia*** shows strong differentiation from *N. sinistra* in allozyme data and DNA sequences from chloroplast regions, nrDNA, and introns of the low copy nuclear genes *idhA*, *idhB*, and *g3pdh*. In macroscopic features, *N. linearifolia* differs from *N. sinistra* primarily in tendencies, rather than absolute differences. Two finer-scale features are diagnostic: pollen sexine sculpturing and mature seed color. The combination ***Navarretia linearifolia*** subsp. ***pinnatisecta*** is made for the large flowered populations of this species geographically restricted to the NW region of the California floristic province. The smaller flowered ***N. linearifolia*** subsp. ***linearifolia*** extends from California to Washington, with a more westwardly distribution compared to *N. sinistra*, which ranges east into Idaho, Utah, and Colorado.

Keywords—cryptic species, *Gilia*, lectotype, species criteria, species delimitation, unified species concept.

Estimates of taxon diversity within genera may depart from biological reality for several reasons. Taxon concepts at both generic and species levels may vary by taxonomist. Some species that can be identified readily may have escaped recognition or acceptance by workers because diagnostic features were overlooked. And, conversely, some named species may be based on the inflation of a novel feature that lacks taxonomic relevance. Additionally, some species may be truly cryptic, with substantial genetic change masked behind indistinguishable or nearly identical external morphologies. These scenarios are not necessarily discrete or mutually exclusive. Differences in taxon concepts often stem from differences in opinion regarding diagnostic features, and many cryptic species complexes dissolve upon discovery of diagnostic characters for distinguishing each species. Regardless of the reason, species circumscriptions that reflect biological reality are important not only for accurate assessments of taxon diversity, but also for conservation planning and studies of character evolution, intraspecific phylogeography, and so forth.

As hypotheses, species circumscriptions are testable and a variety of means for assessing and delimiting species boundaries exist (e.g. Sites and Marshall 2003, 2004; Wiens and Penkrot 2002). Criteria that directly or indirectly assess homogenizing geneflow are particularly useful in distinguishing biological breaks between sibling or cryptic species; that is, among evolutionarily separate lineages not easily distinguished morphologically because their diagnosis requires methods beyond, as Cronquist (1988) stated when discussing criteria for species recognition, "ordinary means." Certain taxa now in *Navarretia* but circumscribed as *Gilia* section *Kelloggia* by Day (1993a) have been confused in a manner consistent with their designation as a cryptic species complex. Grant and Grant (1954) constructed a taxon concept for *Gilia capillaris* Kellogg that recognized this species as variable in several respects. Day (1993a) noted vegetative, calyx, and pollen differences in *G. capillaris* as thus circumscribed and segregated the previously established *Gilia sinistra* M. E. Jones as a distinct species. Day's observations untangled much of the long history of confusion regarding these two species whose morphological similarities are most striking when considered in light of DNA-based phylogenies that indicate they do not form a monophyletic group exclusive of species of the vegetatively distinct genus *Navarretia* (Johnson et al. 1994; Porter and Johnson 2000). An iterative series of investigations within these taxa has revealed an even more striking instance of cryptic diversity. This work, in conjunction with a thorough review of nomenclature indicates that, like *Gilia sinistra* hidden by synonymy in *G. capillaris*, the long neglected name *G. linearifolia* Howell should be reestablished (as *Navarretia linearifolia* (Howell) L. A. Johnson) for material recently considered conspecific with *Gilia sinistra*/*Navarretia sinistra* (M. E. Jones) L. A. Johnson (Day 1993a, b; Grant and Day 1998; Porter and Johnson 2000).

Here, a variety of data used to address species limits in this cryptic complex of nonspiny *Navarrretia* are presented. To facilitate communication, the nomenclature proposed herein (Table 1) is used hereafter, except when discussing names in their historical context. A key to the species of nonspiny navarretias is also provided.

Materials and Methods

The unified species concept (de Queiroz 2007), which equates species to segments of separately evolving metapopulation lineages, was used as the basis of species delimitation. Indirect inferences of gene flow were used as a criterion for recognizing such lineages under the premise that, for sexually reproducing species, gene flow will homogenize populations within a metapopulation lineage, whereas the absence of gene flow ultimately will lead to divergence between distinct metapopulation lineages in molecular characters, morphological characters, or both. Allozymes, DNA sequence variation, and morphology were used to assess divergence between *N. linearifolia* and *N. sinistra* as circumscribed here against the alternative hypothesis that these two entities compose a single species as treated prior to this study.

Allozyme Data—Allozyme variation was surveyed from 30 individuals per population from 10 populations of *N. linearifolia*, two populations of *N. sinistra*, and four populations of *N. capillaris* (included for comparison; Appendix 1). Uneven numbers of populations for each of the two putative species, *Navarretia linearifolia* and *Navarretia sinistra*, were surveyed because populations were sampled before cryptic diversity was suspected. Seven enzymes (10 putative loci) were scored reliably from assays conducted on 11% starch gels using buffer systems as follows. Buffer 6: *pgi-1* and *pgi-2*; buffer 8-: *aat-1*, *aat-2*, *tpi-1*, and *tpi-2*; buffer 11: *idh*; buffer 11+: *g3pd*; buffer M: *6pgd-1*, and *6pgd-2* (buffers 6, 11, and M from Soltis et al. 1983; 8- and 11 + from Haufler 1985). Two control individuals were included on each gel and a summary gel of two individuals from each population was also run to ensure accuracy of allelic scoring.

Allozyme Analysis—Genodive 2.0b15 (Meirmans and van Tienderen 2004) was used to perform several analyses based on allelic diversity. An analysis of molecular variance (AMOVA; Excoffier et al. 1992; Michalakis

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TABLE 1. Comparison of Historical classifications of the nonspiny navarretias, an informal, nonmonophyletic group treated formally as *Gilia* section *Kelloggia* by Day (1993a,b). The placement of these species in *Allophyllum* by Grant and Day (1998) and *Navarretia* by Porter and Johnson is not detailed because those treatments are essentially nomenclatural variations of Day (1993a,b). Additional notes about equivalency and the taxon concepts of these authors are found in the taxonomic treatment section of this paper.

Brand 1907	Grant and Grant 1954	Day 1993a,b	This work
Gilia leptalea subsp. *euleptalea*	*Gilia leptalea* subsp. *leptalea*	*Gilia leptalea* subsp. *leptalea*	*Navarretia leptalea* subsp. *leptalea*
—	*Gilia leptalea* subsp. *bicolor*	*Gilia leptalea* subsp. *bicolor*	*Navarretia leptalea* subsp. *bicolor*
Gilia leptalea subsp. *capillaris*	*Gilia capillaris*	*Gilia capillaris*	*Navarretia capillaris*
Gilia subalpina	Synonym of *Gilia capillaris*	—	Synonym of *Gilia capillaris*
Synonym of *Gilia leptalea* subsp. *capillaris*	Synonym of *Gilia capillaris*	—	*Navarretia linearifolia*
Collomia sinistra	Synonym of *Gilia capillaris*	*Gilia sinistra* subsp. *sinistra*	*Navarretia sinistra*
—	*Gilia leptalea* subsp. *pinnatisecta*	*Gilia sinistra* subsp. *pinnatisecta*	*Navarretia linearifolia* subsp. *pinnatisecta*

and Excoffier 1996) was performed using an infinite allele model with hierarchal nestings of individuals, populations, and species, both with and without *Navarretia capillaris* included. Nei's genetic distance (N; Nei 1978) was also calculated pairwise between populations with the resulting distance matrix imported into PAUP* 4.0b10 (Swofford 2002), which was used to construct an UPGMA cluster phenogram from the distance matrix. GenoDive was also used to conduct a principal components analysis (PCA) based on the covariance matrix of population allele frequencies. The UPGMA phenogram and PCA graph were examined for the presence of a single cluster with the two putative species interspersed, or two well differentiated population clusters; the latter pattern is compatible with a hypothesis of a barrier to homogenizing gene flow (and, by extension, the existence of two species), whereas as the former pattern would fail to support such a hypothesis.

***DNA Sequence Data*—**DNA was isolated and specific gene sequences obtained for the chloroplast *trnL–trnL–trnF* (Taberlet et al. 1991), *trnS–G* (Hamilton 1999), and *trnG–G* (Shaw et al. 2005) regions, the nuclear ITS region (White et al. 1990), and partial sequences of the nuclear *idhA*, *idhB* (Johnson and Johnson 2006), and *g3pdh* (Strand et al. 1997) genes using primers published in these references. For all genes, the PCR profile consisted of 3 min at 95°C, followed by 30 cycles of 1 min at 94°C, 1 min at 52°C, and 1 min at 72°C, followed by 72°C for 8 min. Amplification products were sequenced directly following cleanup for the chloroplast, ITS, and, for most individuals, also the low copy nuclear genes. Amplification products from three individuals were cloned for *idhA* and *g3pdh* using Topo TA kits (Invitrogen Corp, Carlsbad, California) and 3–5 colonies sequenced primarily as an exploratory exercise; in no case did recovered alleles vary by more than 2–4 nucleotides over the length of the sequence and the consensus sequence was used in the data matrix. For all genes, both DNA strands were cycle sequenced (BigDye v.3, Applied Biosystems, Foster City, California) and electrophoresed on an AB 3730xl automated sequencer at Brigham Young University. For nrDNA ITS and the *trnL–trnL–trnF* regions, individuals from ca. 40 populations were initially screened to understand relationships among genotypes, geography, and phenotypes. Given consistent correspondence between major ITS and cpDNA grouping from this initial screening, individuals from sixteen populations each of *N. linearifolia* and *N. sinistra* were sampled from across their geographic distributions and sequenced for all cpDNA regions (Appendix 1). A subset of eight populations of each taxon were also surveyed for *idhA*, and four populations of each were surveyed for *idhB and g3pdh*. Individuals from two to five populations of *Navarretia capillaris* were also sequenced, depending on the DNA region, for comparison (Appendix 1). Individuals of *N. linearifolia* from one population (*Johnson 94–081*) are apparently divergent at the annealing site for one primer in the chloroplast *trnG–trnG* region, and we were unable to obtain this sequence from this single population.

***DNA Sequence Analysis*—**Sequences were assembled into five primary matrices (ITS, cpDNA, *idhA*, *idhB,* and *g3pdh*) and aligned by eye using Se-Al (Rambaut 1996). Matrices (TreeBASE accession number S2646) were analyzed with PAUP* using parsimony as the criterion with 100 replications of random addition, TBR branch swapping, and amb- selected for collapsing zero length branches. Indels were not scored as additional characters in these analyses to assess divergence based on nucleotide substitutions alone. Indels unique to each putative species were identified during the alignment phase of each matrix, however, and these were mapped a posteriori. Resulting phylograms were rooted for presentation purposes only by designating *N. capillaris* as a monophyletic sister to the remaining sequences.

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. The significance of exclusivity was tested by searching for trees incompatible with a constraint tree with forced exclusivity (i.e. reciprocal monophyly) for *N. linearifolia* and *N. sinistra*. The shortest trees incompatible with this constraint were compared with the shortest unconstrained trees for each data set using Templeton's (1983) application of the Wilcoxon signed-rank test.

***Morphological Data*—**Observations were made from the field, extensive new collections housed at BRY, a limited number of common garden plants grown from seed, and over 400 herbarium sheets from BRY, CAS, CIC, GH, JEPS, NY, ORE, POM, RENO, RICKS, RM, RSA, SRP, UC, US, UT, UTC, and WS).

Character surveys covered quantitative and qualitative vegetative and reproductive features. Most observations were made from dried, pressed material but floral features were examined after first rehydrating flowers in Pohl's solution (Pohl 1965). Leaves were measured with a digital caliper, and other features measured from digital images taken with an Olympus SZX-12 dissecting microscope using Image-Pro Plus (Media Cybernetics Inc., Bethesda, Maryland) or MicroSuite Five Basic Edition software (Olympus Soft Imaging Solutions Corp., Lakewood, Colorado). Seed color was determined by comparison of mature seeds under a variety of lighting conditions directly on color standard swatches (Munsell color company 1948). Pollen sexine sculpting was examined on both untreated and acetolized pollen grains and compared with micrographs and descriptions of other pollen grains (Buchner and Weber 2000). Both pollen and seeds were coated with 60% palladium and 40% gold prior to examination under an electron microscope at BYU or Ranch Santa Ana Botanic Garden.

***Morphological Analysis*—**Morphological comparisons centered on discovering features that could distinguish *N. linearifolia* from *N. sinistra* in the context of specimen aggregation analysis (SAA; Snow et al. 2003; see also Davis and Nixon 1992; Wiens and Servedio 2000) rather than statistically describing the range of variation in each species across the all characters examined. For individual qualitative characters, *t* tests for assessing the null-hypothesis of nonsignificance between sample means and box plots for visualizing ranges of variation were used were as exploratory devices (ProStat vs. 5; Poly Software International, Pearl River, New York). When it became evident that a feature was not useful diagnostically, it was eliminated from further consideration. Some features, such as quantitative leaf measurements and presence of upper leaf lobes, were surveyed widely but eliminated as too variable to be informative. Other features, such as pollen morphology and mature seed characteristics, were surveyed from a narrower pool of individuals while endeavoring to maintain wide geographic coverage.

Recognition of morphological groups that correspond to groups also defined by allozyme and DNA data provides strong corroborating evidence for the delimitation of evolutionarily independent metapopulation lineages.

RESULTS

***Allozyme Data*—**The 10 allozyme loci surveyed revealed a total of 21 alleles. GPD, PGI-1, PGD-2, and TPI-2 were monomorphic whereas PGD-2 and PGI-2 had the highest number of alleles per locus with 4 and 5, respectively. The two

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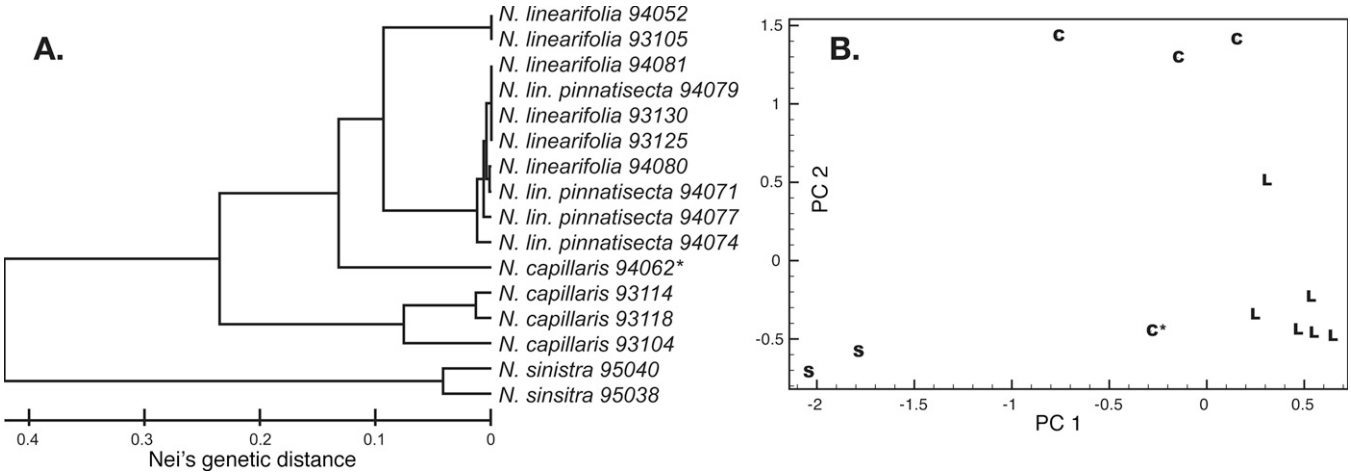


Fig. 1. Genetic differentiation based on allozyme analyses. A. UPGMA phenogram of mean genetic distance (Nei 1978) among populations of *N. capillaris*, *N. linearifolia*, and *N. sinistra*. B. Principle components clustering of populations based on the covariance matrix of population allele frequencies. "C" = *N. capillaris*; "L" = *N. linearifolia*; and "S" = *N. sinistra*. *Navarretia capillaris 94062** (C*) represents a population putatively introgressed with the high elevation race of *N. leptalea* subsp. *bicolor*.

Navarretia sinistra populations were fixed for an allele unique to this species at PGD-2. An AMOVA of the full data set revealed that 66.7% of the allelic variation exists among species, 23.6% among populations within species, 4.3% among individuals within populations, and 5.4% within individuals. Excluding *N. capillaris*, these values shifted to 82.3% among species, 10% among populations within species, 2.7% among individuals within populations, and 5% within individuals. Permutation tests of these data were significant ($p = 0.001$) in all cases. Pairwise comparison of allozyme variation between populations showed considerable divergence between *N. linearifolia* and *N. sinistra* by both UPGMA clustering of Nei's genetic distance (Fig. 1a) and by the PCA analysis of the covariance of population allele frequencies (Fig. 1b). *Navarretia sinistra* shows greater genetic differentiation from *N. linearifolia* (> 40%) than does the outgroup species, *N. capillaris* (12–22%).

DNA Sequence Data—For all DNA regions, maximum parsimony analyses recovered trees (Table 2) that place *N. linearifolia* and *N. sinistra* in exclusive groups with considerable reconstructed (ACCTRANS) base substitutions separating the two groups (Fig. 2). Shortest trees that did not recover *N. linearifolia* and *N. sinistra* as reciprocally exclusive were significantly longer than the shortest unconstrained trees for all DNA regions (Table 2). Additional fixed character differences, in the form of indels unique to *N. linearifolia* or *N. sinistra*, were also observed (Fig. 2).

Morphological Data—Few morphological features discriminate unambiguously between *N. linearifolia* and *N. sinistra*. Variation in the angle of divergence of the pedicel from the stem, and the number of anastomoses per flower (Fig. 3) showed significant differences between their means but with overlapping ranges of variation (Fig. 4). Pollen sexine sculpturing (Fig. 3) and mature seed color are diagnostic and corresponded with the groupings recovered via molecular data in all observations.

Table 2. Descriptors of the DNA sequence data matrices and the maximum parsimony trees resulting from analyses of these data. "STDE" = shortest tree(s) destroying exclusivity; P_{STDE} = probability that the STDE and the unconstrained shortest trees are supported similarly by the data based on the Wilcoxon signed rank test (Templeton 1983).

	ITS	cpDNA	*idhA*	*idhB*	*g3pdh*
Aligned characters	631	2,485	1,260	1,356	964
Variable characters	75	67	182	171	142
Parsimony informative characters	66	65	112	130	105
Number of shortest trees	> 5,000	3	2	1	1
Tree length	84	71	209	193	152
CI	0.98	0.94	0.91	0.96	0.97
RI	0.99	0.99	0.96	0.97	0.98
STDE length	97	85	220	212	171
P_{STDE}	0.008	0.005	0.002	0.0001	< 0.0001

Discussion

Distinguishing between the kind of entities species are and the criteria applied for diagnoses provides a framework for delimiting species empirically (de Quieroz 1998, 2007; Sites and Marshall 2004). As illustrated by de Quieroz, evolution does not occur simultaneously with respect to recognition criteria that form the heart of competing species concepts. Thus, while reciprocal exclusivity (or monophyly on a rooted tree) across many loci provides evidence for species limits (Baum and Shaw 1995), evolutionarily distinct metapopulations at a different stage of speciation may show incomplete lineage sorting at one or more loci (Doyle 1995; Knowles and Carstens 2007). Likewise, examples of strong morphological differentiation between species without much genetic differentiation are known (e.g. Witter and Carr 1988; Soltis et al. 1996), as are examples of strong genetic differentiation without obvious morphological divergence (e.g. Odrzykoski and Szweykowski 1991). Correspondence across multiple data types and recognition criteria provides increasing confidence in the delimitation of species boundaries.

Navarretia sinistra as heretofore circumscribed comprises two evolutionarily independent metapopulation lineages that show strong molecular differentiation, but relatively weak morphological differentiation. These lineages are here

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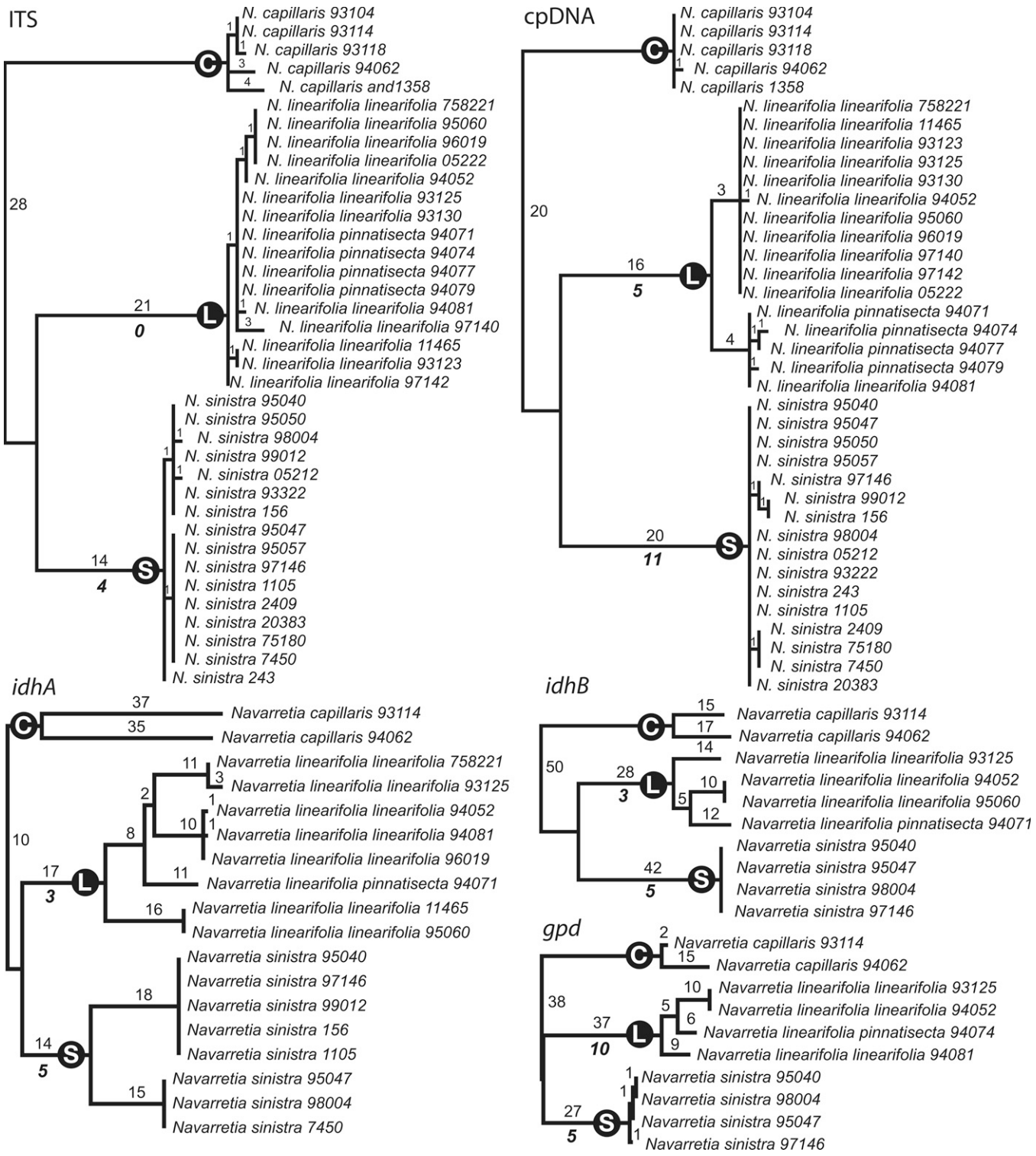


FIG. 2. Phylograms of selected single most parsimonious trees (Table 2) for separate DNA regions showing relative divergences in reconstructed bases substitutions (ACCTRANS) above branches among populations and species. Note that populations of each putative species coalesce into exclusive groups, as indicated by the lettered black circles: C = *N. capillaris*; L = *N. linearifolia*; and S = *N. sinsitra*. Each phylogram is rooted with *N. capillaris* as a monophyletic sister to *N. linearifolia* and *N. sinsistra*. The number of indels unique to, and invariant within, *N. linearifolia* or *N. sinistra* (relative to the other species plus *N. capillaris*) is shown in italics below the branch leading to these species.

recognized as *N. linearifolia* and *N. sinistra*. Continuing a taxonomic convention that formally recognizes significant infraspecific variation within this material, *Navarretia linearifolia* consists of two subspecies: a large flowered, geographically restricted form (*N. linearifolia* subsp. *pinnatisecta*) that intergrades in northwestern California with the typical, small flowered and geographically wide-ranging form (*N. linearifolia* subsp. *linearifolia*). Owing to their similar sized flowers, it is this latter material that is difficult to distinguish morphologically from *N. sinistra*.

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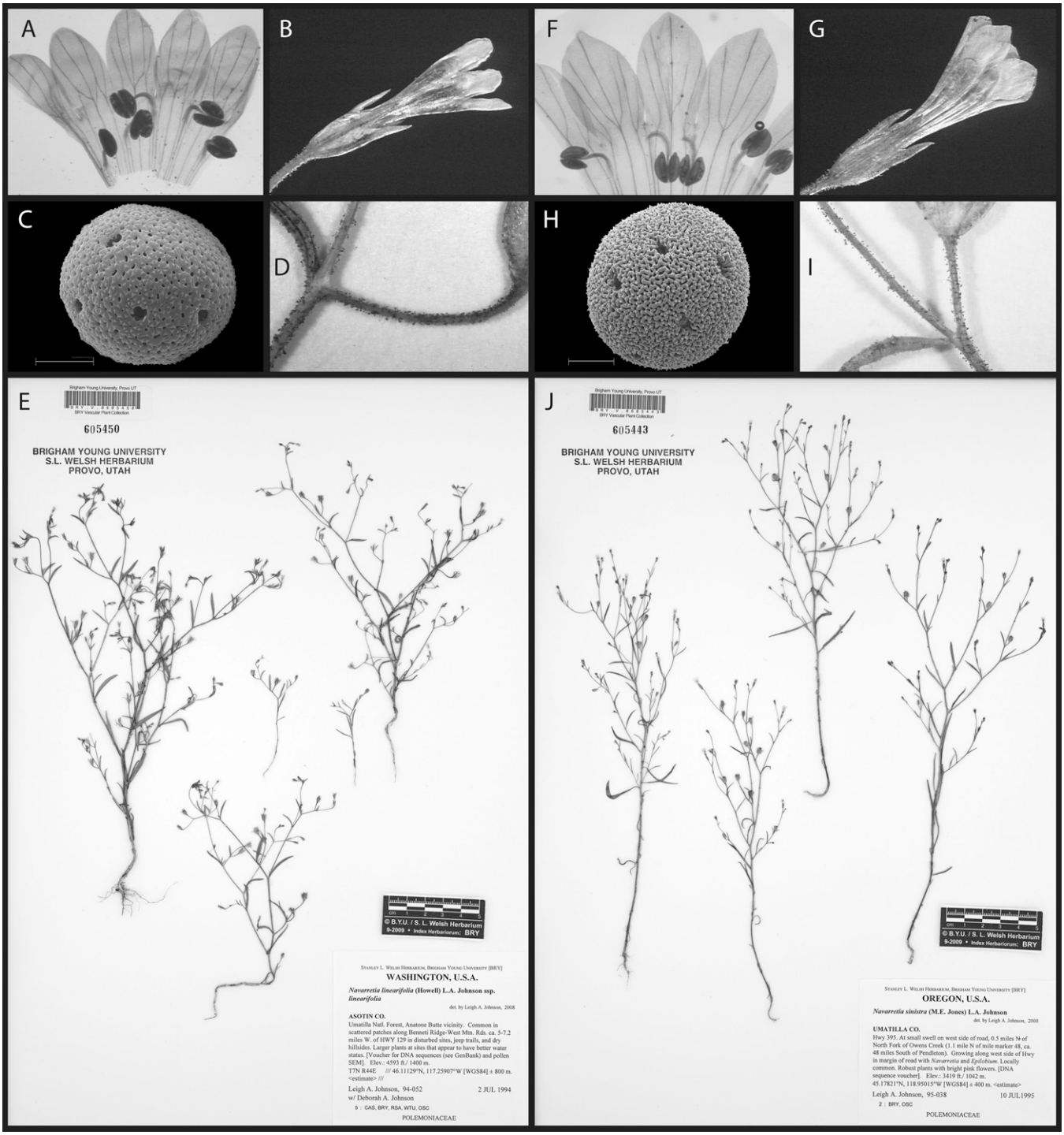


FIG. 3. Comparative morphology; paired images (A and F, B and G, etc., are at the same level of magnification). A–E. *Navarretia linearifolia*. A. corolla venation, *L. Johnson 97–142*. B. pressed flower, *L. Johnson 95–065*. C. pollen grain, *L. Johnson 97–142*. D. pedicel, *L. Johnson 94–052*. E. whole plants, *L. Johnson 94–052*. F–J. *Navarretia sinistra*. F. *L. Johnson 93–085*. G. *L. Johnson 95–057*. H. *L. Johnson 93–085*. I. *L. Johnson 99–012*. J. *L. Johnson 95–038*. All vouchers deposited at BRY.

Cryptic species may be defined, following Mayr's (1942, 1963) discussion of sibling species, as "morphologically similar or identical natural populations that are reproductively isolated" (see also Gornall 1997). The taxonomic literature is replete with studies involving the decrypting of cryptic diversity; new species described from material collected for many years and identified as one species or another before being differentiated and formally recognized. Recent examples of this in the phlox family include *Phlox pattersonii* Prather (Prather 1994), *Navaretia saximontana* S. C. Spencer and *N. willametensis* S. C. Spencer (Spencer and Spencer 2003), *Collomia wilkenii* L. A. Johnson and R. L. Johnson (Johnson and Johnson 2006), and *Dayia grantii* J. M. Porter (Porter and Johnson 2000), among others. In some instances (e.g. Spencer and Spencer 2003), molecular data corroborated patterns first observed from morphological study.

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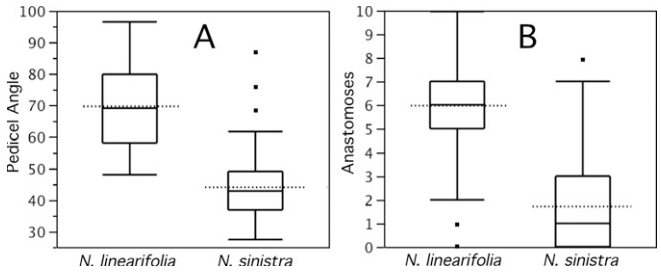


FIG. 4. Box plots for two characters with different means and medians between species (n = 60/species), but substantially overlapping ranges of variation. The upper and lower bounds of the box are the 75th and 25th percentiles, respectively. The solid line within the box is the median, and the dashed line is the mean. The upper and lower whiskers are 1.5 × (interquartile range) above and below the 75th and 25th percentiles, respectively. Outliers are indicated by dots.

In contrast, here, molecular data provided the impetus for a reconsideration of morphology: unexpected molecular variation in two populations from Oregon relative to populations sampled elsewhere in Oregon, Washington, and California led to even more widespread geographic sampling, morphological scrutiny, and a thorough review of nomenclature.

The degree of crypsis between *N. linearifolia* and *N. sinistra* is unusual (Fig. 3; see also representative herbarium sheets BRY0605435-BRY0605469 and BRY0605669-BRY0605672, at http://lib.byu.edu/sites/scholarsarchive/life-sciences/s-l-welsh-herbarium-bry/), particularly in light of phylogenetic analyses that place these species in disparate parts of *Navarretia* (Johnson, in prep). Day's close scrutiny of this material in the 1980s (culminating in Day 1993a), while working to segregate *Gilia sinistra* subsp. *sinistra* from *G. capillaris* (and *G. sinistra* subsp. *pinnatisecta* from *G. leptalea*) resulted in no hints, published or on annotation labels, that she suspected *G. sinistra* subsp. *sinistra* was anything other than a single taxon. Both *N. linearifolia* and *N. sinistra* are diploid annuals with an upright habit, leafy throughout, and equally glandular with structurally similar stipitate glands. *Navarretia sinistra* tends to be taller with a longer, straighter primary axis with branches departing at narrow angles, whereas the primary axis in *N. linearifolia* subsp. *linearifolia* can be more difficult to follow above the bases because branches are often divergent. This pattern extends to the pedicels that generally depart at a narrower angle from the stem in *N. sinistra* than do the pedicels in *N. linearifolia* (Figs. 3, 4). The wider angle of pedicel divergence in *N. linearifolia* often leads to the pedicel bending to form a "sideways J" that presents the flower in a nearly vertical orientation. Leaves in both species are lanceolate and may be palmatifid above, but may also be entire throughout in both species. Flowers in both species are similar in size, shape, color, stamen insertion, style length, and so forth, but the three veins entering each corolla lobe usually remain free from each other in *N. sinistra,* whereas they usually branch and form anastomoses in *N. linearifolia* (Figs. 3, 4). After reviewing hundreds of herbarium sheets and hundreds of plants from recent collections with known genetic identities, a gestalt formed by the angle of stem and pedicel divergence is useful for identification in many, but not all, cases.

As with all generalizations, the difficulty with the comparisons above is that they do not adequately describe the range of variation within either species (Fig. 4). Plants of the larger flowered *N. linearifolia* subsp. *pinnatisecta* often have a well defined, straighter central axis, are often larger in stature, and may lack strongly curved pedicles. Curved pedicels may be wanting on individual plants in any population of *N. linearifolia* subsp. *linearifolia*, but tend to be present on some or most plants and have been observed on even few flowered plants of only 3 or 4 inches in height. Likely based on moisture availability, both species are found in nature in small-stature forms and, in the greenhouse, both can grow to equally large statures. Even the pinnatifid lower leaves more characteristic of *N. linearifolia* subsp. *pinnatisecta* were produced on some plants of *N. linearifolia* subsp. *linearifolia* and *N. sinistra* in the greenhouse. Plants of *N. linearifolia* subsp. *linearifolia* from Humbolt county, California, also tend to have shorter, straighter pedicels like *N. sinistra*, though they also tend to be leafier above with small clusters of immature flowers at the tips that disappear during maturation and elongation of internodes. This pattern of infraspecific variation in larger-scale morphological features that equals or exceeds the interspecific variation between *N. linearifolia* and *N. sinistra* has contributed to the prior lack of taxonomic recognition for these genetically well-differentiated species.

An important finding for morphological diagnoses was the observation of two superficially similar, yet structurally unique pollen grain morphologies that consistently corresponded to the genetic grouping we recognize now as species. *Navarretia linearifolia* has a eutectate pollen sexine that is perforate-foveolate, similar to that observed in *Lavandula angustifolia* Mill. (Fig. 3C; see Buchner and Weber 2000 for *L. angustifolia*). In contrast, *N. sinistra* has a semitectate pollen sexine that is microreticulate and closely resembles that observed in *Dapne cneorum* L. (Fig. 3H; see Buchner and Weber 2000 for *D. cneorum*). This diagnostic morphological character allowed us to survey type specimens and confidently assign proper nomenclature to the two genetic groups. This was particularly helpful with *N. linearifolia*. The specimen available to serve as the type of this name is over 100 yr old and in an early developmental stage such that assigning a correct determination on gross morphology alone was difficult. The determination based on pollen morphology is consistent with the pollen morphology and known genetic make up of other specimens from the same area. Mature seed coloration also appears to be diagnostic, with the caveat that immature seeds may be lighter in both species and thus identification on this feature alone may be tenuous.

The data presented here provide indirect evidence of breeding barriers between *N. linearifolia* and *N. sinistra*. A few attempts to cross flowers in the greenhouse between two populations each of *N. linearifolia* subsp. *linearifolia* and *N. sinistra* failed to produce seed but, lacking experimental design, we consider this effort anecdotal. However, a survey of individuals of both species sampled at a site where they were also collected together over 50 yr ago (Modoc County, California; *Grant & Grant 8015*, UC, WTC; *L. Johnson 09–091,09–092,* BRY), provided no evidence of hybridization or introgression (results not shown). Both species also come into close contact, if not syntopy, in the Ochoco Mountains and Steens Mountain of Oregon (*Johnson 95–040,* BRY; *Johnson 97–142,* BRY; and *Johnson 95–060*, BRY; *Mansfield 93–322*, CIC, respectively). In no case, including the inclusion of one

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Ochoco population (*N. sinistra*) and one Steens population (*N. linearifolia*) in the allozyme survey, did we find any evidence of hybridization or introgression within the sampled individuals.

Navarretia linearifolia and *N. sinistra* differ in no obvious ecological requirements. They inhabit similar sites and, as noted above, co-occur in at least one location where they flower simultaneously. Both subspecies of *N. linearifolia* can occur on serpentine soils, but are found on nonserpentine soils as well. *Navarretia linearifolia* ranges westwardly, from central California and the western edge of Nevada north into Oregon and Washington. *Navarretia sinistra* overlaps this range in Washington, Oregon, Northern California, and Nevada, then eastward into Idaho and with isolated populations in Utah and Colorado (Fig. 5).

The following key and taxonomic treatment includes all four species of nonspiny navarretia because their similar morphologies and long historical association in formal taxonomies make it useful to do so. These species do not, however, form a monophyletic group and the group is not accorded formal taxonomic recognition here.

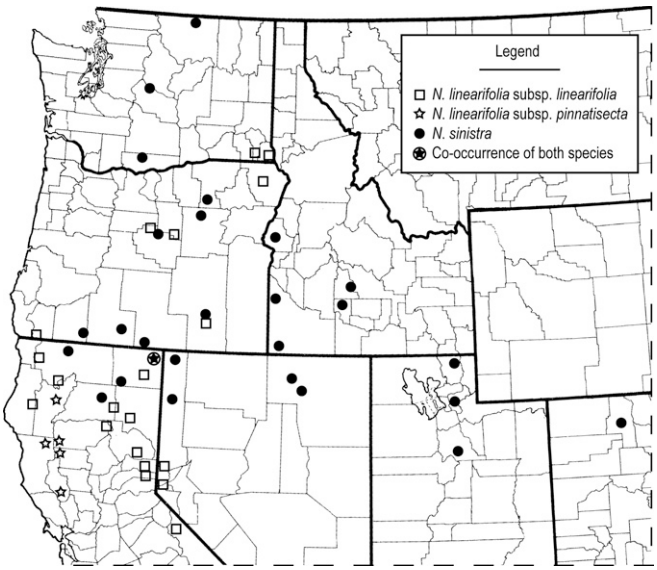


FIG. 5. Distributions of *N. linearifolia* and *N. sinistra* based on representative sampling of known occurrences.

KEY TO NON-SPINY SPECIES OF *NAVARRETIA*

1. Leaves, at least above plant base, pinnatifid to palmatifid, with apices acerose or pungent; flowers several to many in bracteate heads, sessile to subsessile; calyx lobes generally unequal, acerose. ..... other *Navarretia* species
1. Leaves generally linear to lanceolate and entire, infrequently pinnatifid at plant base or palmatifid distally, with apices neither acerose nor pungent; flowers single or paired from long pedicles; calyx lobes equal, acute to acuminate but not acerose. 2
2. External corolla tube minutely long-stalked glandular; upper leaves unlobed; calyx lobes generally long tapered acuminate; pollen sexine semitectate, striate to striato-reticulate, microechinations absent. 3
3. Corolla 6–8 mm, lobes bluish white; calyx densely glandular; branches, leaves ascending. ..... 1. *Navarretia capillaris*
3. Corolla 8–21 mm, lobes pink; calyx sparsely glandular to subglabrous; branches ascending to spreading, leaves spreading. 4
4. Corolla 13–21 mm, throat 6–8 mm, purple. ..... 2a. *Navarretia leptalea* subsp. *leptalea*
4. Corolla 8–15 mm, throat 2–5 mm, yellow, sometimes with short purple marks. ..... 2b. *Navarretia leptalea* subsp. *bicolor*
2. External corolla glabrous; upper leaves often palmately lobed; calyx lobes acute; pollen sexine perforate-foveolate or semitectate and microreticulate, microechinate. 5
5. Corolla 4.5–9 mm; branches and pedicels narrowly ascending; mature seeds dark brown (Munsell hue 10R, value 2, chroma 2 to hue 2.5R, value 2, chroma 4); pollen sexine semitectate, microreticulate. ..... 4. *Navarretia sinistra*
5. Corolla 5–20 mm; if less than 10 mm, branches often divergent and pedicels spreading, frequently curved; mature seeds medium brown (Munsell hue 2.5 YR, value 4, chroma 4 to value 3, chroma 4); pollen sexine eutectate, perforate-foveolate. 6
6. Corolla 5–10 mm, style included. ..... 3b. *Navarretia linearifolia* subsp. *linearifolia*
6. Corolla 10–20 mm, style exserted. ..... 3a. *Navarretia linearifolia* subsp. *pinnatisecta*

TAXONOMIC TREATMENT

1. NAVARRETIA CAPILLARIS (Kellogg) Kuntze, Revis. Gen. Pl. 2: 433. 1891. *Gilia capillaris* Kellogg, Proc. Calif. Acad. Sci 5: 46. 1873. *Gilia leptalea* subsp. *capillaris* (Kellogg) Brand, Pflanzer. (Engler) 4, Fam. 250: 98. 1907. *Allophyllum capillare* (Kellogg) A. G. Day & V. E. Grant, Phytologia 84: 375. 1998 [1999].—TYPE: U. S. A. California: Placer Co., Cisco, C. P. R. R., Sierra Nevada Mountains, 6 July 1870, *A. Kellogg s. n.* (holotype: GH!).

Gilia subalpina Greene ex Brand, Pflzr 4: 98. 1907.— TYPE: U. S. A. California: Nevada Co., above Donner Lake toward Donner Pass, 29 July 1903, *A. Heller 7042* (lectotype [first step] designated by Jepson (1943); lectotype [second step] here designated: UC 58466!; isolectotypes: BRY!, DS, GH!, NY × 2!, RM!, UNR!).

Notes—Brand (1907) did not view the type of *Gilia capillaris* and apparently formed a concept for this taxon based largely on material now excluded from it. Of the four specimens cited as representative of *Gilia leptalea* subsp. *capillaris* by Brand, one is *N. capillaris* as treated here (*Baker 1355*), two are *N. sinistra* (*Elmer 1226* and *Baker 3560;* the latter specimen is more accurately cited as *Copeland 3560*, distributed by Baker) and one (*Howell s.n*, near Waldo) is *N. linearifolia* subsp. *linearifolia*. In contrast, all specimens cited by Brand as syntypes for *G. subalpina* (*Heller 7042*, *Jones 2424*, *Hansen 511*, *Abrams 2063*, and *Baker 1358*; see lectotype above and representative specimens examined below) are here determined as *N. capillaris*.

Jepson (1943) indicated the type locality of *Gilia subalpina* as Donner Pass, *Heller 7042*, effectively providing a first level lectotypification for this species. Cronquist (1984) also cites only *Heller 7042* of Brand's syntypes. We designate the UC specimen of *Heller 7042*, which Jepson would have seen, as second level lectotype to complete the lectotypification of this species. Of Brand's syntypes for *G. subalpina*, *Heller 7042* is the

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most widely distributed, best preserved, and most representative of the protologue.

Gilia columbiana Piper ex Brand (Brand 1907) is a manuscript name cited as a synonym under *Gilia leptalea* subsp. *capillaris* by Brand based on a handwritten description and specimen annotation by Piper (*Elmer 1226*, WS!). The actual specimen collected by Elmer is determined, on the basis of gross morphology and pollen exine sculpturing, to belong to *N. sinistra*.

Representative Specimens Examined—(* = pollen examined with SEM; also for *Heller 7042* cited as lectotype above); U. S. A. California: Alpine Co., Woods Lake Region, 14 August 1939, *F. W. Peirson 12863* (RSA, UC); Bear Valley, 23 July 1893, *G. Hansen 511* (NY, POM); Calvaras Co., S. end of Tamarack in vicinity of a stream, 11 July 1997, *L. Johnson 07–162* (BRY); Fresno Co., along trail into canyon of Mono Creek at turn ca. 1 mile above E end of Vermillion Valley, 10 July 1953, *C. H. Quibell & E. M. Quibell 2683* (RSA); Modoc Co., Warner Mtns., Cedarville Pass, swale along intermittent streamlet, 20 June 1959, *A. Cronquist & A. Holmgren 8522** (GH, UTC, NY, WTU; some sheets contain mixed collections with *N. linearifolia* subsp. *linearifolia*); Mono Co., Toiyabe Natl. Forest, near Molybdinite Creek and road to Emma Lake, 30 June 1993, *L. Johnson 03–104* (BRY, WS); Nevada Co., Soda Springs, 21 July 1881, *Jones 2423* (GH, NY, POM, UTC); Placer Co., Hwy 80, just E of Norden on trail ¾ miles above Sierra Club Lodge, 13 July 1982, *A. Day & O. Robinson 82–83* (RSA); San Bernardino Co., E. end of Bluff Lake, in runoff channel, 16 August 1975, *C. Davidson 3130* (RSA); San Bernardino Mtns., Green Valley, July 1901, *L. Abrams 2063* (NY); Sierra Co., SFSC Sierra Field Station near Haskell Creek, 2 July 1993, *L. Johnson 93–118** (BRY); off Yuba Pass Road across from FS Rd 1210, 11 July 1997, *L. Johnson 97–151** (BRY); Siskiyou Co., Siskiyou Mtns., Jaynes Canyon, 26 July 1935, *L. C. Wheeler 3699* (NY, RENO, RSA); Tulare Co., Mineral King vicinity, 2.5–3 miles along trail to White Chief Lake from Eagle-Mosquito Parking area, 8 July 1994, *L. Johnson 94–062** (BRY, CAS); Idaho: Franklin Co., Bear River Range, Franklin Basin, 12 July 1942, *B. Maguire 21625* (NY, UTC); Nevada: Washoe Co., Little Valley, 24 June 1902, *C. Baker 1355* (GH, NY, POM); Little Valley, 24 June 1902, *Baker 1358** (GH, NY, POM, US); Mt. Rose, N side of Tahoe Meadows, 3 August 1982, *A. Day et al. 82–87* (RSA); Big Meadows, Carson Range, 28 July 1978, *M. J. Williams et al. 78–255–17* (RENO); Oregon: Harney Co., Steens Mtn., S side of Fish Creek, 1/2 mi S of Fish Lake, 27 July 1995, *D. Mansfield 95–44** (CIC); Steens Mtn., T32 or 33S R33E, head of McCoy Creek, just N of the head of Fish Creek, 26 July 1959, *A. Cronquist 8768** (NY, RM, UC, UTC, WTU; some sheets contain mixed collections with *N. linearifolia* subsp. *linearifolia*); Klamath Co., Crater Lake, Vitae Falls, 21 July 1935, *J. W. Thompson 12252* (MONTU, POM, UC, WTU,); Utah: Cache Co., 0.2 miles S of Idaho state line beside Logan River below Franklin Basin, 15 July 1958, *L. Anderson 1358** (NY, UTC).

2. Navarretia leptalea (A. Gray) L. A. Johnson, Aliso 19: 68. 2000. *Collomia leptalea* A. Gray, Proc. Amer. Acad. Arts 8: 261. 1870. *Gilia leptalea* (A. Gray) Greene, Erythea 4: 58. 1896. *Allophyllum leptaleum* (A. Gray) A. G. Day & V. E. Grant, Phytologia 84: 375. 1998 [1999].—TYPE: U. S. A. California: Yosemite Valley, 1866, *H. N. Bolander 4918* (lectotype designated by Grant and Grant (1954: p. 89): GH!).

2a. Navarretia leptalea (A. Gray) L. A. Johnson subsp. leptalea. *Gilia leptalea* subsp. *eu-leptalea* Brand, Pflzr. (Engler) 4: 250: 97. 1907.

Notes—Though distinctive in areas of their range, collections intermediate and intergrading between subspecies are known.

Representative Specimens Examined—(* = pollen examined with SEM). U. S. A. California: Butte Co., Colby, July 1986, *R. M. Austin 258* (RSA); Jonesville, Scotch John meadow, 28 June 1930, *E. B. Copeland 444* (RSA); Calavaras Co., 2 miles NE of Big Trees, State Hwy 4, Ebbetts Pass Road, 11 July 1956, *P. C. Everett & E. K. Balls 22049* (RSA); El Dorado Co., several miles above Kyburz in Echo Pass, 9 August 1952, *V. Grant 18000* (RSA); Fresno Co., Shaver Lake vicinty, along old logging road S of Hwy 168, 9 July 1994, *L. Johnson 94–068** (BRY); Huntington Lake, 19 July 1947, *E. Carter 107* (POM); Auberry Rd., ½ mile above Meadow Lakes, 12 July 1951, *C. H. Quibell 145* (RSA) Lassen Co., between Hwy 44 and N edge of Log Lake, 28 July 2005, *L. Johnson 05–224* (BRY); Camp Fredonyer, on road from Westwood to Susanville, 13 July 1950, *V. Grant and A. Grant 8943* (RSA); Madera Co., Roadside, Nelder Grove, above Oakhurst, 16 July 1940, P. A. Munz 15977 (POM); Nevada Co., E side of Hwy 89 at Sierra/Nevada Co. line, 2 July 1993, *L. Johnson 93–127** (BRY); W side of Hwy 89 at top of grade 1.8 miles N of Hobbart Mills, 2 July 1993, *L. Johnson* 93–129*; Plumas Co., on abandoned logging road 2 mils SW of jct wth Hwy 89 on Gold Lake Forest Hwy., 2 July 1993, *L. Johnson 93–120* (BRY); Lake Davis vicinity, 0.4 miles N of Hwy 70 on Grizzley Road, 2 July 1993, *L. Johnson 93–122* (BRY); Shasta Co., 1 mile W of Hatchet Creek summit on Hwy 299, 13 July 1947, *V. Grant & A. Grant 8020* (RSA); Burney Spring, 9 July 1932, *F. W. Peirson 10288* (RSA); Sierra Co., along Hwy 89 ca. 4.5 miles N of jct. with Hwy 49, *L. Johnson 97–148** (BRY); Tehama Co., Wilson Lake vicinity, 0.3 miles N of Hwy 89 along Lost Creek Road, 3 July 1993, *L. Johnson 93–131** (BRY); Tulare Co., Big Meadow, jct of rd to Mt. Maddox, 3 miles from "General's Hwy", 25 July 1950, *R. S. Ferris & L. Lorraine 12219* (RSA); Tuolumne Co., Lily Creek between Long barn and Hull Meadow, 18 August 1942, *I. L. Wiggins 10154* (POM).

2b. Navarretia leptalea (A. Gray) L. A. Johnson subsp. bicolor (H. Mason & A. D. Grant) L. A. Johnson, Aliso 19: 68. 2000. *Gilia leptalea* subsp. *bicolor* H. Mason & A. D. Grant, Madrono 9: 220. 1948. *Allophyllum leptaleum* (A. Gray) A. G. Day & V. E. Grant subsp. *bicolor* (H. Mason & A. D. Grant) A. G. Day & V. E. Grant, Phytologia 84: 376. 1998 [1999]—TYPE: U. S. A. California: Toulumne Co., Dardanelle, 21 June 1944, *A. M. Alexander & L. Kellogg 3736* (holotype: UC!).

Representative Specimens Examined—(* = pollen examined with SEM). U. S. A. California: Alpine Co., Hermit Valley vicinity, 0.4 miles SE of Stanislaus Meadow Trail along Hwy 4, 1 July 1993, *L. Johnson 93–106** (BRY); One mile N of Red Lake (NE of Carson Pass), 27 September 1943, *A. M. Alexander & L. Kellogg 3544* (RSA); Faith Valley, 16 July 1959, *A. Day s.n.* (RSA 299503); Calavaras Co., 1 mile SW of Big Meadows camp near Hwy 4, 1 July 1993, *L. Johnson 93–110** (BRY); S. end of Tamarack in vicinity of a stream, 1 July 1993, *L. Johnson 93–115** (BRY); El Dorado Co., Trail to Grass Lake, Lake Tahoe Region, 19 August 1943, *A. M. Alexander & L. Kellogg 3460* (RSA); 3 miles E of Echo Summit on St Hwy 50, 26 July 1974, *C. Davidson 2502*; Fresno Co., W. side of Mono Crk, 1/8 mile above E end of Vermillion Valley, 8 July 1953, *C. H. Quibell & E. M. Quibell* 2559 (RSA); Mariposa Co., Tioga Rd., W of Olmstead Pt., 21 July 1972, *J. R. Shevock 2115* (RSA); Nevada Co., W of Hwy 89 at UC Sagehen Field Station, 8 August 1983, *A. Day & B. Trowbridge 83–77b* (RSA); Sierra Co., Gold Lake, open slope, 4 July 1934, *L. S. Rose 34316* (POM); Tuolumne Co., ca 11 airmiles NE of Pinecrest, S side of FS Rd 5N01 to Eagle Peak, 11 July 1987, *B. Ertter & A. Carter 7237* (RSA).

3. **Navarretia linearifolia** (Howell) L. A. Johnson, comb nov. *Gilia linearifolia* Howell. Fl. N. W. Amer. 1: 461 1901.—TYPE: U. S. A. Oregon, Siskiou (sic) Mts., 8 July 1886, *Thomas Howell s. n.* (lectotype here designated: ORE 96501!).

Notes—Considered a synonym for *G. capillaris* by most workers, *G. linearifolia* has not been recognized as a distinct taxon beyond its original publication. This is likely, in part, because the protologue is ambiguous regarding specimens upon which to base the name and an effort to lectotypify the name has not been made previously despite several annotations on the Howell specimen at ORE that indicate this specimen may serve as the type. Both Abrams (1951) and Grant and Grant (1954) cite the year of publication for *G. linearifolia* as 1903 (the year the final pages of Howell's work were published) rather than 1901 (the year the fascicle containing this species was published; Howell 1901). Other works with generally extensive synonomy, such as Munz (1959) and Cronquist (1984), omit the name entirely. In reestablishing *G. sinistra*, Day (1993a) provided no synonomy. It is unclear whether this is because she considered *G. linearifolia* synonymous with *G. capillaris* (in which case there were no synonyms for *G. sinistra*) or because she elected not to list synonyms even though she considered *G. linearifolia* synonymous with *G. sinistra* and considered *G. sinistra* to have priority (following the mistaken date of publication of *G. linearifolia* from her earlier publication,

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Grant and Grant 1954). As lectotypified here, *G. linearifolia* clearly falls into Day's taxon concept for *G. sinistra*.

The ORE specimen was selected as lectotype because it is consistent with the protologue and was certainly in the possession of Howell at the time his *Flora of Northwest America* was published (Howell's personal collection was eventually purchased by ORE). Though this is the only Howell specimen we could locate with this location and date, it is also possible that the ORE sheet is from the same collection by Howell that yielded four additional specimens now housed at GH, NY, US, and WTC (note that none of the sheets have any handwriting of Howell's on them). These latter specimens, also consistent with the protologue, are labeled "June 1884, Waldo, Oregon", two years and a month earlier and a more specific location than the label on the specified lectotype. That all four specimens are from a single collection is possible (and even likely) despite the differences in the label between the ORE and the other three sheets (see online supplemental data for personal correspondence with K. Chambers, ORE, that contributed to the following line of reasoning). Howell often sent plants to others for identification, including Asa Gray (Ornduff 2008). The GH collection is annotated in Gray's handwriting, "*Gilia capillaris* forma *rigidula*" on a "Syn. Fl. of N. Am. Ed. 2" label, with "new var. *rigidula*," also in Gray's handwriting written to the left. The ORE specimen is similarly labeled "*Gilia capillaris* var. *rigidiuscula* Gr." Importantly, both sheets include a number "203" that links the two specimens. Howell did not keep a numbering series for his collections, but likely numbered plants sent unlabeled to Gray to keep track of the determinations he received back, thus, the number 203 links the two specimens and suggests they are from a single collection. The information received back from Gray was used as the basis for the ORE label given Gray's subspecific epithet was never published. The ORE sheet's label is written in the hand of Louis Henderson, a close friend and associate of Howell's and later curator of ORE. Why Henderson labeled the ORE specimen, and not Howell, is unclear, but opens the possibility for an error in transcribing the information (or, alternatively, for correcting an earlier error in date). Also, all four sheets are at a similar state of phenology (though the NY specimens are smaller plants). As stated previously, Gray never published this new variety and Howell did not recognize it in his flora. Instead, Howell recognized a new species (which he favored over varieties; Ornduff 2008) likely based on the same material: *G. linearifolia*, but he apparently did not annotate the specimen now at ORE to reflect this change. Brand (1907) cited Howell's 1884 Waldo collection as a representative of *G. leptalea* subsp. *capillaris*; Day, in 1987, annotated the WTC specimen of this collection "*Gilia sinistra*." We have, as yet, found no specimens of Howell's labeled "*Gilia linearifolia*," or labeled otherwise but conspecific with the basionyms of *G. capillaris* or *G. sinistra*, that would dispute the lectotype designation made here.

3a. **Navarretia linearifolia** subsp. **linearifolia**.

Notes—Chromosome counts of *N. linearifolia* subsp. *linearifolia* by A. Day are recorded on several herbarium labels as follows: *A. Day & O. Robinson 84–17*, $n = 9$; *A. Day & O. Robinson 82–85*, n = ca. 9; *A. Day & B. Trowbridge 83–75*, diploid, $n = 9$ or $n > 9$; *A. Day, M. Williams, & A. Tiehm 82–92*; $n = 11$. Aneuploidy has not been further investigated, but intraspecific aneuploidy is known to occur in *Allophyllum*, a near relative.

Representative Specimens Examined—(* = pollen examined with SEM; also for *Howell s.n.* (ORE) cited as lectotype above. † = chromosome count). U. S. A. California: Alpine Co., Silver Creek at Forestry Camp Ground, 28 July 1955, *P. A. Munz 21304* (RSA); Humbolt Co., jct of USFS Rd. 5N01 and USFS Rd. 1, 12 miles S of Berry Summit on Hwy 299, 10 July 1990, *R. Spellenberg 10238* (RSA); Mono Co., Toiyabe Natl. Forest, near Molybdinite Creek and road to Emma Lake, 30 June 1993, *L. Johnson 03–105* (BRY); Nevada Co., at top of grade 1.8 miles of Hobbart Mills, W side of Hwy 89, 2 July 1993, *L. Johnson 93–128* (BRY); W of Hwy 89 and 2.4 miles W of UC Sagehen Field Station along Sagehen Creek below Sheep Spring, 8 August 1983, *A. Day & B. Trowbridge 83–75*† (RSA); N end of Buck Ridge, 2 air miles SE of Hischdale, 4 August 1982, *A. Day, M. Williams, & A. Tiehm 82–92*† (RSA) Lassen Co., between Hwy 44 and N edge of Long Lake, 28 July 2005, *L. Johnson 05–220* (BRY); Plumas Co., N side of Lake Davis, 0.2 miles W of Coot Bay, 15 July 1982, *A. Day & O. Robinson 82–85*† (RSA); Sierra Co., 5.5 miles N of Sierra co. line on either side of Hwy 89, 11 July 1997, *L. Johnson 97–157* (BRY); Siskiyou Co., Hwy 3, summit just W of Scott Mtn., near county line, 29 June 1984, *A. Day & O. Robinson 84–18* (RSA); Hwy 3, 5.4 miles S of jct with Callahan-Gazelle Rd., 0.9 miles N of Scott Mtn. Summit, 28 Jun 1984, *A. Day & O. Robinson 84–17*† (RSA); Scott Mtn., south of Calahan, 3 July 1961, *C. B. Hardham 8114* (RSA); Trinity Co., In wet bog, summit of grade, Scott Mtn., 15 July 1950, *H. L. Mason 14049* (GH, NY, RM, UC, UTC, WTU). Nevada: Washoe Co., Peavine Mtn., W. of Peavine Peak, 6 July 1975, *Margaret Williams & A. Tiehm 75–82–21* (NY); Oregon: Crook Co., 4.9 miles S of Jct with Hwy 26 on Hwy 27, S of Prineville, 9 July 1997, *L. Johnson 97–140**; Harney Co., Steens Mtn., 7.4 miles toward Fish Lake from mile marker 2, 13 July 1995, *L. Johnson 95–060** (BRY); Josephine Co., Siskiyou Natl. Forest, ca. 3 miles SW of O'Brien along FS road 4402, 12 July 1994, *L. Johnson 94–081** (BRY, CAS); Waldo, June 1884, *T. Howell s.n /203** (GH!, NY! WTU!); Wheeler Co., Buck Point vicinity on NF 12, 10 July 1997, *L. Johnson 97–142* (BRY); Wallowa Co., Buckhorn Springs, 29 June 1934, *M. E. Peck 18335* (NY); Washington: Asotin Co., S slope just under crest of ridge, summit of Blue Mountains, 0.5 miles W of Anatone Butte, T7N R44E S1, 2 July 1949, *Cronquist 5915* (BRY, GH, NY, UC, UTC, WTU); along Benneti Ridge-West Mtn. Rds, 5–7.5 miles W of Hwy 129, *L. Johnson & D. Johnson 94–052** (CAS, BRY); Garfield Co., Teal Springs Camp vicinity, 15 Jun 1996, *L. Johnson & D. Johnson 96–019* (BRY).

3b. **Navarretia linearifolia** Howell (L. A. Johnson) subsp. **pinnatisecta** (H. Mason & A. D. Grant) L. A. Johnson, comb. nov. *Gilia leptalea* (A. Gray) Greene subsp. *pinnatisecta* H. Mason & A. D. Grant, Madroño 9: 220. 1948. *Gilia sinistra* M. E. Jones subsp. *pinnatisecta* (H. Mason & A. D. Grant) A. G. Day, Novon 3: 332. 1993. *Allophyllum sinistrum* (M. E. Jones) A. G. Day & V. E. Grant subsp. *pinnatisectum* (H. Mason & A. D. Grant) A. G. Day & V. E. Grant, Phytologia 84: 376. 1998 [1999]. *Navarretia sinistra* (M. E. Jones) L. A. Johnson subsp. *pinnatisecta* (H. Mason & A. D. Grant) L. A. Johnson, Aliso 19: 68. 2000.—TYPE: U. S. A. California: Lake Co., open ground about Whispering Pines resort, base of Cobb Mountain, 5 July 1927, *Baker 2299a* (holotype: UC!).

Representative Specimens Examined—(* = pollen examined with SEM). U. S. A. California: Glenn Co. Plaskett Meadow vicinity along Hwy 162, 8 July 1997, *L. Johnson 97–129** (BRY); Summit Covelo-Willows Hwy, 4 August 1943, *M. S. Baker 10556* (RSA); Lake Co., Boggs Lake, along W shore, 10 July 1994, *L. Johnson 94–071* (BRY); Near Hullville on ridge between Eel River and Rice Creek, 2 August 1902, *A. A. Heller 6019* (POM); dry margin of Snow Lake, 21 June 1957, *M. S. Baker 12338* (JEPS, RSA, UC); Wash of Kelsey Creek, near Kelseyville, 29 June 1945, *H. L. Mason 12612* (RSA, UC); Mendocino Co., Ham Pass vicinity, along small side road N off of Bland's Cove Road, 11 July 1994, *L. Johnson 94–077** (BRY, CAS); West Spring, Read Mountain, Ukiah, 24 July 1909, *J. McMurphy s.n.* (RSA 262233); *Napa Co.*, East side of Mt. St. Helena, 24 August 1941, *R. F. Hoover 5576* (UC); Tehama Co., 10.3 miles NE of Paskenta at Jct of roads to Eagle Peak and Ball Rock, 13 July 1951, *H. K. Sharsmith 4028* (POM, UC); 1 mile E of Square Lake, 25 July 1951, *P. A. Munz 16878*; Trinity Co., 12 miles E of Forest Glen, 12 August 1936, *P. A. Munz 14374* (POM); along Rd. 5E25 south of Senteney Rock, 9 July 1976, *T. Nelson 2983* (RSA).

4. Navarretia sinistra (M. E. Jones) L. A. Johnson. Aliso 19: 68. 2000. *Gilia sinistra* M. E. Jones Contr. W. Bot. 10: 57. 1902. *Collomia sinistra* (M. E. Jones) Brand, Pflanzer. (Engler) 4, Fam. 250: 54. 1907. *Allophyllum sinistrum*

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(M. E. Jones) A. G. Day & V. E. Grant, Phytologia 84: 376. 1998 [1999]—TYPE: U. S. A. California: Middle Valley, southern Idaho, 7 July 1899, *M. E. Jones 6458* (holotype, POM!; isotypes, ORE!, US!, CAS!, US!)

Notes—The Marcus E. Jones Herbarium is now at POM, and the POM specimen was annotated as holotype by A. G. Day in 1984. All viewed specimens are dated July 8, 1899, apparently from a lead type press, rather than July 7, 1899, as stated by Jones (1902). Jones' field notes record he was in Middle Valley on July 7, and in Salubria on July 8, indicating that the labels, rather than the original description, are in error (Jones 1965). In transferring this species to *Collomia*, Brand (1907) states he did not actually see the specimen; he did, however, view two specimens here considered conspecific that he placed in *Gilia leptalea* subsp. *capillaris* (*Elmer 1226* and *Baker 3560*; actually *Copeland 3560* distributed by Baker). *Elmer 1226* is the basis for *Gilia columbiana* Piper ex Brand nom. illegit., a name published only as a synonym of *G. leptalea* subsp. *capillaris* (see notes under *G. capillaris* above). The notes by Piper attached to this specimen describe cobwebby hairs on the lower stem, but these are only foreign trichomes adhering to the plant's stipitate glandular trichomes. A chromosome count for *N. sinistra* made by M. Windham (now at DUKE) is $n = 9$ (*L. Johnson 97–146*).

Representative Specimens Examined—(* = pollen examined with SEM; also for *M. E. Jones 6458* cited as type above. † = chromosome count). U. S. A. California: Lassen Co., Susanville, Perkin's Ranch, 26 June 1897, *M. E. Jones 10226* (POM); Modoc Co., 9 miles N of Lookout, 15 June 1940, *A. Eastwood & J. T. Howell 8290** (GH); Service Gulch, 4.3 km W of County Rd. 91 on Forest Service road 42N03, 6 July 1991, *Bartholomew 5970** (NY); Siskiyou Co., Klamathon, 3 July 1903, *Baker* (actually *Copeland*) *3560* (GH, NY, RM, UC POM); Shasta Co., off road 37, 0.8 miles W of Rock Creek, along unused spur road, 28 July 2005, *L. Johnson 05–212* (BRY); Colorado: Routte Co., Hwy 27 between Oak Creek and Hwy 40, 2 August 1999, *L. Johnson 99–012** (BRY); Idaho: Camas Co., S. edge of Macon Flat at foot of Mt. Bennett Hills, 21 July 1978, *B. Ertter 2409* (BRY, CIC, NY, UTC, MONTU); Nevada: Elko Co., 6.6 miles along road to Bull Run Reservoir from jct with Hwy 226, 26 Jun 2006, *L. Johnson 06–089* (BRY); Independence Mtns., Mahoney Springs, 30 July 1982, *A. Tiehm & R. Eckert 7450* (NY, UTC, UNLV); Washoe Co., Bald Mt., Peterson Canyon, T45N R21E S8, 30 June 1978, B. Rogers & A. Tiehm 1105 (NY, RENO, UTC); Oregon: Crook Co., Ochoco Pass vicinity, ca 2 mile E of Hwy 26 off NFD-2630 on Rd 020, 10 July 1995, *L. Johnson 95–040* (BRY); Grant Co., 85.5 miles S of Pendleton along Hwy 395, 10 July 1997, *L. Johnson 97–146*†* (BRY, CAS); Harney Co., Steen's Mtn., T34S R32E S11 NE1/4, in drying mud of large playas, 7 July 1993, *D. Mansfield 93–322** (CIC); Klamath Co., 2 miles S of Bly Pass summit along Hwy 140, in sagbrush flat, 12 July 1995, *L. Johnson 95–050** (BRY); Utah: Cache Co., 1/2 mile down Logan Cayon from Twin Creek Road along Hwy 89, 1 July 1962, *D. Anderson 243* (UTC); Morgan Co., ca 3 miles NW of Mountain Green on Dry Creek, 27 June 1976, *B. Albee 3244* (UT); Utah Co., Payson Cyn., near jct of Jones Ranch Trail #123 and main road, 13 July 1998, *L. Johnson 98–004** (BRY); Washington: Kittitas Co., Mt. Stuart, *Elmer 1226** (WS); Klickitat Co., Simcoe Mtns., 6 June 1884, *Suksdorf 395** (GH).

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Appendix 1. Voucher information for populations sampled for the allozyme and DNA sequence-based analyses included in this study. Information is included in the following order for each population: State, county, collector and number (herbarium acronym following Index Herbariorum) "A + D" (if used for allozymes and DNA sequences) or "A" or "D" (for one type of data only). Sequences can be obtained from GenBank using the following numbers: nuITS, AF008200, AF008198, AF208210, GU734283–GU734316; *trnL–trnL–trnF*, AF208177, EU628504, GU734138–GU734172; *trnS–trnG*, EU628241, GU734173–GU734208; *trnG–trnG*, GU734209–GU734244; *idhA*, GU734265–GU734282; *idhB*, GU734255–GU734264; *g3pdh*, GU734245–GU734254.

Navarretia capillaris. Utah, Cache Co., *Anderson 1358* (UTC); D. California, Mono Co., *Johnson 93-104* (BRY) A + D. California, Calaveras Co., *Johnson 93-114* (BRY) A + D. California, Sierra Co., *Johnson 93-118* (BRY) A + D. California, Tulare Co., *Johnson 94-062* (BRY) A + D.

Navarretia linearifolia subsp. ***linearifolia.*** California, Mono Co., *Atwood et al. 11465* (BRY) D. California, Mono Co., *Johnson 93-105* (BRY) A + D. California, Plumas Co., *Johnson 93-123* (BRY) D. California, Sierra Co., *Johnson 93-125* (BRY) A + D. California, Tehama Co., *Johnson 93-130* (BRY) A + D. Washington, Asotin Co., *Johnson & Johnson 94-052* (BRY) A + D. California, Trinity Co., *Johnson 94-080* (BRY) A + D. Oregon, Josephine Co., *Johnson 94-081* (BRY) A + D. Oregon, Harney Co., *Johnson 95-060* (BRY) D. Washington, Garfield Co., *Johnson & Johnson 96-019* (BRY) D. Oregon, Crook Co., *Johnson 97-140* (BRY) D. Johnson, Wheeler Co., *Johnson 97-142* (BRY) D. California, Lassen Co., *Johnson 05-222* (BRY) D. Nevada, Washoe Co., *Williams and Tiehm 75-82-21* (UTC) D.

Navarretia linearifolia subsp. ***pinnatisecta.*** California, Lake Co., *Johnson 94-071* (BRY) A + D. California, Glenn Co., *Johnson 94-074* (BRY) A + D. California, Mendocino Co., *Johnson 94-077* (BRY) A + D. California, Trinity Co., *Johnson 94-079* (BRY) A + D.

Navarretia sinistra. Utah, Cache Co., *Anderson 243* (UTC) D. Idaho, Owyhee Co., *Atwood 20383* (BRY) D. Idaho, Camas Co., *Ertter 2409* (UTC) D. Idaho, Gooding Co., *Ertter 75-180* (UTC) D. Oregon, Umatilla Co., *Johnson 95-038* (BRY) A. Oregon, Crook Co., *Johnson 95-040* (BRY) A + D. Oregon, Jackson Co., *Johnson 95-047* (BRY) D. Oregon, Jackson Co., *Johnson 95-050* (BRY) D. Oregon, Lake Co., *Johnson 95-057* (BRY) D. Oregon, Grant Co., *Johnson 97-146* (BRY) D. Utah, Utah Co., *Johnson 98-004* (BRY) D. Colorado, Routte Co., *Johnson 99-012* (BRY) D. California, Shasta Co., *Johnson 05-212* (BRY) D. Oregon, Harney Co., *Mansfield 93-322* (CIC) D. Nevada, Washoe Co., *Rogers and Tiehm 1105* (UTC) D. Idaho, Washington Co., *Saab 156* (SRP) D. Nevada, Elko Co., *Tiehm and Eckert 7450* (UTC) D.

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