

Recognizing a new species of *Silene* (Caryophyllaceae) from California: a splitter's game?

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Silene krantzii T.R. Stoughton is a new species endemic to higher elevation, alpine habitats in the San Bernardino Mountains, San Bernardino County, California. The new species appears to be abundant in locations where it has been observed, but it is narrowly restricted in overall distribution, presumably due to the limited availability of suitable habitat. *Silene krantzii* sp. nov. is morphologically similar to a closely related species in the San Bernardino Mountains, *Silene verecunda* S. Watson, but differs from this taxon in the San Bernardino Mountains by the presence of glandular trichomes on the basal leaves and proximal stems, smaller leaf size, a red calyx that is inflated at flowering, and a short-statured, spreading habit. *Silene krantzii* also occurs in a unique ecological setting. Qualitative evidence of these differences is summarized for the new species and relevant information regarding ongoing study of genetic diversity within the *S. verecunda* complex is discussed.

Key words: alpine, catchfly, morphology, natural history, San Bernardino Mountains, San Gorgonio Mountain, *Silene krantzii*, *Silene verecunda*, Southern California, species concepts

Over the course of multiple botanical forays to the alpine zone of San Gorgonio Mountain, located in the San Bernardino Mountains, California, several plants resembling *Silene verecunda* S. Watson (1875) were collected by the first author. All known specimens previously identified as *Silene verecunda* subsp. *platyota* (S. Watson) C. L. Hitchcock & Maguire (1947) from subalpine (<3,000 meters), mixed conifer forests of the San Bernardino Mountains held at RSA/POM and UC/JEPS herbaria were examined. We observed several distinct differences between *S. verecunda* subsp. *platyota* and the unidentified *Silene* collections from the alpine zone of San Gorgonio Mountain. We now propose that these differences are sufficient to recognize the populations on San Gorgonio Mountain as a

new species of *Silene* in the San Bernardino Mountains, utilizing a taxonomic concept proposed by Cronquist (1978) in which taxa are circumscribed based on discontinuity of morphological features. Natural history information included here lends additional support for the recognition of a new species of *Silene* endemic to the San Gorgonio summit region of the San Bernardino Mountains drawing on aspects of more contemporary species discourse recently articulated by Baum (2009).

TAXONOMY

Silene krantzii T.R. Stoughton, sp. nov. (Figures 1–4).—TYPE: USA, California, San Bernardino Mountains, ‘The Tarn’ just below (south of) the San Gorgonio summit region (Figure 1A), alpine gravel fell-field with *Festuca saximontana*, *Raillardella argentea*, *Calyptridium umbellatum*, *Hulsea vestita* subsp. *pygmaea* and *Elymus elymoides*, granitic substrates, 3,272 m elev., 34° 5’ 34.37” N, 116° 49’ 23.30” W, 23 July 2011, Thomas Stoughton 1391, with R. Shores, M. Seccombe, and P. Boyd (Holotype: RSA806300; Isotypes: GB, JEPS, CAS, NY, UCR).

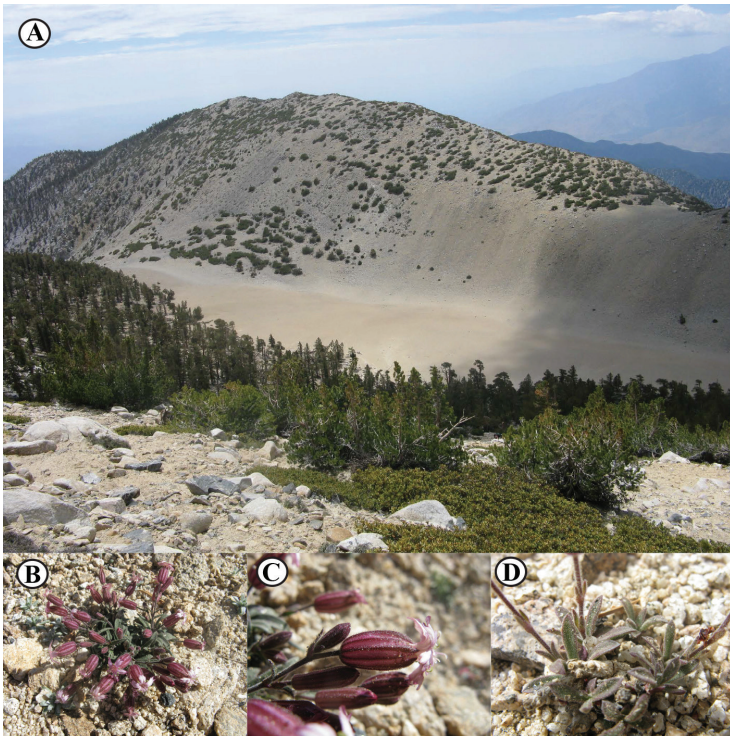


FIGURE 1.—*Silene krantzii* in native habitat. A. Alpine fell-field habitat at the type locality, “The Tarn” just below the south face of San Gorgonio Mountain in the San Bernardino Mountains, San Bernardino County, California. B. Overall plant habit demonstrating prostrate nature of stems and racemose inflorescences. C. Flower displayed in side-view, showing inflated and ribbed condition of the mature calyx in flowering. D. Basal leaves and stems, showing oblanceolate shape and presence of glandular trichomes. Photographs by Thomas R. Stoughton.

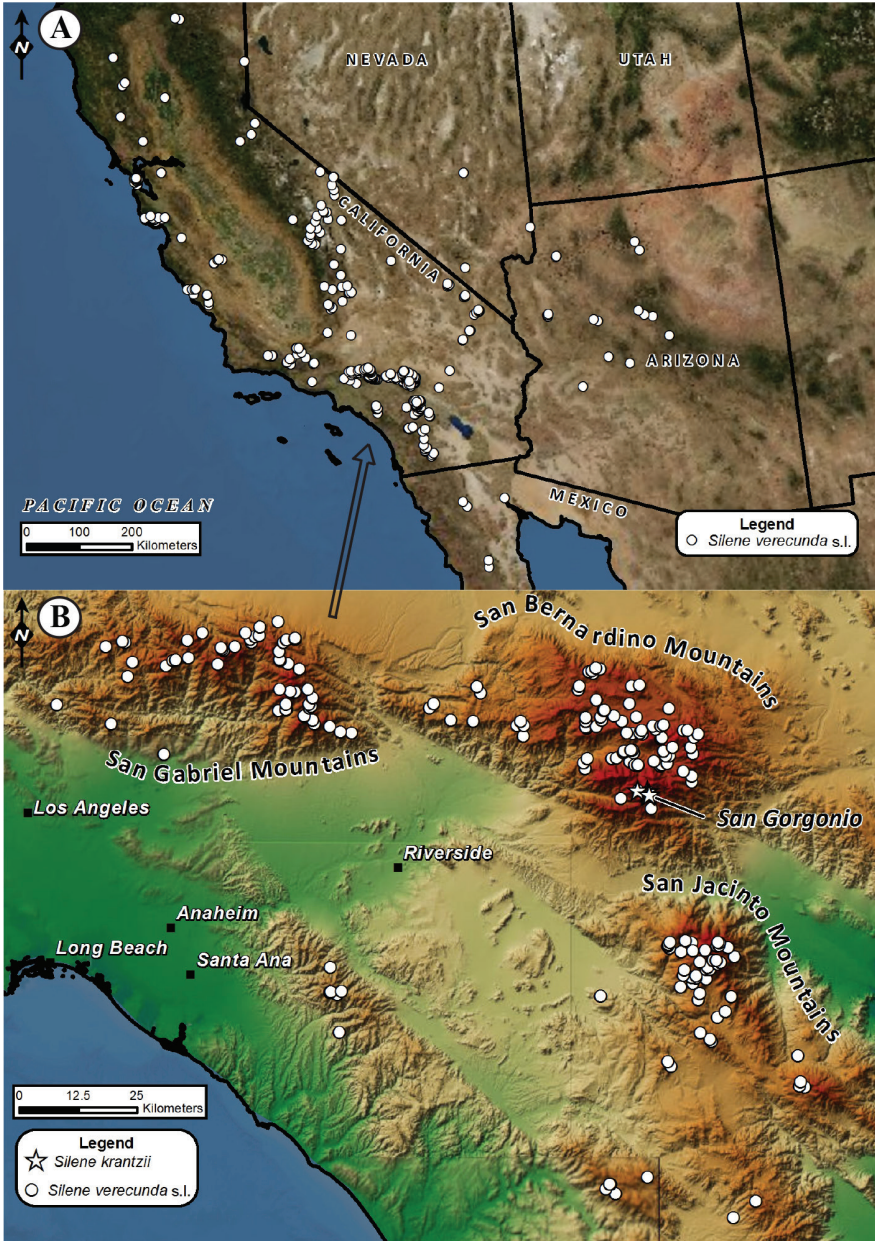


FIGURE 2.—Distribution of the *Silene verecunda* complex. A-B. Locality information downloaded from the Consortium of California Herbaria and Intermountain Regional Herbarium Network. A. The easternmost taxon in the *S. verecunda* complex (circles) is subsp. *andersonii* (Clokey) C. L. Hitchcock & Maguire, whereas the majority of the morphological variation exhibited by this species is attributed to subsp. *platyota* (S. Watson) C. L. Hitchcock & Maguire in the Sierra Nevada, Transverse Ranges and Peninsular Ranges of California (including Baja, MEX). Plants from the Coast Ranges of California represent the 'typical' variety, with the type specimen for *S. verecunda* S. Watson reported from serpentine substrates on Mt. Davidson in the San Francisco Bay Area. B. Inset showing the Transverse and Peninsular Ranges of southern California, with the location of *S. krantzii* (stars) on San Gorgonio Mountain indicated in the southern portion of the San Bernardino Mountains, San Bernardino County, California.



FIGURE 3.—*Silene krantzii*. Illustration by Diana D. Jolles.

Caespitose perennial herb, caudex branches few to many below ground, many fertile shoots at the base 2–10(14) cm long, spreading to ascending, generally unbranched, glandular-viscid throughout, hairs generally less than 0.5 mm, glands stipitate. Basal leaves linear-oblongate, (5)8–30 × 1–3 mm, apex acute, base attenuate into short petiole, both surfaces glandular-viscid, 1-veined or venation obscure, in opposite pairs of 2. Cauline leaves similar to basal leaves, but gradually reduced apically, linear-lanceolate, few, sessile, often with fertile axillary branches, opposite. Inflorescence generally an open cyme, monochasial (generally not a compound dichasium), 1–4 flowered with ascending branches. Bracts linear-lanceolate, margins membranaceous. Peduncles 0.5–2.5(3.5) cm long. Bracteoles similar to cauline leaves, but lanceolate-ovate and gradually smaller than bracts. Pedicels up to 2.5(3.5) cm long, generally longer than calyx. Calyx 10-nerved, 8–15 mm long, cylindrical-campanulate to campanulate-clavate, narrowed proximally around carpophore, reddish, densely glandular-viscid, generally somewhat inflated at flowering with pale commissures between prominent parallel veins, not clearly papery in fruit; teeth keeled, broadly ovate to triangular, *ca.* 1–3 × 1–1.5 mm, obtuse, with membranaceous and ciliate margins. Carpophore *ca.* 0.5–1(1.5) mm long, hairy. Petals pink, (7)9–17 mm long; limb broadly obovate, *ca.* 2.5–4 mm long, distinctly divided to *ca.* 2/5 total length; lobes broadly oblong, *ca.* 0.5–1.5 × 0.5 mm, margins laciniate at base; claw elliptic-oblong to obovate, slightly exserted beyond calyx, *ca.* (5)6–9(10) × 0.3–1.2 mm, ciliate near base; coronal scales 2, oblong, 0.5–1.5(2) mm long, rounded at tip or toothed, sometimes with laciniate margins. Stamens exserted from the calyx but ± equal to corolla, styles slightly more exserted; filaments usually sparsely pilose proximally. Styles 5.5–8 mm long. Capsules narrowly elliptic-obovate to clavate, (5.5)7–10 × 4–5.5 mm, included in the calyx. Seeds brownish, usually orbicular-reniform to oblong, 1–1.5 mm long, flattened, papillate-tuberculate with papillae developed into a low crest along margin.



FIGURE 4.—*Silene krantzii*. Scan of the type specimen, Stoughton *et al.* 1391 (RSA806300), collected from "the Tarn" in the San Gorgonio Wilderness, San Bernardino National Forest, San Bernardino County, California.

Silene krantzii is morphologically similar to the broad interpretation of *S. verecunda* S. Watson by Morton (2005) in some respects, but differs in its ecological setting and the presence of glandular trichomes on the basal leaves and proximal stems, smaller leaf size, a red calyx that is inflated at flowering, and a low-stature, spreading habit.

Silene krantzii is typically found on sand or gravel substrates of primarily igneous origin. Most records describe it in open, exposed areas above tree line with mixed shrubs and herbs (including *Festuca saximontana*, *Raillardella argentea*, *Hulsea vestita* subsp. *pygmaea*, *Calyptridium umbellatum*, and *Elymus elymoides*), although some records describe the habitat as rocky rather than sandy or gravelly. The species is cited as being scarce to common in different localities and habitats around the summit region of San Gorgonio Mountain, but personal observations by the first author suggest it is densely abundant at the type locality and in other areas around the summit region of San Gorgonio Mountain. That said, *S. krantzii* is thus far known only from high elevation (3000–3500 m) locations in the San Bernardino Mountains of southern California. Plants flower from as early as mid-May to as late as early September and develop mature fruits from June to October.

The specific epithet, *krantzii*, refers to the first author's botanical mentor and friend, Timothy Krantz, who has greatly enriched our knowledge of the flora of the San Bernardino Mountains (Krantz 1994). The suggested common name for the species is Krantz's catchfly.

Paratypes: USA, California, Transverse Ranges, San Bernardino Mountains District, San Gorgonio summit region, San Bernardino County: RSA793545, *Bell 3757*, 6 Jul 2012; RSA498876, *Cooper 2994*, 2 Sep 1948; RSA436977, *Dunkle 3787*, 3 Sep 1933; CAS35901, *Howell 23678*, 25 Jul 1947; POM17581, *Munz 9596*, 24 Aug 1923; RSA39583, *Munz 12081*, 25 Jul 1947; RSA65065, *Peirson 615*, 24 Apr 1923; CAS408760, *Raven 11145*, 11 Aug 1957; RSA806301, *Stoughton et al. 1407*, 7 Aug 2011; RSA806302, *Stoughton et al. 1432*, 20 Aug 2011; RSA281181, *Thorne 49871*, 20 Jul 1977; RSA438861, *Wallace k-III*, 17 Aug 1938.

TAXONOMIC RELATIONSHIPS

Silene krantzii appears to be a close relative of *Silene verecunda* S. Watson (1875), a staggeringly variable species of *Silene* that is widespread in southwest North America. *Silene verecunda* (Figure 5) occurs in California, Nevada, Utah, Arizona, and in Baja California, Mexico (Morton 2005), with unsubstantiated reports of the species from Oregon. Disregarding all subspecies in the most recent treatment, Morton (2005) suggested that separation of taxa would be arbitrary and that the species complex is in need of in-depth study. Despite this conclusion, Morton provides numerous morphological characters and disparate ecological settings for distinguishing taxa associated with the group. Morton's taxonomic concept of *Silene* is in direct contrast to later findings of Popp and Oxelman (2007), who used base pair substitutions from both nuclear and plastid markers to assess relationships among many members of *Silene* in North America. Popp and Oxelman (2007) found *Silene andersonii* Clokey [= *S. verecunda* subsp. *andersonii* (Clokey) C. L. Hitchcock & Maguire] to be resolved in a separate clade than that of two other accessions of *S. verecunda* they included in their analyses. A more recent study (Petri and Oxelman 2011) further substantiates paraphyly of *S. verecunda* as circumscribed by Morton (2005). This suggests that some of the morphological variation observed by previous authors (Watson 1875, 1882, 1888; Jepson 1914; Clokey 1939; Hitchcock and Maguire 1947) may



FIGURE 5.—*Silene verecunda* subsp. *verecunda* in native habitat near the type locality of *S. verecunda* S. Watson on Mt. Davidson, in the vicinity of San Francisco Bay, California. A. Overall plant habit demonstrating decumbent to erect nature of the stems of these considerably larger plants. *Silene verecunda* subsp. *verecunda* occupies coastal, lower elevation habitats in California, which is in stark contrast to the inland, alpine habitat of *S. krantzii*. B. Basal leaves and stems, showing oblanceolate shape with much more pronounced petioles compared to *S. krantzii*. *Silene verecunda* subsp. *verecunda* does exhibit glandularity on the proximal stems and leaves like *S. krantzii*, but these trichomes are larger, less-dense, and of a different structural arrangement. C. Flower displayed in side-view, showing somewhat inflated condition of the mature calyx in flowering similar to *S. krantzii*. Note that calyces are considerably less red in color than *S. krantzii* and a noticeable keel on the calyx teeth is lacking. Photographs used by permission from Scott Simono, San Francisco State University, California.

have a genetic basis and that the associated ecological affinities may represent locally adapted genotypes (with corresponding morphotypes) rather than phenotypic plasticity in a widespread, generalist species.

QUALITATIVE ANALYSES AND CLASSIFICATION

Specimens of all members of the *S. verecunda* complex (including *S. krantzii*) from herbaria at RSA/POM and UC/JEPS were examined (Appendix I) as part of a larger project (T. Stoughton *et al.*, Rancho Santa Ana Botanic Garden, unpublished data) evaluating the taxonomic validity of the previously recognized subspecies of *S. verecunda* using molecular phylogenetics. A total of 130 specimens of *S. verecunda* s.l. (Morton 2005) collected from California (including Baja) were examined, including 82 specimens of *S. verecunda* subsp. *platyota* and 11 specimens of *S. krantzii* collected from the San Bernardino Mountains. A limited number of representative specimens for the other subspecies of *S. verecunda* outside of the San Bernardino Mountains are listed in Appendix I, including 9 specimens of subsp. *andersonii*, 20 specimens of subsp. *platyota*, and 8 specimens of subsp. *verecunda*.

We considered treating the new taxon as a variety or subspecies of *S. verecunda* because, like *S. verecunda* s.l., it is ciliate on the petal claw with two petal limb lobes that have lacinate margins. *Silene krantzii* overlaps morphologically with *S. verecunda* s.l. in portions of its geographic range in several other features. The branching pattern of *S. krantzii* is similar to that of *S. verecunda* subsp. *platyota*, but the primary axes of *S. krantzii* are generally more prostrate to spreading in comparison and *S. verecunda* subsp. *platyota* tends to have inflorescences that are compound dichasia. Plants of *S. krantzii* are smaller than *S. verecunda* subsp. *platyota*, which occurs at lower elevations in the San Bernardino Mountains (below 3,000 m). The range of corolla size among *S. krantzii* plants is similar to that of *S. verecunda* s.l. Seeds of *S. krantzii* appear to be smaller than that of *S. verecunda* s.l., but are similar to the latter species in being flattened, papillate-tuberculate, and orbicular-reniform to oblong in shape with papillae that are developed into a low crest along the margin. The principal distinction between *S. krantzii* and the subspecies of *S. verecunda sensu* Hitchcock and Maguire (1947) is the unique combination of: (1) glandular trichomes on the basal leaves and proximal stems; (2) leaves of reduced size; (3) a red calyx that is inflated at flowering; and (4) a low-stature, spreading habit (see Appendix II, Key to *Silene verecunda* species complex). These distinctive morphological features of *S. krantzii*, along with its isolated geographic distribution in the alpine zone of the San Bernardino Mountains having no known intergradation with *S. verecunda* s.l., warrant its species status by a taxonomic (morphologic) species concept (Cronquist 1978) that incorporates information regarding natural history of the species.

Physical isolation of *S. krantzii* populations at high elevation in the San Bernardino Mountains region and the evolution of unique morphological and ecological features suggest that this species has either a restricted niche, limited dispersal ability, or both. In general, we know very little about the phylogenetic relationships within the *S. verecunda* complex (Popp and Oxelman 2007, Petri and Oxelman 2011), so gaining a better understanding of these relationships should be the goal of future molecular studies of California *Silene* species. Although no explicit attempts have been made to characterize genetic diversity in the group, recent research (Popp and Oxelman 2007, Petri and Oxelman 2011) indicates that the *S. verecunda* complex, like the rest of the genus, is relatively slow to accumulate genetic synapomorphies at loci traditionally used for phylogenetic inference. Adopting a metapopulation view of monophyletic species circumscription (De Queiroz 2007) has recently increased in popularity because it can accommodate a greater number of natural processes, including ones causing reticulate patterns of evolution like hybridization and introgression. However, as Baum (2009) points out, monophyly is a feature of taxa that

arises after metapopulation lineages have been isolated for sufficiently long enough to accumulate fixed mutations. Given the lack of resolution in *Silene* phylogeny estimates to date (e.g., Oxelman *et al.* 1997; Popp and Oxelman 2004, 2007; Popp *et al.* 2005; Petri and Oxelman 2011), a ‘long time’ in *Silene* may be relatively much longer than in other Angiosperm lineages. It is not possible for us to evaluate Baum’s (2009) concepts of predictive power or robustness for *S. krantzii* at this time due to a paucity of genetic data, but recognition of this new species does have biological significance, utility, and precedent (Baum 2009). *Silene krantzii* is ecologically distinct from *S. verecunda*, occurs sympatrically only with another phylogenetically distant *Silene* species (*S. parishii* S. Watson), and can be distinguished phenotypically from putative close relatives. Additionally, we argue that there is taxonomic precedence for species recognition of *S. krantzii* despite the fact that putative close relatives have been previously treated both as separate species (Watson 1875, 1882, 1888; Jepson 1914; Clokey 1939) and subspecies (Jepson 1914, Hitchcock and Maguire 1947) of *S. verecunda*. All of the subspecies of *S. verecunda* treated by Hitchcock and Maguire (1947) were described as unique species in previous works (Watson 1875, 1882; Clokey 1939). Preliminary genetic evidence from nuclear and chloroplast loci suggest that numerous monophyletic taxa exist in the *S. verecunda* complex (T. Stoughton *et al.*, Rancho Santa Ana Botanic Garden, unpublished data), including but not limited to all of the subspecies previously recognized by Hitchcock and Maguire (1947) included in our key (Appendix II). Additionally, botanists who are familiar with the *S. verecunda* complex have confirmed that this ‘species’ has served as a taxonomic dumping ground for numerous entities possessing some, but not all, of the diagnostic morphology of *S. verecunda* S. Watson (D. Taylor, Jepson Herbarium, personal communication). These taxa may be the products of recent, rapid radiation following hybridization and allopolyploidization (Petri and Oxelman 2011), but the signature is phenotypic diversification with minimal corresponding genetic change. Lest this phenotypic polymorphism be mistaken for plasticity, it should be noted that *S. krantzii* is supported by genetic synapomorphies, albeit extremely few at present, and a pilot common garden study in which phenotypic differences among *S. krantzii* and *S. verecunda* subsp. *platyota* from the San Bernardino Mountains were retained in flowering individuals (T. Stoughton, Rancho Santa Ana Botanic Garden, unpublished data).

Does the circumscription of *S. krantzii* represent one more slice in the *ad nauseum* splitting process of micro-taxonomists? Perhaps! Before elucidating the reasons why we think it is not only beneficial but our responsibility to recognize *S. krantzii* as distinct from *S. verecunda* s.l., we briefly discuss the negative aspects of so-called ‘taxonomic splitting’. Philosophically, it is undesirable to reduce species phylogenetically to their elements (i.e., genotypes). Species are meant to represent groups of individuals that share synapomorphies (shared, derived characters) rather than subgroups sharing particular alleles (i.e., genotypes). Recognizing genotypes as species predictably leads to species breakdown as a result of sexual reproduction and gene flow, and underestimation of intraspecific genetic diversity. From a conservation standpoint, taxonomic splitting may lead to increased, positive efforts to conserve particular species assemblages based on species richness. However, overestimates of richness due to taxonomic splitting may result in the conservation of certain genotypes rather than the species containing them (Zachos 2013). Conservation efforts based on inaccurate species circumscription resulting from overzealous taxonomic splitting could create a genetic bottleneck, which would then artificially put the species at very high risk. That said, a survey by Morrison *et al.* (2009) indicated that taxonomic splitting, relative to ‘lumping’ or making no taxonomic change, has produced only positive effects, increasing

awareness of particular groups and increasing their protection as well.

Disintegration of *S. verecunda* s.l. seems eminent and arguably represents taxonomic splitting. However, as our ability to understand phylogenetic relationships among taxonomic entities increases, our ability to understand morphological evolution and geographic distributions increases in turn. We think that it is our responsibility as taxonomists not only to circumscribe *S. krantzii* as distinct based on the evidence laid out in this study, but to learn everything we can about its natural history, testing its taxonomic status with new data when it is available. To this end, we hope that recognition of the narrowly endemic *S. krantzii* at the species level will also catalyze a re-evaluation of conservation needs for the entire *S. verecunda* complex. Although synonymized by Hartman et al. (2012) in the current treatment of *The Jepson Manual*, the infraspecific taxon *Silene verecunda* subsp. *verecunda* is still recognized as a rare plant (Rank 1B.2 — plants rare, threatened, or endangered in California and elsewhere; moderately threatened in California) by the California Native Plant Society (CNPS 2013).

BIOGEOGRAPHY

The San Bernardino Mountains make up a floristically and geologically diverse region of significant botanical importance (Krantz 1994). San Gorgonio Mountain was the southernmost glaciated peak in western North America (Sharp et al. 1959, Owen et al. 2003) and consequently represents the southernmost limit of several widespread alpine plant taxa (Krantz 1994). A vast majority of high elevation (i.e., >3,000 m) areas in the San Bernardino Mountains are designated by the San Bernardino National Forest as the San Gorgonio Wilderness, the only place that *Silene krantzii* is currently known to occur. Krantz (1994) reviewed the vascular plant flora of the San Bernardino Mountains, citing nearly 1,600 taxa native to this region. Nineteen flowering plant species that grow in the alpine zone of San Gorgonio Mountain (ca. 40% of the total number of species surveyed by Krantz) are not found elsewhere in the San Bernardino Mountains but occur more widely to the north (Krantz 1994). With this study we add one additional species, increasing our knowledge of the endemic flora (ca. 8%) of the very rich and interesting summit region of San Gorgonio Mountain.

The geographic range of *S. krantzii* is intriguing given the distribution of other taxa in the *S. verecunda* complex (Figure 2). Other subspecies of *Silene verecunda* s.l. in the southwest U.S. include *S. verecunda* subsp. *platyota*, a common understory component in pine forests at lower elevations (<3,000 m) in the San Bernardino Mountains, and *S. verecunda* subsp. *andersonii*, a more xeric-adapted taxon that grows in the desert mountains, primarily to the northeast and not overlapping in distribution with *S. krantzii*. As mentioned previously, preliminary molecular assays suggest that *S. krantzii* is distantly related to *S. verecunda* subsp. *andersonii* and that other subspecies in the *S. verecunda* complex appear to be unique evolutionary lineages (Popp and Oxelman 2007; Petri and Oxelman 2011; T. Stoughton et al., Rancho Santa Ana Botanic Garden, unpublished data). *Silene krantzii* has been found only around the summit region of San Gorgonio Mountain thus far, but we recommend looking for this species on adjacent high peaks in southern California, particularly in the White Mountains of Inyo County, and the nearby San Gabriel Mountains (San Bernardino and Los Angeles counties) to the west. In the higher elevations of the eastern San Gabriel Mountains, Philip Munz collected individuals from “little baldy” that resemble *S. krantzii* (Munz 6119, POM13373 and UC218196) but differ in that they do not have leaves of reduced

size or a low-statured, spreading habit. The Munz collection also has inflorescences that are strict dichasia, more similar to those typical of *S. verecunda* subsp. *platyota*. This and other collections from the higher elevation habitats in the San Gabriel Mountains did not escape the attention of Hitchcock and Maguire (1947) during preparation of their monograph on North American *Silene*, but ultimately they did not offer a name.

Silene krantzii may represent just one example of many plant lineages in southern California that have become widely disjunct from close congeners in the southern Rocky Mountains during the Pleistocene, as explained by the hypothesis of Major and Bamberg (1967) and others (e.g., Morefield 1992, Krantz 1994). The hypothesis of Cordilleran disjunction, sensu Major and Bamberg (1967), has been rejected by some authors (e.g., Chabot and Billings 1972, Raven and Axelrod 1978) who have instead favored more direct north to south dispersal along the Sierran-Cascadian axis. Although *S. krantzii* is currently known only from the San Bernardino Mountains, the preponderance of examples of other species on San Gorgonio Mountain would lend support to either of the two competing hypotheses. Many widespread species that inhabit the alpine zone on San Gorgonio Mountain occur also in the alpine habitats of the eastern Sierra Nevada and White Mountains of California (Morefield 1992, Krantz 1994). Discontinuous populations of these plants are spread across the Basin and Range Province linking populations in the western mountain ranges to populations in the southern Rocky Mountains (Major and Bamberg 1967, Morefield 1992, Krantz 1994). Therefore, locating additional populations of *S. krantzii* and an understanding of the phylogenetic relationship of this new species will be essential for developing hypotheses regarding its origin and evolution over time.

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**APPENDIX I: LIST OF VOUCHER SPECIMENS OF *SILENE KRANTZII* AND *S. VERECUNDA*
EXAMINED FOR THIS STUDY**

USA, California, Transverse Ranges, San Bernardino Mountains District, San Bernardino County: ***S. krantzii* specimens.**—RSA793545, *Bell 3757*, 6 Jul 2012; RSA498876, *Cooper 2994*, 2 Sep 1948; RSA436977, *Dunkle 3787*, 3 Sep 1933; POM17581, *Munz 9596*, 24 Aug 1923; RSA39583, *Munz 12081*, 25 Jul 1947; RSA65065, *Peirson 615*, 24 Apr 1923; RSA806300, *Stoughton 1391*, 23 Jul 2011; RSA806301, *Stoughton et al. 1407*, 7 Aug 2011; RSA806302, *Stoughton et al. 1432*, 20 Aug 2011; RSA281181, *Thorne 49871*, 20 Jul 1977; RSA438861, *Wallace k-111*, 17 Aug 1938. ***S. verecunda* subsp. *platyota* specimens.**—POM283, *Abrams 2039*, 30 Jul 1901; POM158085, *Abrams 2911*, 5 Aug 1902; RSA743190, *Adams s.n.*, 18 Aug 2001; RSA752761, *Bell 457*, 26 Sep 2009; RSA767348, *Bell 1349*, 21 Jun 2010; RSA767029, *Bell 1370*, 23 Jun 2010; RSA767021, *Bell 1445*, 29 Jun 2010; RSA766995, *Bell 1547*, 7 Jul 2010; RSA769000, *Bell 1703*, 28 Jul 2010; RSA779190, *Bell 2687*, 15 Jun 2011; RSA779746, *Bell 2747*, 5 Jul 2011; RSA781783, *Bell 2857*, 3 Aug 2011; RSA615913, *Boyd 10272*, 10 Aug 1998; RSA477824, *Cooper 2910*, 24 Aug 1948; RSA438874, *Davidson 2145*, Jul 1905; RSA438873, *Davidson 2322*, Jul 1905; RSA438860, *Davidson 3094*, 16 Aug 1975; RSA438871, *Davidson 3147*, 16 Aug 1975; RSA438872, *Davidson 4599*, 14 Aug 1976; RSA753631, *De Groot 6057*, 8 Jun 2009; RSA438878, *Detmers s.n.*, 15 Jun 1929; RSA438875, *Fosberg 55871*, 3 Aug 1931; RSA753792, *Fraga 2870*, 3 Jun 2009; RSA753874, *Fraga 2878*, 4 Jun 2009; RSA753399, *Fraga 2997*, 16 Jun 2009; RSA780520, *Fraga 3544*, 12 Jul 2010; RSA616039, *Gross 40*, 2 Aug 1998; RSA749476, *Gross 4077*, 15 Jun 2009; POM11670, *Harwood 4316*, 4 Jul 1920; POM9373, *Harwood 4327*, 4 Jul 1930; RSA761653, *Honer 3537*, 28 Jun 2010; RSA760901, *Honer 3604*, 16 Jul 2010; RSA41849, *Howe s.n.*, 24 Jun 1947; RSA287, *Howell 349*, 10 Jul 1927; POM123149, UC311416, *Jones 6183*, 19 Jul 1900; RSA741121, *Mistretta 3414*, 17 Jul 2008; RSA740480, *Mistretta 3448*, 18 Jul 2008; RSA752705, *Mistretta 3823*, 9 Jun 2009; RSA753115, *Mistretta 3917*, 22 Jun 2009; RSA767691, *Mistretta 5377*, 12 Jul 2010; RSA767424, *Mistretta 5612*, 9 Aug 2010; RSA768252, *Mistretta 5623*, 11 Aug 2010; RSA768946, *Mistretta 5668*, 27 Aug 2010; POM12832, *Munz 6246*, 25 Aug 1922; POM48822, *Munz 8673*, 17 Jul 1924; POM96546, UC310485, *Munz 10544*, 29 Jun 1926; POM96621, *Munz 10710*, 14 Jun 1926; RSA38752, *Munz 11992*, 22 Jul 1947; POM184179, *Munz 12787*, 9 Jun 1932; RSA102380, *Parish 930*, May 1881; RSA102382, UC136296, *Parish 931*, May 1881; RSA102381, *Parish 3064*, 24 June 1894; UC8498, *Parish 3728*, 25 Jun 1895; RSA65062, *Peirson 3270*, 25 Aug 1922; RSA65050, *Peirson s.n.*, 24 Jun 1941; POM306370, *Ramsey 1463*, 2 Jul 1939; RSA692071, *Sanders 14940*, 26 Jun 1994; RSA438879, *Spalding s.n.*, 6 Aug 1931; RSA438896, *Templeton 76H371B*, 18 Jul 1932; RSA369513, *Thorne 47341*, 11 Aug 1975; RSA370810, UC1536094, *Thorne 47704*, 15 Jul 1976; RSA371147, *Thorne 47729*, 15 Jul 1976; RSA337855, *Thorne 53246*, 15 Jun 1979; RSA302740, *Thorne 53358*, 3 Jul 1979; RSA611493, *Wheeler 1097*, 24 Jul 1932; RSA554044, *White 91-199*, 20 Jul 1991; RSA554483, *White 715*, 29 Aug 1992; RSA632097, *White 6924*, 27 Jul 1998; RSA627588, *White 7072*, 13 Aug 1998; RSA674800, *White 8623*, 24 Jun 2001; RSA674819, *White 8689*, 2 Jul 2001; RSA682583, *White 9656*, 29 Jul 2003; RSA715743, *White 11530*, 20 Jun 2006; RSA752960, *White 13322*, 24 Jul 2009; RSA752333, *Wood 942*, 18 Jun 2009; RSA752331, *Wood 947*, 18 Jun 2009; RSA764869, *Wood 2105*, 1 Jul 2010; RSA766694, *Wood 2127*, 2 Jul 2010; UC1137880, *Yates 6616*, 24 Jun 1937.

USA, California, Desert Mountains District (including White and Inyo Mountains), Inyo and San Bernardino Counties: ***S. verecunda* subsp. *andersonii* specimens.**—RSA296490, *Castagnoli 198*, 6 Jun 1980; RSA624136, *DeDecker 3310*, 27 Jul 1973; RSA270672, *Henrickson 13986*, 13 May 1974; UC1549855, *Morefield 4148*, 18 Jul 1986; RSA486336, *Morefield 4804*, 19 Jul 1988; RSA352210, *Peterson 601*, 15 Jun 1982; RSA552077, *Romsper 425*, 11 Aug 1977; RSA290816, *Thorne 44874*, 10 Jul 1974; RSA334384, *Thorne 54802*, 21 Sep 1980.

USA and MEX, California (including Baja), Sierra Nevada, Transverse Ranges, and Peninsular Ranges Districts, Fresno, Kern, Los Angeles, Orange, Riverside, San Bernardino, and Tulare Counties: ***S. verecunda* subsp. *platyota* specimens.**—RSA507942, *Boyd 2260*, 28 May 1988; RSA507251, *Boyd 2373*, 4 Jun 1988; RSA519440, *Boyd 2762*, 20 Jul 1988; RSA438862, *Davidson 2978*, 3 Jul 1975; UC1618234, *Ertter 6311*, 9 Jun 1986; RSA727590, *Fraga 735*, 19 May 2003; RSA727455, *Fraga 1265*, 18 Jun 2004; RSA680009, *Gross 1020*, 10 Jun 2003; RSA795882, *Gross 5573*, 11 Jul 2012; RSA225227, *Moran 14479*, 21 Aug 1967; RSA659142, *Moran 28862*, 21 Jun 1980; RSA679167, *Roberts 5936*, 25 Jun 2003; RSA546449, *Ross 3063*, 2 Jul 1990; RSA637501, *Soza 514*, 10 Jun 1999; RSA682367, *Soza 1701*, 25 Jun 2003; RSA599719, *Swinney 3942*, 29 Jun 1995; RSA596614, *Swinney 3974*, 6 Jul 1995; RSA733088, *Swinney 7994*, 20 Jun 2001; RSA774867, *Swinney 11253*, 24 Jun 2009; RSA673473, *White 7712*, 20 Apr 2000.

USA, California, Coast Ranges and San Francisco Bay Area Districts, Monterey, San Benito, San Francisco, San Louis Obispo, and Santa Cruz Counties: ***S. verecunda* subsp. *verecunda* specimens.**—JEPS102187, *Douglas HL369b*, 20 May 1994; UC1583623, *Keil 20704*, 11 Jun 1988; RSA330449, *Norris 4829*, 14 Mar 1985; JEPS81534, *Stone 462*, 13 May 1982; RSA502348, *Taylor 9617*, 29 Apr 1988; JEPS90790, *Taylor 11942*, 30 Jun 1991; JEPS82771, *West 43*, 11 Apr 1983; JEPS82967, *West 80*, 11 May 1983.

APPENDIX II: KEY TO THE *S. VERECUNDA* SPECIES COMPLEX

1. Flowering calyx somewhat inflated (slightly at times), generally reddish in color, lobes (teeth) keeled or not; basal leaves generally (5)8-60 mm long
 2. Alpine (high elevation) habitats, trichomes glandular on proximal-most leaves; flowering calyx lobes generally strongly keeled; inflorescence a monochasium, branches spreading to ascending *S. krantzii*
 - 2' Coastal (low elevation) habitats, at least some non-glandular trichomes on petioles of proximal-most leaves; flowering calyx teeth generally not keeled; inflorescence a compound dichasium (occasionally simple, sometimes monochasial below), branches ascending to erect *S. verecunda* subsp. *verecunda*
 - 1' Flowering calyx tubular, generally greenish in color (rarely reddish), lobes (teeth) not keeled; basal leaves generally 60-100 mm long (sometimes withering early)
 3. Proximal-most leaves sparsely minute-glandular with noticeably thickened midribs and marcescent bases, generally withering early; transmontane pine and oak woodlands; inflorescence a monochasium (rarely dichasial)
..... *S. verecunda* subsp. *andersonii*
 - 3' Proximal-most leaves generally non-glandular (if glandular, then not sparsely so) and lacking noticeably thickened midribs or marcescent bases, not withering early; generally cismontane pine and oak woodlands; inflorescence a dichasium (sometimes monochasial below) *S. verecunda* subsp. *platyota*