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Erratum

Linanthus bigelovii specimens collected in San Luis Obispo County (Keil 27219, Keil and Riggins 30129, and Hoover 8146) were deposited at OBI, not SLO (page 64).

A FISTFUL OF POLEMONIACEAE: NEW NAMES AND COMBINATIONS

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ABSTRACT

New taxa, names, and combinations are provided for five genera in Polemoniaceae: *Dayia*, *Giliastrum*, *Leptosiphon*, *Linanthus*, and *Loeselia*. Combinations include the transfer to *Dayia* of two species formerly included in *Ipomopsis* and one in *Bryantiella* (*Dayia glutinosa*, *D. havardii*, and *D. sonorae*), as well as the return of *Giliastrum stewartii* to species rank. A new name is offered for *Linanthus aureus* when transferred into *Leptosiphon*: *Leptosiphon chrysanthus* and its subspecies, *L. chrysanthus* subsp. *decorus*. New combinations for infraspecific taxa are made available for *Linanthus californicus* (subsp. *glandulosus* and *tomentosus*) and *L. pungens* (subsp. *hookeri*, *pulchriflorus* and *hallii*). New subspecies are described for *Linanthus bigelovii* (subsp. *johnsonii*), *L. dichotomus* (subsp. *pattersonii*), *L. maculatus* (subsp. *emaculatus*), *L. watsonii* (subsp. *laccolithicus* and *dolomiticus*), and *Loeselia glandulosa* (subsp. *sonorae*). *Linanthus maricopensis* is described as new. In addition, 10 lectotypes are designated, associated with *Dayia*, *Leptosiphon*, and *Linanthus*.

Key words: *Dayia*, *Dayia glutinosa*, *Dayia havardii*, *Dayia sonorae*, elliptical Fourier analysis, *Giliastrum stewartii*, lectotypes, *Leptosiphon aureus*, *Leptosiphon chrysanthus*, *Leptosiphon chrysanthus* subsp. *decorus*, *Linanthus bigelovii* subsp. *johnsonii*, *Linanthus dichotomus* subsp. *pattersonii*, *Linanthus maculatus* subsp. *emaculatus*, *Linanthus maricopensis*, *Linanthus watsonii* subsp. *dolomiticus*, *Linanthus watsonii* subsp. *laccolithicus*, *Loeselia glandulosa* subsp. *sonorae*, Polemoniaceae.

In anticipation of the forthcoming publication of the *Flora of North America*, Vol. 15: *Magnoliophyta: Fouquieriaceae to Boraginaceae* (Flora of North America Editorial Committee 1993+), the volume including Polemoniaceae, a significant number of nomenclatural innovations and changes are necessary. These include expansion of *Dayia* J.M. Porter, a new combination in *Giliastrum* Rydb., provision of a new name in *Leptosiphon* Benth., descriptions of a number of new taxa and new combinations in *Linanthus* Benth., and a new subspecies of *Loeselia glandulosa* (Cav.) G. Don.

REALIGNMENT OF THREE SPECIES INTO *DAYIA*

The genus *Dayia* J.M. Porter was described a little more than a decade ago (Porter and Johnson 2000). Porter and Johnson included two species, *Dayia scabra* (Brandege) J.M. Porter and *D. grantii* J.M. Porter, both endemic to Baja California Sur, Mexico. Subsequently, the genus has received little attention. Grant (2004) suggested that *D. scabra* and *D. grantii* were properly placed within the genus *Gilia*, in section *Giliastrum*; however, he made no nomenclatural change for *D. grantii*. A recent series of analyses of DNA sequences focusing on *Ipomopsis* Michx. (Porter et al. 2010; see also Johnson et al. 2008) sampled all genera of Tribe Loeseliaceae (sensu Porter and Johnson 2000, not Grant 1997 [1998]), the tribe that includes *Dayia*. Their maximum likelihood analysis of combined chloroplast *trnL* intron and *trnL-trnF* intergenic spacer, and

nuclear ribosomal internal transcribed spacer (ITS) region (i.e., ITS1, 5.8S, and ITS2) inferred that the two species of *Dayia* (*D. scabra* and *D. grantii*) share recent common ancestry with three other species that have historically proved difficult to place generically (see Porter et al. 2010: 189, Fig. 5). These species include *Ipomopsis havardii* (A. Gray) V.E. Grant (originally described as a species of *Loeselia* L. and later transferred to *Gilia* Ruiz & Pav.), *Ipomopsis sonorae* (Rose) A.D. Grant (an endemic of the Mexican Sonoran Desert, originally described in *Gilia*), and *Bryantiella glutinosa* (Phil.) J.M. Porter (a South American species originally described in *Gilia*). *Bryantiella glutinosa* shares more recent common ancestry with *D. scabra* than does *D. grantii*. *Ipomopsis havardii* and *I. sonorae* form a lineage that is sister to the rest of *Dayia* (Fig. 1–5).

A consequence of these analyses is the realization that *Dayia* would not be monophyletic if *Ipomopsis havardii*, *I. sonorae*, and *Bryantiella glutinosa* remained within the respective genera where they have been placed. The phylogenetic relationships among *Dayia grantii*, *D. scabra*, and *B. glutinosa* unambiguously place the latter into the genus *Dayia*. While *Ipomopsis havardii* and *I. sonorae* are inferred to be sister species and the closest lineage to *Dayia*, they are also less morphologically cohesive with the other members of *Dayia*. Even so, they share with *Dayia* once-pinnatifid leaves with filiform segments, zonocolporate pollen with striato-reticulate exine, and exceptionally small, mucilaginous seeds (among the smallest in the family). Despite the morphological diversity, *Dayia* can easily be expanded to incorporate these three species. Moreover because the genus has not been discussed taxonomically, aside from Porter and Johnson (2000), the modest change in circumscription does not present significant taxonomic upheaval or confusion. Below are the necessary combinations to make this change:



Fig. 1–5. Floral morphology of species of the genus *Dayia*.—1. *Dayia scabra* (Brandege) J.M. Porter.—2. *Dayia glutinosa* (Phil.) J.M. Porter [formerly *Bryantiella glutinosa* (Phil.) J.M. Porter].—3. *Dayia grantii* J.M. Porter.—4. *Dayia havardii* (A. Gray) J.M. Porter [formerly *Ipomopsis havardii* (A. Gray) V.E. Grant].—5. *Dayia sonora* (Rose) J.M. Porter [formerly *I. sonora* (Rose) A.D. Grant]. All scale bars = 3 mm.

***Dayia havardii* (A. Gray) J.M. Porter, comb. nov.**

Basionym: *Loeselia havardii* A. Gray, *Proc. Amer. Acad. Arts Sci.* **19**: 87 (1883).

Gilia havardii (A. Gray) A. Gray, *Syn. Fl. N. Am.* **2**(1): 411 (1886). *Ipomopsis havardii* (A. Gray) V.E. Grant, *El Aliso* **3**: 357 (1956).—TYPE: *V. Havard* 247, United States of America, Texas, Presidio del Norte, west Texas, 11 Mar 1881 (holotype GH [247007]; isotype US 145865 [147758]).

***Dayia sonora* (Rose) J.M. Porter, comb. nov.**

Basionym: *Gilia sonora* Rose, in Vasey & Rose, *Contr. U.S. Natl. Herb.* **1**: 90 (1890).

Ipomopsis sonora (Rose) A.D. Grant in V. Grant, *El Aliso* **3**: 361 (1956).—TYPE: *E. Palmer* 170, Mexico, Guaymas, February 1890 (holotype US 41252 [110354]; isotype GH [91163]).

***Dayia glutinosa* (Phil.) J.M. Porter, comb. nov.**

Basionym: *Gilia glutinosa* Phil., *Linnaea* **30**: 196 (1854).

Gilia glutinosa Phil., *Anales Univ. Chile* **90**: 212 (1895). *Bryantiella glutinosa* (Phil.) J.M. Porter, *Aliso* **19**: 71 (2000).—TYPE: *R.A. Philippi* 550, Chile, Coquimbo, November 1853 (holotype SGO 054277). *Gilia ramosissima* Phil., *Anales Mus. Nac., Santiago de Chile* 1891: 53 (1891).—TYPE: Philippi's protologue states, "Prope Socaire et Chismisa c. 280 m.s.m. lecta." Collections at SGO include *F. Philippi s.n.*, Chile, Cuesta de Chismisa, 17 Mar 1885 (054278) and *F. Philippi s.n.*, Chile, Socaire, February 1885 (042116). Lectotype [here designated] *F. Philippi s.n.*, Chile, Prov. San Pedro de Atacama, Socaire, February 1885; SGO 042116. This mount closely matches the original description and includes more plant material from which observation can be made than SGO 054278.

Gilia glabrata Phil., *Anales Univ. Chile* **90**: 213 (1895). *Gilia ramosissima* Phil. var. *glabrata* Reiche, *Anales Univ. Chile* **120**: 194 (1907).—TYPE: Syntypes are *F. Philippi s.n.*, Chile, Prov. Atacama, Chañarcillo, September 1885, SGO 054250; *J. King s.n.*, Chile, Carrizal, 1885; SGO 054248 & 054249. Lectotype [here designated] *J. King s.n.*, Chile, Carrizal, 1885; SGO 054248. This mount well matches the original description and represents the most complete specimen, bearing both flowers and fruit.

Gilia chachanensis I.M. Johnston, *Contr. Gray Herb.* **70**: 82 (1924).—TYPE: *F. E. Hinkley & Mrs. F. E. Hinkley* 25, Peru, Arequipa, Chachani Mountain, 3300 m, March 1920 (holotype GH; isotype US).

TRANSFER OF *GILIA STEWARTII* TO SPECIES RANK IN *GILIASTRUM*

The genus *Giliastrum* (Brand) Rydb. (Rydberg 1906) was reincarnated (Porter 1997) following over 80 years of disuse (but see Grant 1959, 2004; Turner 1994). The justification for its segregation from *Gilia* Ruiz & Pav. is overwhelming. While *Gilia* is closely related phylogenetically to *Allophylum* (Nutt.) A.D. Grant & V.E. Grant, *Collomia* Nutt., *Lathrocasis* L.A. Johnson and *Navarretia* Ruiz & Pav., *Giliastrum* is more closely related (among other genera) to *Eriastrum* Wooton & Standl., *Ipomopsis* Michx., *Loeselia* L., and *Dayia* J.M. Porter. So distant are these relationships that they have been placed in

different tribes of Polemoniaceae (Porter and Johnson 2000): *Gilia* in tribe *Gilieae* V.E. Grant and *Giliastrum* in tribe *Loeseliae* J.M. Porter & L.A. Johnson. Further, species of *Giliastrum* are characteristically perennials, with rotate corollas, the corolla lobes longer than the fused portion and have a unique, zonopororate-peritectate pollen type. Species of *Gilia*, in contrast, are annuals, with funnellform corollas, the lobes shorter than the fused portion and have a more common zonocolporate-striate pollen type.

Giliastrum's current circumscription includes nine species (Porter and Johnson 2000). One, *Giliastrum purpusii* (Brandegee) J.M. Porter, incorporates three subspecies. A reevaluation of these subspecies in light of their interrelationships and relationship with the Argentine species, *G. castillanosii* J.M. Porter, based on comparative DNA sequencing of the chloroplast *trnL-F* region and nuclear ribosomal ITS region (J. M. Porter and V. W. Steinmann, unpubl.) and comparative morphology has prompted a change in nomenclature.

Giliastrum stewartii (I.M. Johnst.) J.M. Porter, comb. nov.

Basionym: *Gilia stewartii* I.M. Johnst., *J. Arnold Arb.* **24**: 94 (1943).

Giliastrum purpusii (K. Brandegee) J.M. Porter subsp. *stewartii* (I.M. Johnst.) J.M. Porter, *Aliso* **17**: 84 (1998).—**TYPE**: I. M. Johnston & C. H. Muller 1258, Mexico, Coahuila, 5 mi S of San Jose on the road to Esmeralda (via Norias), 13 Sep 1940 (holotype GH 00219769; isotype MICH 1192662).

A NEW NAME FOR *LINANTHUS AUREUS* AND THE APPLICATION OF *LEPTOSIPHON AUREUS*

Polemoniaceae has experienced more than its share of taxonomic and nomenclatural turmoil. Taxon circumscriptions at all ranks have fluctuated wildly over the past 200 years (compare Bentham 1833, 1845; Gray 1870, 1878; Grant 1959; Porter and Johnson 2000). This has contributed to a complex and bewildering nomenclature. Because many of the original names predated the requirement for type specimens, the precise application of many names has been a matter of supposition, as lectotypification has not been accomplished for many species. Recently, a series of investigations into the phylogeny and generic boundaries in Polemoniaceae (Johnson et al. 1996, 2008; Porter 1997; Bell et al. 1999; Bell and Patterson 2000) have made it very clear that *Linanthus* in the traditional sense (e.g., Grant 1959; Patterson 1993) is not monophyletic. In their revised classification of Polemoniaceae, Porter and Johnson (2000) divided *Linanthus* into two genera, resurrecting and expanding *Leptosiphon* Benth., in addition to *Linanthus*. As part of this change, they transferred *Linanthus aureus* (Nutt.) Greene into *Leptosiphon*. They were unaware that their combination was a later homonym of *Leptosiphon aureus* Benth. ex E. Vilm. Unfortunately, these two names do not refer to the same species. Here we correct this error by providing a legitimate transfer of *Gilia aurea* Nutt. into *Leptosiphon* and clear up nomenclatural confusion involving the species known as *Leptosiphon aureus*.

Scattered across the arid lands of the southwestern USA and adjacent Mexico is a delicate spring annual with striking golden-yellow flowers, filamentous stems and opposite, palmate leaves. Although originally included in the genus *Gilia* by Thomas Nuttall (1848), for the last century it has been known as

Linanthus aureus (Greene 1892; Fig. 6). While there seems no controversy concerning the application of Nuttall's name, there has been no clear identification of type material. Nuttall's protologue indicates that a collection by W. Gambel, made in (or around) Santa Barbara, California, was the basis for *Gilia aurea*. Three specimens are believed to be those of W. Gambel, GH 78819, K 000769037 and PH 1068920/12188. The specimen in Gray Herbarium states, "*Gilia* * (§ *Chrysanthus* * *aurea*, St. Barb Angels," in Nuttall's hand and "Nutt., Gambel" in Gray's hand. This specimen was presented to GH by E. Durand in 1866 (fide annotation). The mount at K states, "*Gilia* * *aurea*, Sta. Barbara, in Nuttall's hand and includes three plants. The specimen at Philadelphia Academy of Sciences states "*G. chrysanthus*, Nutt., Calif., Durand." The GH and PH specimens have the same source, the Durand Herbarium, where much of Nuttall's materials, including some of Gambel's collections ultimately resided. A large collection of Nuttall's materials is also found at K. While the GH specimen bears a label in Nuttall's hand, the location—St. Angels (Los Angeles)—is in conflict with the protologue. It is possible that the protologue was in error, as the change in location on the GH sheet was made by Nuttall, and subsequent comments by Gray (1870: 264) suggest that there was a question whether the specimen was collected in Santa Barbara or Los Angeles. Note that no other historic or modern collections have been made at Santa Barbara, but the species is historically known from Los Angeles. Regardless, the specimen at K is not in conflict with the protologue and most closely matches the illustration and description provided by Nuttall. The lectotype is therefore designated as K 000769037. The mounts at GH (78819) and PH (1068920/12188) are here interpreted as islectotypes (material from the same W. Gambel collection).

In addition to the absence of a lectotype, an error in synonymy has resulted in further confusion. It is not clear precisely when the error in synonymy began, but a specimen from the herbarium of J. Gay, collected on 7 Jul 1855 along Rue de Reuilly, Paris (K000750982), is identified with *Leptosiphon aureus* Benth. and *Gilia aurea* Nutt., implying the names are synonymous. Mason in Abrams (1951, 3: 419) includes "*Leptosiphon aureus* Benth. ex Vilm.-Andre" in synonymy under *Linanthus aureus*. However, "*Gilia micrantha* var. *aurea* Benth.," the source of *Leptosiphon aureus* Benth. ex Vilm., is included in synonymy under *Linanthus acicularis* Greene (Abrams 1951, 3: 431). Similarly, Cronquist (1984) included *Leptosiphon aureus* Benth. ex Vilm. as a synonym of *Linanthus aureus*. This confusion has persisted and several modern authors have employed the name "*Leptosiphon aureus* (Nutt.) E. Vilm.," although Vilmorin did not propose a new combination involving Nuttall's *G. aurea*. Below we show that *Gilia micrantha* Steud. var. *aurea* Benth. and *Leptosiphon aureus* E. Vilm. are synonymous.

Within the second edition of *Les Fleurs de Pleine Terre* (1866), Elisa de Vilmorin (director of Vilmorin-Andrieux and Co.) discusses five species under the generic name *Leptosiphon*. The third of these is "*Leptosiphon* jaune d'or.—*L. aureus*, Benth." No indication of the source of the epithet *aureus*, other than the name Bentham is provided. However, it is also relevant to note that Vilmorin described the flowers in some detail: "Les fleurs, très-nombreuses, disposées en corymbe, sont entourées chacune par un calice dont les 5 segments, de même forme que les feuilles, se confondent avec elles; le tube de la corolle est long d'un centimètre et demi; sa couleur est

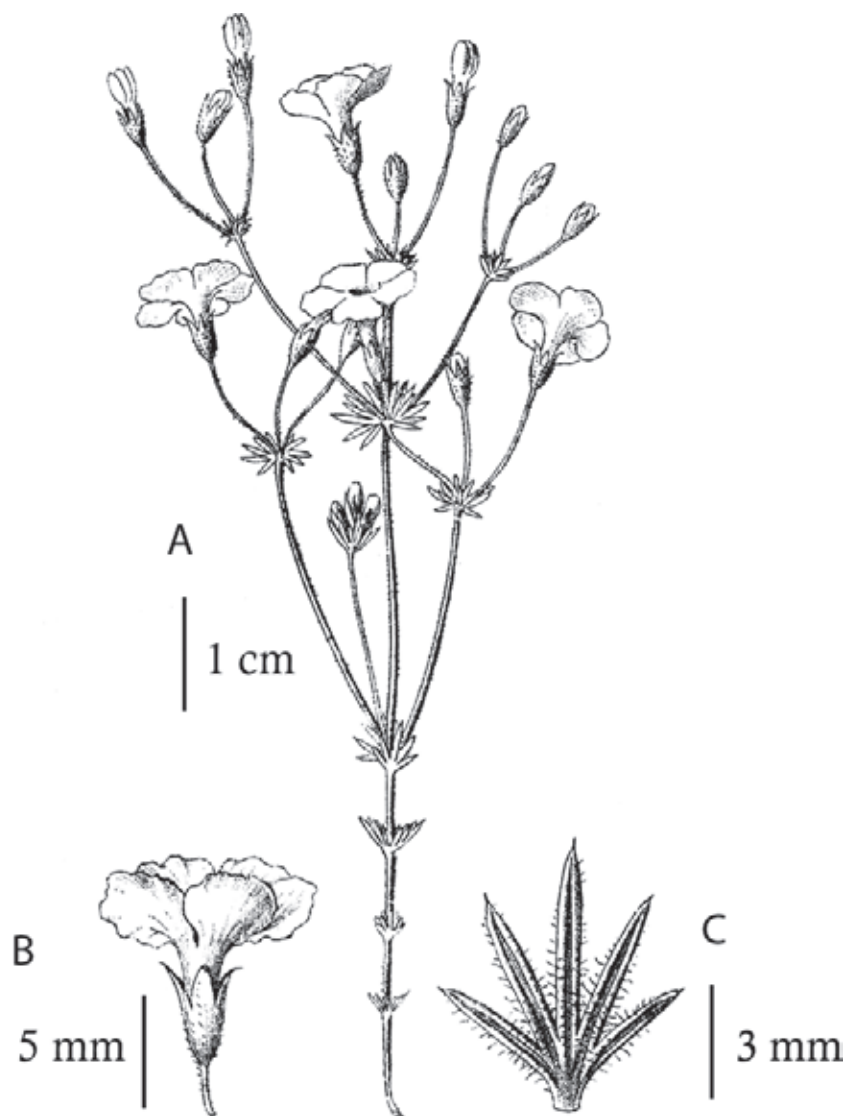


Fig. 6. *Leptosiphon chrysanthus* J.M. Porter & R. Patt. [formerly *Linanthus aureus* (Nutt.) Greene]: (A) plant; (B) flower; (C) leaf. Figure from Brand (1907).

d'un blanc jaunâtre analogue à celle de la partie inférieure du limbe; ce limbe est à 5 divisions ovales, étalées et d'un jaune doré; chacune de ces divisions est marquée à la base de deux petites taches purpurines qui forment par leur ensemble une jolie petite couronne; étamines et pistil saillants, de couleur orangée" (pp. 470–471). The description indicates that this species has a long, narrow corolla tube approximately 1.5 cm long, as do many species of *Leptosiphon*. This description clearly excludes Nuttall's *Gilia aurea*, but is consistent with a number of other species, including the yellow-flowered *Leptosiphon acicularis* (Greene) Jeps.

Bentham's (1833) treatment of Polemoniaceae, in which he described the genus *Leptosiphon*, does not include the epithet *aureus*. However, in *Plantae Hartwegianae* (1849), Bentham provides the name *Gilia* (*Leptosiphon*) *micrantha* Steud. var. *aurea*, based upon Hartweg 234. Interestingly, of this taxon Bentham says only, "nec aliter a species differre videtur" (not otherwise different from the species it seems), providing no description. This apparently indicates that Bentham did not accept the taxon as different from *G. micrantha*. Given that

Vilmorin cited *Plantae Hartwegianae* often, this is unquestionably the source of the epithet *aureus*. Subsequent editions of *Les Fleurs de Pleine Terre*, e.g., the 3rd–5th editions (1870, 1894, 1909), continued to recognize *L. aureus*, but also stated, "syn. lat. *Gilia lutea* Steud. var. *aurea* Hort." (pp. 594, 549, 591, respectively). In addition to the citation, an illustration is also provided of *Leptosiphon* jaune d'or (Fig. 7).

Vilmorin's basis for *Leptosiphon aureus* is also clear from Voss's Vilmorin Blumengärtnerei (Siebert and Voss 1896). In this treatment, Siebert and Voss followed contemporary authors, e.g., Asa Gray (1878), in subsuming *Leptosiphon* (and many other genera) under *Gilia*. In discussing the various cultivated forms of *Gilia micrantha* Steud., Voss provides a nomenclatural innovation, *Gilia micrantha* Steud. forma *aurea*, citing "syn. *Leptosiphon aureus* Benth. (Siebert and Voss 1894: 683)" as the basis for the name. This indicates that *L. aureus* Benth., as cited by Vilmorin, was considered to be very closely related to *Gilia micrantha* (= *Leptosiphon parviflora* Benth.).

Brand's monograph of Polemoniaceae (1907) also includes many of Vilmorin's names. Like Gray's treatment in the

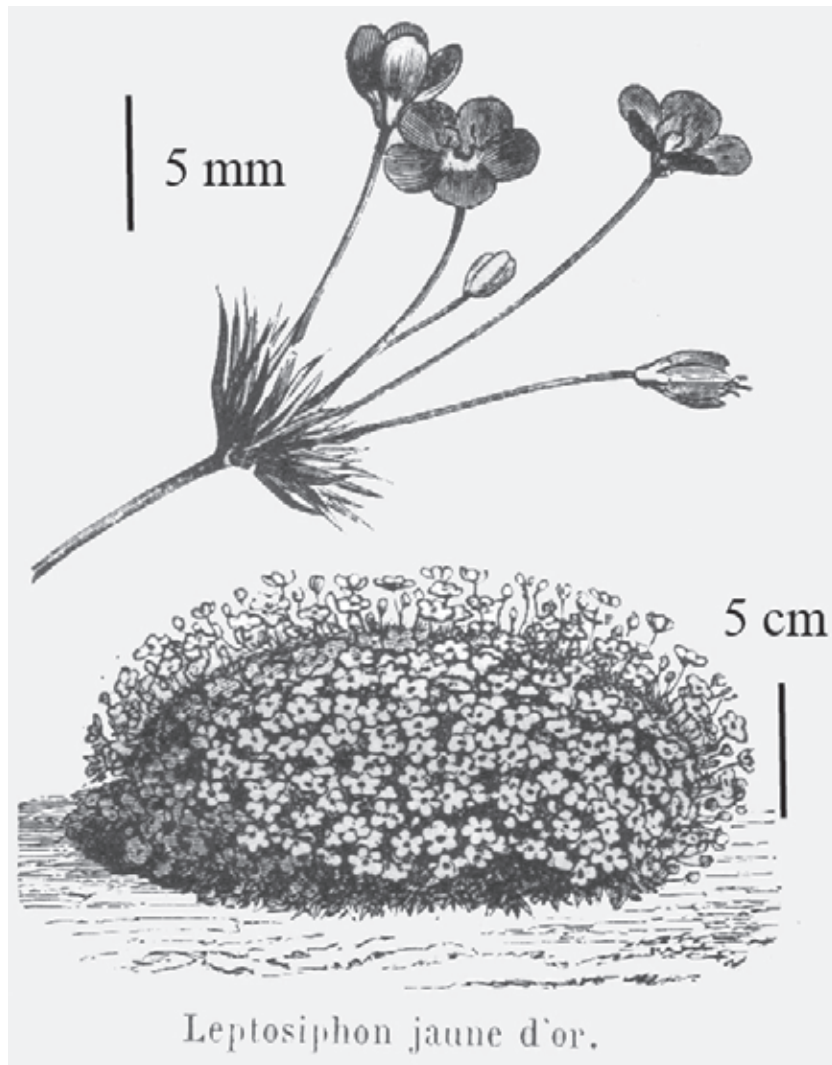


Fig. 7. *Leptosiphon jaune d'or*, *Leptosiphon aureus* Benth. ex E. Vilm. [= *Leptosiphon acicularis* (Greene) Jeps.] line drawing. Below: plant habit. Above: capitulate inflorescence head. Figure from Vilmorin et Cie. (1866: 470) and Vilmorin (1870: 594).

Synoptical Flora (1878), Brand incorporated many of the previously segregated genera, such as *Linanthus* and *Leptosiphon*, into *Gilia*. In particular, associated with his species 90, *Gilia lutea* (Benth.) Steud., Brand provided a new combination, “Var. c. *aurea* Benth.! Pl. Hartweg. (1849) 325.—*Leptosiphon aureus* Benth. ex Vilm.-Andr. Fleurs pleine terre ed. 2. (1866) 470”.

This rather lengthy explanation provides the justification for proposing that *Gilia micrantha* var. *aurea* Benth, nom. nud., and *Leptosiphon aureus* Benth. ex E. Vilm. are the same taxon. This conclusion is further supported by collections at K (000750977) and P (04591512). The former is a collection of Hartweg, identified as *G. micrantha* var. *aurea*, the latter identified as *Leptosiphon aureus* Benth. (Hortus Parisiensis, 1869). Both of these specimens represent the same taxon, *Leptosiphon acicularis* (Greene) Jeps. Although the name *L. acicularis* has been applied for over a century, it is now evident that the earliest legitimate name for this taxon is *L. aureus*. This also means that *Linanthus* (*Gilia*) *aureus* cannot be transferred to *Leptosiphon* using the original epithet. Here we provide a new name:

***Leptosiphon chrysanthus* J.M. Porter & R. Patt., nom. nov.**

Replaced name: *Gilia aurea* Nutt., *Proc. Acad. Nat. Sci. Philadelphia* 4: 11 (1848).

Navarretia aurea (Nutt.) Kuntze, *Revis. Gen. Pl.* 2: 433 (1891). *Linanthus aureus* (Nutt.) Greene, *Pittonia* 2: 257 (1892). *Dactylophyllum aureum* (Nutt.) A. Heller, *Muhlenbergia* 2: 231 (1906). *Leptosiphon aureus* (Nutt.) J.M. Porter & L.A. Johnson, *Aliso* 19: 80 (2000), *nomen illegitimum*: later homonym [not *Leptosiphon aureus* Benth. ex E. Vilm., *Fl. Pleine Terre* (ed. 2) 470 (1866). = *Gilia micrantha* Steud. var. *aurea* Benth.].—TYPE: *W. Gambel s.n.*, USA, California, Santa Barbara, flowering April (fide protologue); lectotype (here designated) K 000769037; isolectotypes GH 78819, PH 1068920/12188.

Etymology.—The epithet *chrysanthus* (Greek, golden) refers to the brilliant yellow flower color.

***Leptosiphon chrysanthus* J.M. Porter & R. Patt. subsp. *decorus* (A. Gray) J.M. Porter & R. Patt., comb. nov.**

Basionym: *Gilia aurea* Nutt. var. *decora* A. Gray, *Proc. Amer. Acad. Arts* 8: 264 (1870).

Gilia aurea Nutt. forma *decora* (A. Gray) Brand, *Pflanzenr.* (Engler) 4, Fam. 250: 131 (1907). *Linanthus aureus* (Nutt.) Greene var. *decora* (A. Gray) Jeps., *Man. Fl. Pl. Calif.* [Jepson] 803 (1925). *Linanthus aureus* (Nutt.) Greene subsp. *decorus* (A. Gray) H. Mason, III, *Fl. Pacific States* (Abrams) 3: 419 (1951). *Leptosiphon aureus* (Nutt.) J.M. Porter & L.A. Johnson subsp. *decorus* (A. Gray) J.M. Porter & L.A. Johnson, *Aliso* 19: 80 (2000).—TYPE: Protologue states, “California, Fremont, Brewer, the latter on Monte Diablo.” Note that the protologue is possibly in error as this taxon is known only from Imperial, Kern, Los Angeles, Riverside, and San Bernardino counties, in the Mojave and Colorado Deserts; whereas, Mt. Diablo is in the Coast Ranges (Contra Costa County), near San Francisco Bay. Syntypes: *J.C. Frémont s.n.*, California; *W.H. Brewer 1204*, California, 1860. Gray Herbarium holds only a collection by J. C. Frémont (GH00078820). Mounts of *J.C. Frémont 334*, *J.C. Frémont 324* and *W.H. Brewer 1204* can be found at NY (all on the same sheet). Lectotype (here designated) GH (*J.C. Frémont s.n.*, California, 00078820).

While it is important to correct the confusion involving *Leptosiphon chrysanthus*, it is also critical to make clear the application of the name “*Leptosiphon aureus*.” Below we provide the correct nomenclature and synonymy for *Leptosiphon aureus*, including lectotype designation:

Gilia micrantha Steud. var. *aurea* Benth. nom. nud., *Pl. Hartw.* 325 (1849). Based on *T. Hartweg 1851/234*, USA, California, “in valle Sacramento,” 1837.—Note: Collections of *Hartweg 1851/234* at K (K000750977) and P (P00640841) represent two different species. It is possible that labels and/or specimens were at some time inadvertently switched at one of the herbaria. Because the name was not validly published, it is not necessary to specify a type; however, we have treated the name as corresponding to K000750977.

Leptosiphon aureus Benth. ex E. Vilm., *Fl. Pleine Terre* (ed. 2) 470 (1866). *Gilia micrantha* Steud. f. *aurea* (Benth. ex E. Vilm.) Voss, *Vilm. Blumengärtn.*, ed. 3, 1: 683 (1894). *Gilia lutea* (Benth.) Steud. var. *aurea* (Benth. ex E. Vilm.) Brand, *Pflanzenr.* (Engler) 4, Fam. 250: 143 (1907).—TYPE: (lectotype here designated, closely matching the protologue). *Collector unknown*, France, Paris, cultivated, 1869 (P 04591512).

Linanthus acicularis Greene, *Pittonia* 2: 259 (1892). *Leptosiphon acicularis* (Greene) Jeps., *A School Flora for the Pacific Coast* 77 (1902).—TYPE: the protologue identifies no collector or location, stating only that *L. acicularis* co-occurs with *L. parviflorus*. Described while Greene was at Berkeley, the materials that he consulted are most likely at UC (and/or CAS). These include *W. H. Brewer 983*, Sonoma County, Sonoma, 18 Apr 1862 (UC); *H. N. Bolander 3853*, Sonoma County, Russian River Bed, 1864 (UC); *W. H. Brewer 1274*, 1800s; *H. P. Chandler 1082*, Mendocino County, North Coast Ranges. Greene’s herbarium is at Notre Dame and has no specimens attributable to this species (B. Hellenthal, pers. comm.). Lectotype (here designated) *H. N. Bolander 3853*, Sonoma County, Russian River Bed, 1864 (UC). This specimen closely matches the protologue.

The nomenclatural changes proposed above are unfortunate but necessary. Unfortunate in the sense that two names for well-known species formerly of *Linanthus* (*Linanthus acicularis*

and *L. aureus*) cannot retain their specific epithets when transferred to *Leptosiphon*. This change also results in the confusing situation in which the name *Leptosiphon aureus* remains a legitimate name of priority; however, it refers **not** to the species formerly called *Linanthus aureus*, but to the species formerly called *Linanthus acicularis*. While this is unsatisfying, it is the only recourse aside from a proposal to conserve, which would have no guarantee of success.

A NEW SUBSPECIES OF *LINANTHUS BIGELOVII*

Field studies and examination of herbarium collections, with special attention to the type, has revealed considerable variation across the range (western Texas to California) of *Linanthus bigelovii* (A. Gray) Greene. This variation has resulted in some degree of confusion and mischaracterization concerning *L. bigelovii* and differences between it and *L. jonesii* (A. Gray) Greene. Specifically, populations of *L. bigelovii* in California have correctly been described as glabrous and glaucous (occasionally a few glandular trichomes may be present); however, those from the eastern portion of the range, including the type, are sparsely beset with glandular trichomes, particularly on the pedicels, but also sparsely so on the calyx (Fig. 8). *Linanthus jonesii*, with its coarsely glandular pedicels and calyx, is easily distinguished from *L. bigelovii* in California, but the distinction is less clear in Arizona, where *L. bigelovii* tends to also have glandular trichomes. The glandular trichomes of *L. bigelovii* are uniseriate with globular terminal glands and differ from the coarse multiseriate glandular trichomes with flattened, tack-like terminal glands found on *L. jonesii* (Fig. 8). In contrast with the eastern populations, the populations of *L. bigelovii* in California have glabrous pedicels and calyces. A somewhat more subtle difference is found in seed morphology. Seeds of *L. bigelovii* from the eastern portions of its range are small, elliptical to oblong in outline, usually notched at the hilum, and sometimes with narrow winged margins (Fig. 9A). Importantly, sometimes the seeds lack the winged margins and are nearly indistinguishable from those of *L. jonesii* (Fig. 9C). *Linanthus bigelovii* from California has seeds that are slightly larger, elliptical to oblong in outline, sometimes with very narrow wing-like edges, but generally lacking the notching at the hilum (Fig. 9B). As found in the eastern populations of *L. bigelovii*, the western phase has glabrous filaments that diverge about mid-length of the corolla tube (Fig. 10). Here we describe the western, glabrous phase of *L. bigelovii* at the rank of subspecies:

LINANTHUS BIGELOVII (A. Gray) Greene subsp. **johnsonii** J.M. Porter & R. Patt., subsp. nov.—TYPE: *J. M. Porter & S. J. De Groot 14254*, USA, California, Riverside County, Colorado Desert, Little San Bernardino Mountains region, S of State Route 62, at the base of granite outcrop, just E of Joshua Tree National Park, 794 m elev., 9 Mar 2005 (holotype RSA).

Erect, taprooted annual 4.5–47 cm tall, simple to more often freely, dichotomously branched; cotyledons 5.2–9.5 mm long, linear or narrowly linear-lanceolate, sheathing, sparsely ciliate villous proximally. Stems nearly glabrous throughout, or with a few eglandular and rarely glandular trichomes at the nodes; nodes generally opposite throughout. Leaves 1.4–6.5 cm long, simple and linear or linear-filiform at the lower nodes, 3-cleft essentially to the base into linear-filiform segments at the more distal nodes, the central lobe the longest, leaf base somewhat

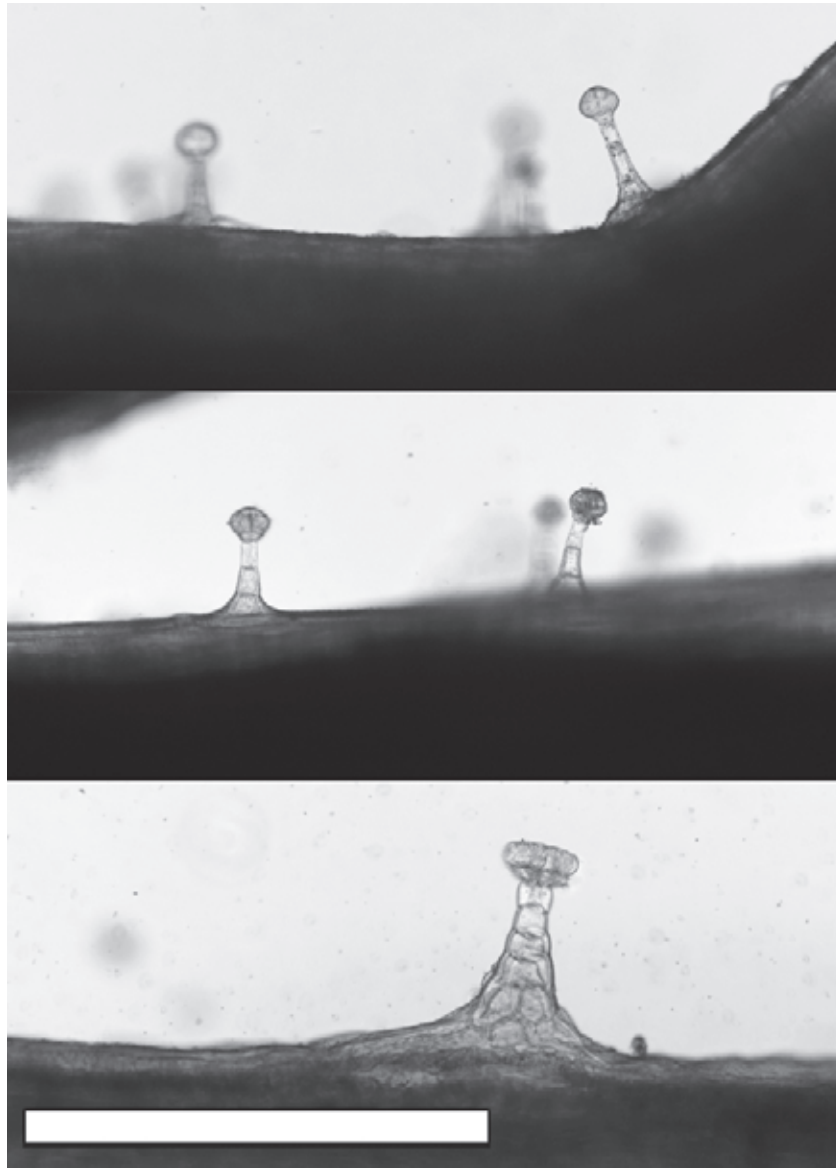


Fig. 8. Glandular trichomes from the calyx (above) and pedicels (center) of *Linanthus bigelovii* (A. Gray) Greene subsp. *bigelovii* and from the calyx of *L. jonesii* (A. Gray) Greene (below). Note the uniseriate stalk with globular, multicellular distal gland of *L. bigelovii* subsp. *bigelovii* (above and center) and the multiseriate stalk and bi-tiered, flat-topped, multicellular, terminal gland of *L. jonesii* (below). Scale bar = 0.5 mm.

sheathing, very sparsely ciliate-villous, stipitate-glandular or glabrous at the leaf base. Inflorescence cymose, diffuse and branching, more or less regularly dichotomous, the terminal flower subsessile or pedicellate, the pedicel 0.6–10 mm long, commonly closely subtended by a pair of leafy bracts, similar to the leaves, 5–30 mm long, simple entire and linear or 3-lobed, the lobes linear. Flowers vespertine (nocturnal), closed during the day, opening in the late afternoon or evening and remaining open through the night. Calyx 8–18 mm long, the green, herbaceous costae terminating in unequal lobes; the lobes 2.4–6.9 mm long, apex acute acicular or mucronate; the tube 6–11 mm long, the conspicuous white-hyaline intervals of the tube as wide as or generally wider than the green and herbaceous costae, glabrous abaxially, sparsely to moderately villous, sometimes also glandular adaxially on the distal tube and proximal lobes. Corolla 8–16.3 mm long, the lobes (2.5–)4–7.5(–9) mm long, 1.7–5.2 mm wide, white, generally flecked with purple, maroon or

brownish on the abaxial lobe margin exposed in bud, and a band of purple adaxially in the upper tube or throat, glabrous. Stamens equally or sub-equally inserted 3.5–5.6 mm above corolla insertion, generally 2 mm or more above the apex of the ovary; filaments slender, glabrous, 0.6–1.1(–1.6) mm long; anthers 0.5–0.7 mm long, included; pollen yellow. Ovary 1.9–3.5 mm long, 0.6–1.4 mm in diameter, glabrous; style 0.4–0.8 mm long; stigma lobes 1.2–2.1 mm long. Capsule cylindroid, 7–11 mm long, 1.5–2.8 mm in diameter, dehiscent from the apex down 1.8–2.5 mm, held for some time within the slightly accrescent calyx, the valves remaining attached toward the base at least for a time after dehiscence. Seeds 12–21 seeds per locule, 0.6–1.5 mm long, 0.4–0.7 mm in diameter, pale, more or less ellipsoid, angular, not reniform nor much indented at the hilum, often with very narrow marginal wings along the angular edges, the hilum generally along one of the angled edges, inconspicuous, swelling when wet, and becoming somewhat mucilaginous. $2n = 18$.

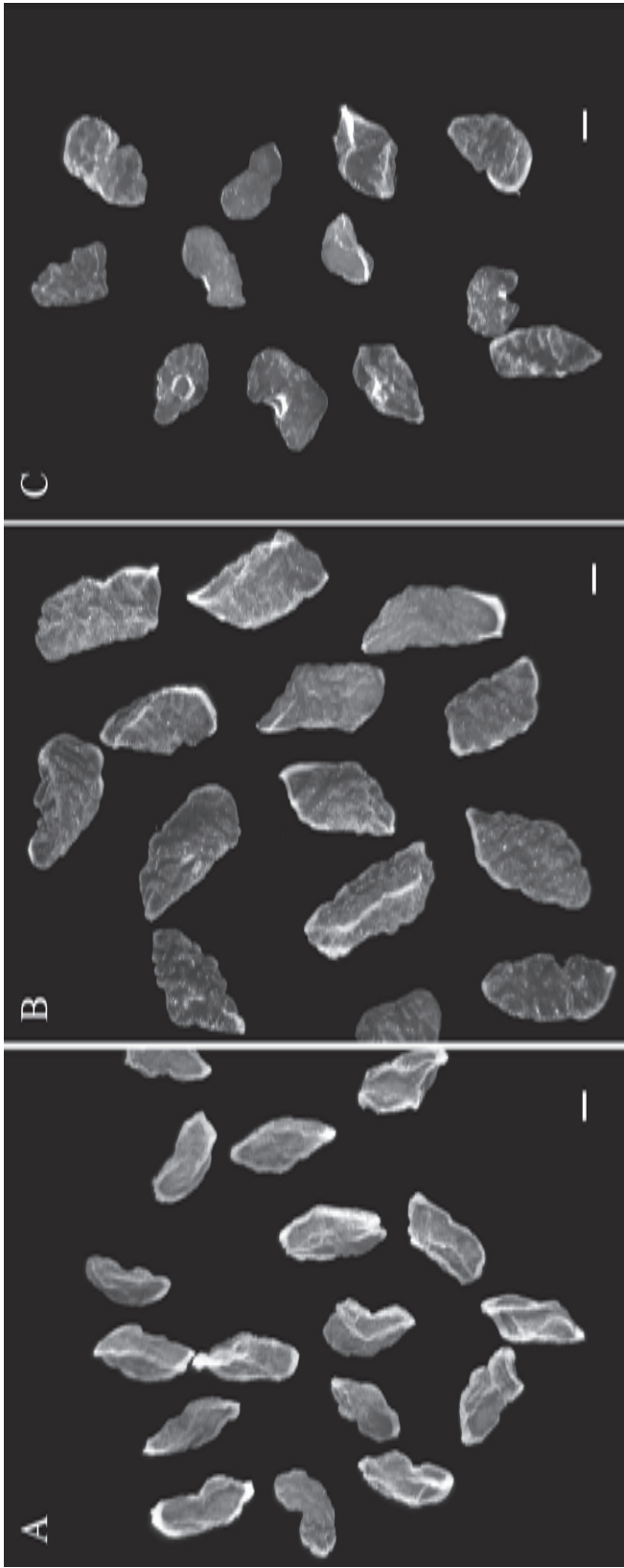


Fig. 9. Seeds of *Linanthus bigelovii* (A. Gray) Greene sampled from (A) near the type locality in El Paso County, Texas, and (B) from the western extent of its range in California; and seeds of *Linanthus jonesii* (A. Gray) Greene (C) sampled from near its type locality at Needles, California. Scale bar = 0.4 mm.

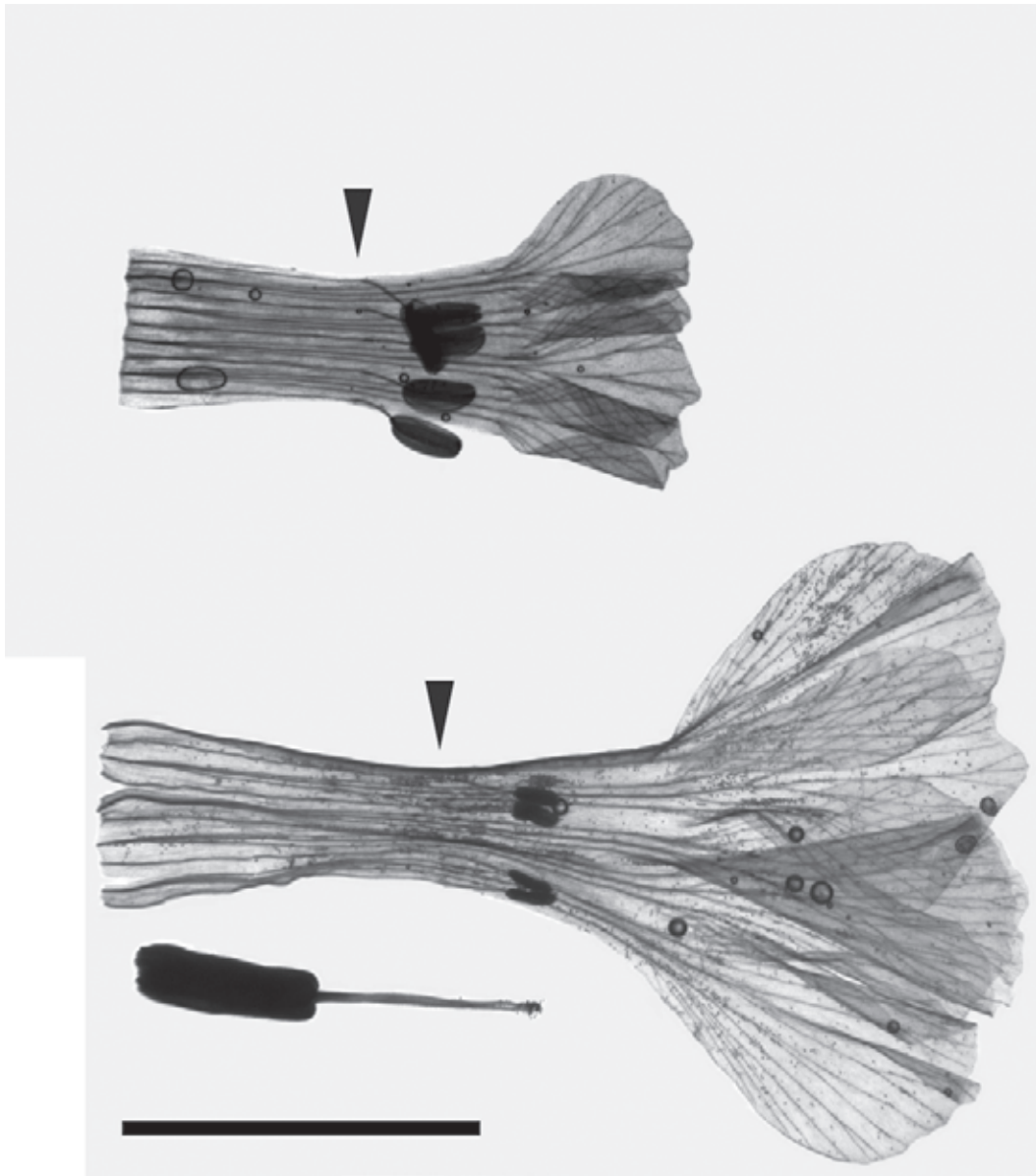


Fig. 10. Corolla dissections of *Linanthus bigelovii* (A. Gray) Greene. The smaller flower (above) is from near the type locality of subsp. *bigelovii* in the Organ Mountains near El Paso, Texas, while the larger flower (below) is from near the type locality of *L. bigelovii* subsp. **johnsonii** J.M. Porter & R. Patt. on the northern foothills of the San Gabriel Mountains, Los Angeles County, California. The arrow indicates the point of insertion of the filaments in the mid-tube. Scale bar = 2.0 mm.

Key to the Subspecies of Linanthus bigelovii

1. Distal stems, pedicels, and calyx stipitate-glandular; proximal leaf margins densely villous with eglandular trichomes and stipitate-glandular trichomes; seeds angular reniform, sometimes with narrow marginal wings, the hilum indented and often white margined *Linanthus bigelovii* subsp. *bigelovii*
- 1' Distal stems, pedicels, and calyx glabrous, or with very sparse eglandular, villous trichomes or very sparse stipitate glands on the proximal leaf margins; seeds ellipsoid, angular, not reniform nor much indented at the hilum, hilum not white margined, sometimes with very narrow marginal wings along the angular edges *Linanthus bigelovii* subsp. **johnsonii**

On steep rocky slopes, sandy or clay soil, limestone or granitic loams, alluvial benches, colluvial bajadas, washes, canyons and flats, associated with chaparral, shadscale scrub, greasewood scrub, pinyon-juniper woodlands, creosote scrub, desert grasslands, sagebrush scrub of the Colorado, Mohave, and Sonoran deserts, at 370–1800 m, from California (Imperial, Inyo, Kern, Los Angeles, Mono, Monterey, Riverside, San Bernardino, San Diego, and Ventura Counties), Arizona (Mohave County), and Nevada (Clark and Lincoln Counties). Flowering April–May, fruiting late April through June.

Etymology.—The commemorative epithet *johnsonii* honors Leigh Johnson, student of Polemoniaceae, Professor of Biology at Brigham Young University, Herbarium Curator and Associate Museum Director of the Monte L. Bean Life Science Museum.

Selected representative specimens.—USA. ARIZONA. Mo-have County: Grizelle's, near Kingman, 21 Apr 1927, *S. Braem s.n.* (POM). CALIFORNIA. Inyo County: Owens Valley, W slopes of Red Hill cinder cone, just N of Little Lakes, S of Coso Jct., 1033 m, 15 Apr 2011, *J. André 17671* (RSA); White Mtns, W base of Black Mtn, 2.5 mi S, 77° W of its summit. Owens Valley drainage, 1250 m, 1 Apr 1986, *J. D. Morefield & D. H. McCarty 3308* (UCR); Southern Sierra Nevada region, Sierra Nevada foothills, S of Lone Pine, Lubkin Canyon Rd., hills below pheasant club, 26 Apr 1998, *J. M. Porter 11811* (RSA); Mojave Desert, North Mojave Desert region, Owens Valley, E of Black Rock Springs, 3810 ft elev., 15 May 1978, *M. DeDecker 4674* (RSA). Kern County: Los Padres National Forest, Lockwood Valley, S of the San Emigdio Mountain Range, on the N side of Lockwood Valley Road, ca. 0.8 mi, by road, SW of the junction with Cuddy Valley Rd., 27 May 2005, *J. M. Porter & T. Anderson 14418* (RSA); West Mojave Desert region, Jct of Hwy 58 and Neuralia Road, S of Red Rock Canyon State Park and W of Jawbone Canyon; elev. 2500 ft, 5 Apr 1991, *D. Charlton 4727* (RSA). Los Angeles County: West Mojave Desert region, Antelope Valley, hill N of Saddleback Butte State Park (N of Avenue J), 27 Apr 1998, *J. M. Porter 11831* (RSA); West Mojave Desert region, Black Butte: rocky easterly and northeasterly slopes, 960–1082 m elev., 27 Apr 1991, *T. S. Ross 4708* (RSA); Transverse Ranges, San Gabriel Mountains region, Santiago Canyon, canyon and slopes draining W slopes of Santiago Canyon ca. 1 mi SW of confluence with Little Rock creek, 3300 ft elev., 11 Apr 1995, *O. Mistretta 1623* (RSA); Mono County: White Mtns, low hills S of Rock Creek drainage, 1549 m elev., 20 Apr 1986, *J. D. Morefield & D. H. McCarty 3471* (UCR); S of Rock Creek drainage, White Mountains, Owens Valley, 5080 ft elev., 20 Apr 1986, *J. D. Morefield & D. H. McCarty 3471* (UC). Monterey County: Santa Lucia Mtns, NW of San Antonio Mission, 20 Apr 1962, *C. B. Hardham 9047* (SBBG); Lewis Creek, NE of Lonoak (2 mi from intersection of Bitterwater Road), 25 Apr 1934, *D. D. Keck 2769* (POM). Riverside County: Colorado Desert, western Colorado Desert region, Palm Springs, *A. Davidson s.n.* (POM); Split Rock, Joshua Tree National Monument, 4300 ft elev., 7 May 1941, *A. M. Alexander & L. Kellogg 2134* (UC); Transverse Ranges, San Bernardino Mountains region, Whitewater Canyon, E of the Paw, near the mouth of Catclaw Flat Canyon, 871–914 m elev., 12 Apr 2010, *L. Gross, J. McConaughy, D. Monks, T. Stoughton, J. Tirrell & M. Volke s.n.* (RSA); Colorado Desert, Little San Bernardino Mountains region, S of State Route 62, at the base of granite outcrop, just E of Joshua Tree National Park, 794 m elev., 9 Mar 2005, *J. M. Porter & S. De Groot 14254* (RSA). San Bernardino County: south-central Mojave Desert region, transition between San Bernardino Mountains and Little San Bernardino Mountains, Big Horn Sheep Wilderness, New Dixie Mine Road, just W of Hwy 247, 1153 m elev., 4 May 2011, *T. Stoughton, S. Rockwood & C. Gabriel 1189* (RSA); Whipple Mountains, hill in drainage below cove NE of highest peak along summit ridge, 1012 m elev., 24 Apr 2010, *S. J. De Groot 6299* (RSA); East Mojave Desert region, N base of Old Woman Mountains, S of Essex, Honeymoon Wash along Willow Springs road, 0.5 mi W of Sunflower Springs Road, 1000 m elev., 19 Mar 1993, *S. Boyd, W. Appleby & T. S. Ross 7868B* (RSA); New York Mountains, Mojave National Preserve, along dirt road to Mail Spring,

0.2 mi SW of spring area, 1538 m elev., 2 Jun 2010, *J. André 15540* (RSA). San Diego County: Peninsular Ranges, Cuyamaca–Laguna Mountains region, summit of Mt. Springs Grade, 3500 ft elev., 17 Apr 1927, *F. W. Peirson 7231* (RSA). San Luis Obispo County: Caliente Range, 5.1 mi from Soda Lake Rd., along Selby Rd., oak-juniper woodland, 11 May 1998, *D. Keil 27219* (SLO); Caliente Range, along main ridge NW of Caliente Pk., ca. 4125 ft elev., 23 Apr 2003, *D. Keil & R. Riggins 30129* (SLO); between San Juan River and Carrizo Plain, on sandy slopes, 20 Apr 1952, *R. F. Hoover 8146* (SLO). Ventura County: Transverse Ranges, Mount Pinos region, Camp Ozena, 2 mi E of U.S. Hwy 399, Ozena Valley, 3900 ft elev., 19 Apr 1962, *D. E. Breedlove 2408* (RSA). NEVADA. Clark County: Virgin Valley, along E base of Mormon Mesa, S of junction of Mormon Mesa road and road going N along Virgin River, 7 Apr 1995, *J. S. Holland 3345* (UCR); Lincoln County: Meadow Valley Mountains, 1.9 road mi ESE of Kane Springs Valley Road on road to Lyman Crossing, 2 May 2006, *A. Tiehm s.n.* (NY). UTAH. Washington County: St. George, 4 Apr 1880, *M.E. Jones 122* (POM); Lytle Ranch Preserve, 12 Apr 1991, *L. Higgins 18651* (RSA).

A NEW SPECIES OF *LINANTHUS* FROM THE SONORAN DESERT

In the course of reinvestigating the *Linanthus* species of Arizona, an unusual new taxon was discovered in the central portion of the state. In the past, these populations have consistently been identified as *Linanthus dichotomus*, owing to their large corollas. However, these populations lack three diagnostic traits of *L. dichotomus*: (1) inflated and densely pilose filament bases; (2) seeds with a pith-like, whitish and finely cellular-reticulate seed coat; and (3) a glabrous and somewhat glaucous calyx. Rather, the filaments are undilated and glabrous (Fig. 11), seeds are reniform, brown and rugose, and the calyx is coarsely glandular. In particular, the coarse glandular trichomes are similar to those of *L. jonesii*. The glandular trichomes of *L. jonesii* have stalk cells that are multiseriate, bearing large, tack-like terminal glands that are multicellular (Fig. 8). They differ from the trichomes of *L. bigelovii* which have uniseriate stalks with terminal, 1–8-celled, globular glands (Fig. 8). What distinguishes these plants from *L. jonesii* are the exceptionally large corollas and the tendency for glandular trichomes of the calyx and pedicel to have uniseriate stalks. Because both *L. jonesii* and this large-flowered taxon are sympatric throughout the range of the new taxon, we believe that there must be isolation between the two. We therefore treat the new taxon at the rank of species:

Linanthus maricopensis J.M. Porter & R. Patt., sp. nov.—

TYPE: *M. Chamberland 1846* with *R. Felger & C. Funicelli*, USA, Arizona, Maricopa County, South Maricopa Mountains, N of Highway 8, NE of Big Horn, 32.8667° N, 112.3667° W, 24 Mar 2001 (holotype ARIZ) (Fig. 12).

Erect, taprooted annual 6–25 cm tall, simple to more often freely, dichotomously branched; cotyledons 2.5–4.8 mm long, linear-filiform, sheathing, glabrous or very sparsely ciliate villous proximally. Stems sparsely but coarsely stipitate-glandular throughout, more densely stipitate-glandular at and just below the nodes and in the inflorescence; nodes generally opposite, rarely subopposite or alternate. Leaves 8.9–33 mm long, simple and linear or linear-filiform (rarely 3-lobed



Fig. 11. Corolla dissections of *Linanthus maricopensis* J.M. Porter & R. Patt. and *L. jonesii* (A. Gray) Greene. The larger flower is from near the type locality of *L. maricopensis* in the Maricopa Mountains, Yavapai County, Arizona (left), while the smaller is from near the type locality of *L. jonesii* near Needles, California (right). The arrow indicates the point of insertion of the filaments, in the mid-tube. Scale bar = 2.0 mm.

and the central lobe longest), leaf base somewhat sheathing, coarsely stipitate-glandular on the adaxial proximal surface and margin (ciliate). Inflorescence cymose, diffuse and branching, more or less regularly dichotomous, the pedicel of the terminal flower 1.5–13.5 mm long, coarsely stipitate-glandular, closely subtended by a pair of leafy bracts; bracts 9–32 mm long, simple, entire linear-filiform, very rarely 2(–3)-cleft into linear-filiform segments, the central lobe the longest, petiole to 2 mm long, coarsely stipitate-glandular. Flowers opening in the late afternoon, or vespertine (nocturnal), closed during the day, opening in the evening and remaining open through the night. Calyx 8–13.2 mm long, the green, herbaceous costae terminating in unequal lobes, 2–7.9 mm long, the tube 5.4–7.5 mm long, the conspicuous white-hyaline intervals of the tube wider than the costae, glandular (the trichomes coarse, with multiseriate stalks and multicellular terminal glands) abaxially, sparsely to moderately villous and glandular adaxially on the distal tube and lobes. Corolla 14–30 mm long, the lobes 7.9–20.6 mm long, 5.4–10.2 mm wide, cream to white, generally flecked with purple abaxially and a band of purple adaxially in the upper tube, glabrous. Stamens equally or subequally inserted 4.4–6.2 mm above corolla insertion, filaments slender, glabrous, 1.1–1.6 mm long, anthers 1.1–1.5 mm long, included, pollen yellow. Ovary 2–2.5 mm long, 0.8–1.0 mm in diameter, narrowly pyriform to cylindric, glabrous, style 0.6–1.3 mm long, stigma lobes 1.4–2.5 mm long. Capsule cylindric, 4.5–9.1 mm long, 1.8–2.5 mm in diameter, held for some time within the slightly accrescent calyx, the valves remaining attached toward the base at least for a time after dehiscence.

Seeds 18–32 seeds per locule, ca. 1 mm long, 0.4 mm in diameter, pale, more or less angular reniform, the hilum indented and white margined, seed coat rugose, swelling when wet, and becoming somewhat mucilaginous.

Key Distinguishing *Linanthus bigelovii*, *L. dichotomus*, *L. jonesii*, and *L. maricopensis*

1. Seeds 5–10 per locule, 1–1.5 mm long, irregularly angular, the outer seed-coat pithy, whitish, finely cellular-reticulate, not becoming mucilaginous when wetted *L. dichotomus*
- 1' Seeds 12–21 per locule, 0.6–1.1 mm long, more or less ellipsoid, angular reniform, the hilum indented and white margined, or not reniform nor much indented at the hilum, swelling when wet, and becoming somewhat mucilaginous 2.
2. Calyx glabrous or sparsely beset with uniseriate glandular trichomes, the terminal gland globose, 1–8-celled *L. bigelovii*
- 2' Calyx glandular, usually coarsely so, at least some glandular trichomes with multiseriate stalks and disc-like terminal glands, 8–36-celled, also with uniseriate glandular trichomes, the terminal gland globose, 1–8-celled 3.
3. Corolla 8.5–16.5 mm long, the lobes 3.5–7.5 mm long, 2.4–4.8 mm wide *L. jonesii*
- 3' Corolla 14–30 mm long, the lobes 7.9–20.6 mm long, 5.4–10.2 mm wide *L. maricopensis*



Fig. 12. The holotype specimen of *Linthus maricopensis* J.M. Porter & R. Patt.

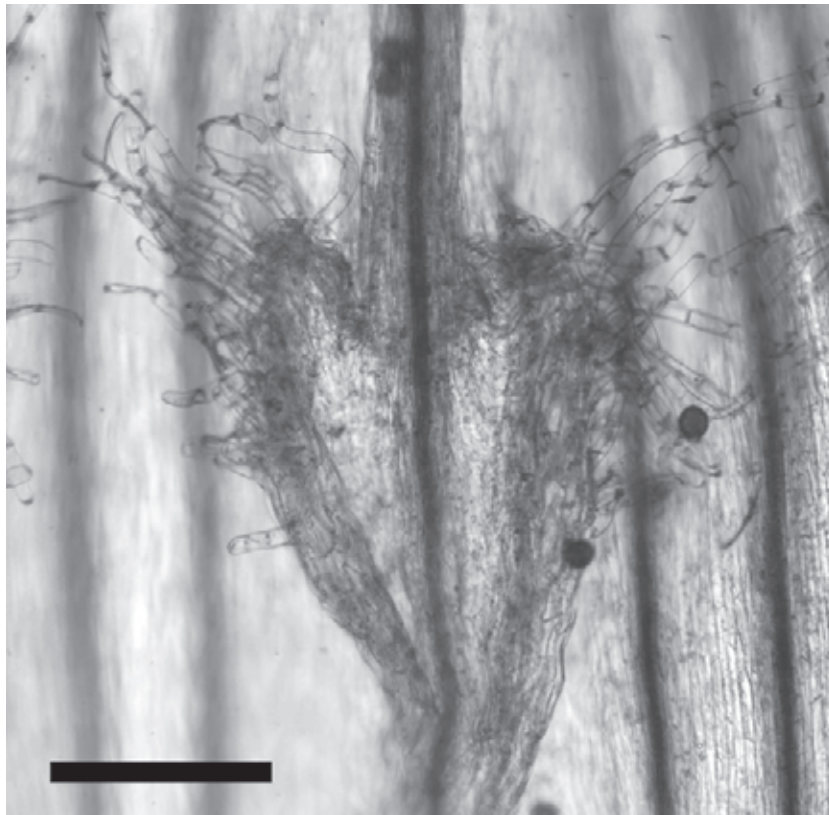


Fig. 13. The dilated, villous pad located at the point of filament insertion in the corolla of *Linthanthus dichotomus* Benth. subsp. **pattersonii** J.M. Porter. Scale bar = 0.2 mm.

Linthanthus maricopensis occurs on sand, granite, gravel, loam, rhyolitic soil, occasionally sandstone, shale and conglomerate intermixed with basalt at the foot of desert mountains, on hillsides, in washes and on bajadas or occasionally on roadsides, associated with Sonoran Desert scrub, 200–900 m elev. Flowering late January–March(–April), fruiting in April. This species is apparently restricted to Maricopa and adjacent Pinal Counties, Arizona.

Etymology.—The epithet *maricopensis* (Latinized geographic location) denotes Maricopa County, Arizona, location of the known populations of this unusual taxon.

Selected representative specimens.—USA. ARIZONA. **Maricopa County**: Sonoran Desert National Monument, Butterfield Trail, 365 m elev., 20 Mar 2001, *R. S. Felger 01-189* (ARIZ); Sonoran Desert National Monument, South Maricopa Mountains, 591 m elev., 24 Mar 2001, *R. S. Felger 01-219* (ARIZ); Sonoran Desert National Monument, North Maricopa Mountains, 580 m elev., 31 Jan 2003, *R. S. Felger 03-140* (ARIZ); Sonoran Desert National Monument, North Maricopa Wilderness, vicinity of Margie's Cove campground, 329 m elev., 25 Feb 2008, *B. Boyle 8036* (ARIZ).

A NEW SUBSPECIES OF *LINTANTHUS DICHOTOMUS*

The distinction between *Linthanthus dichotomus* Benth. and *L. bigelovii* (A. Gray) Greene has long been recognized and the traits used to diagnose them are straightforward, if somewhat cryptic. *Linthanthus dichotomus* has large flowers (corolla lobes

10–16 mm long, Patterson 1993), the epipetalous stamens are inflated and densely pilose at their point of attachment (Fig. 13), and the outer seed-coat is pith-like, whitish and finely cellular-reticulate (Fig. 14), unchanged when wetted (not producing mucilage). By contrast, *L. bigelovii* has smaller flowers (corolla lobes 7–8 mm long, Patterson 1993), the epipetalous stamens are narrow and glabrous at their point of attachment (Fig. 10), and the outer seed-coat is smooth to rugose (at 10×) brownish, either angled and narrowly winged or reniform, becoming slightly mucilaginous when wetted. Even so, it seems that there has been some confusion between the two species. For example in the Intermountain Flora, Cronquist (1984) describes the seeds of *L. bigelovii* as “sometimes approaching those of *L. dichotomus* in structure.”

Examination of materials of both *Linthanthus dichotomus* and *L. bigelovii* has revealed a series of populations in California, Nevada and Baja California, Mexico that possess small flowers like those of *L. bigelovii* (and have been identified as such) but display the seed (Fig. 14) and stamen features of *L. dichotomus* (Fig. 15). These populations represent a small-flowered phase of *L. dichotomus* and are here described as a new subspecies:

LINTANTHUS DICHOTOMUS Benth. subsp. **pattersonii** J.M. Porter, subsp. nov.—TYPE: *O. Mistretta & C. Mistretta 2415*, USA, California, Los Angeles County, Liebre Mountains, Ritter Ridge, SW of Quartz Hill, along SCE transmission lines, S of California Aqueduct, UTM Zone 11S 3832983N

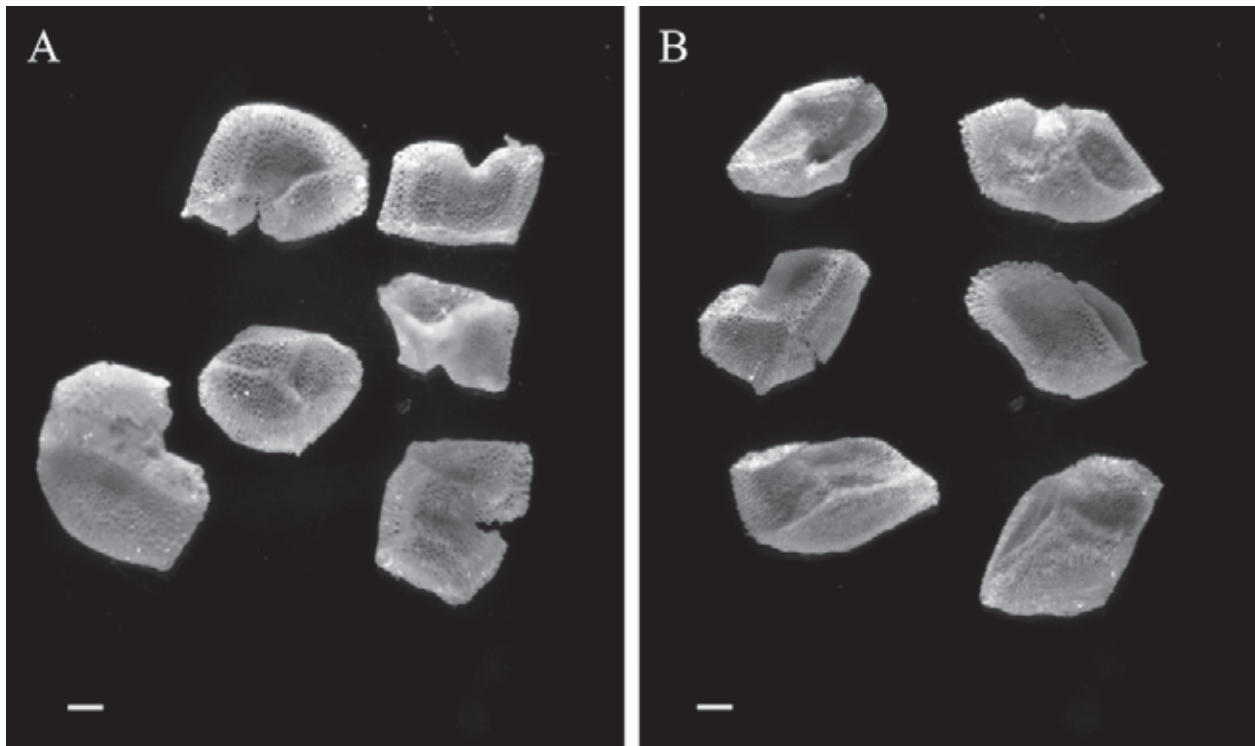


Fig. 14. Seed morphology of *Linthanthus dichotomus* Benth., illustrating the whitish, pithy seed coat that remains unchanged when wetted: (A) seeds of subsp. *dichotomus*; (B) seeds of subsp. *pattersonii* J.M. Porter. Scale bars = 0.4 mm.

0384700E, desert sage scrub/juniper woodland transition zone, 10 Apr 2008 (holotype RSA) (Fig. 16).

Plants 1–19(–22) cm tall; cotyledons linear, sometimes slightly broader distally, 3.5–12.5 mm long, 0.3–0.4 mm wide. Stems glabrous, the primary axis (0.3–)2–18 mm long, 2–7(–8) nodes to the terminal flower; lateral (secondary branches dimorphic, those of the lower nodes to 12 or more cm long, 2–4 nodes to the terminal flower; branches of the uppermost nodes 0.3–6.5 cm long, one node to terminal flower. Flowers

vespertine, opening in evening and closing in daylight. Calyx 7–15 mm, membrane much wider than herbaceous costae, the membrane sinus V-shaped or somewhat truncate. Corolla narrowly funnelform, 13–17.5 mm long, tube 6.8–10 mm, purple more distally but orifice white or cream, lobes 4.6–11 mm long, white with light purple shading on abaxial margins. Stamens inserted 2–2.5 mm above the base (insertion) of the corolla, diverging adjacent to the apex of the ovary; filaments 2–2.4 mm long, dilated and villous at the insertion, anthers 1–1.6 mm long.



Fig. 15. Dissected portion of the corolla of *Linthanthus dichotomus* Benth. subsp. *pattersonii* J.M. Porter. Two of the five lobes are shown and the arrow indicates the position where the filaments diverge from the corolla tube (note the villous, dilated pads at this position). Scale bar = 2.0 mm.



Fig. 16. The holotype specimen of *Linanthus dichotomus* Benth. subsp. **pattersonii** J.M. Porter.

Key to the Subspecies of Linanthus dichotomus

1. Flowers opening in the morning and remaining open during the day, closed at night *L. dichotomus* subsp. *meridianus*
- 1' Flowers opening in the evening and remaining open during the night, closed during day.
 2. Corolla 15–33 mm long, tube 10–12.5 mm
 *L. dichotomus* subsp. *dichotomus*
 - 2' Corolla 13–17.5 mm long, tube 7–10 mm
 *L. dichotomus* subsp. **pattersonii**

Linthanthus dichotomus subsp. **pattersonii** occurs in the Mojave Desert-chaparral ecotone, chaparral, chaparral-pinyon-juniper ecotone, chaparral-Sonoran (Colorado) desert ecotone; Imperial, Los Angeles, Riverside, San Bernardino, and San Diego Counties, California, as well as Nevada, USA, and Baja California, Mexico.

We note that three infraspecific taxa have historically been associated with *Linthanthus dichotomus* in addition to subsp. *meridianus*. The earliest name is *Gilia dichotoma* var. *parviflora* Torr. in Emory, Rep. U. S. & Mex. Bound. Surv. (Bot.) 147 (1858) [July–December 1858]. This is synonymous with *Linthanthus bigelovii* subsp. *bigelovii*, bearing the same type specimen (lectotype Cronquist 1984). The second taxon is *Gilia dichotoma* var. *uniflora* Brand, Pflanzenr. 4, Fam. 250: 144 (1907). This taxon is based upon an H. Bolander collection of 1867. We have been unsuccessful at locating this collection; however, Brand's description suggests that the corolla is larger than the taxon we describe here and, as such, we consider var. *uniflora* to be synonymous with subsp. *dichotomus*. Even so, without a type the application of the name is uncertain. The third and final name is *Gilia dichotoma* var. *integra* M.E. Jones, Contr. West. Bot. 12: 53 (1908). Evident from an examination of the type (*M.E. Jones s.n.*, USA, California, San Bernardino County, Victor, 2600 ft, 18 May 1903, POM!) is that this taxon has large flowers and mostly simple leaves. This too falls within our circumscription of subsp. *dichotomus*.

Etymology.—The commemorative epithet *pattersonii* honors Robert W. Patterson, student of *Leptosiphon* Benth. and *Linthanthus* (Polemoniaceae) and inspiring professor at San Francisco State University.

Selected representative specimens.—USA. CALIFORNIA. Los Angeles County: Liebre Mountains, Parker Mountain and ridge to SW; SW Acton & NNE Ravenna, 3670–4131 ft elev., 29 Apr 1991, *T. Ross* 4856; Liebre Mountains, Between Boquet Jctn and Bonelli Ranch, 1300 ft elev., 8 May 1967, *L.C. Wheeler* 9343; Liebre Mountains, Soledad Canyon area, N of Soledad Cyn. Road, S of I-14 freeway, E of Bee Canyon and W of Agua Dulce Canyon, 1900–2500 ft elev., 20 Apr 1998, *S.D. White* 6315; Liebre Mountains, Soledad Canyon Wash, ca. 0.5 mi E of Acton, 2720 ft elev., 30 Apr 1991, *T. Ross* 4960; Mojave Desert, Lovejoy Buttes, on the Mojave Desert, NE portion of Buttes, 3040–3090 ft elev., 23 Mar 1991, *T. Ross* 4263; Mojave Desert, NE corner of county, ca. 3 mi SSE of Jackrabbit Hill (Kern Co.), ca. 1.45 mi S of Kern County line and 0.2–0.5 mi W of San Bernardino County line, 2880–2900 ft elev., 23 Mar 1991, *T. Ross* 4280; San Gabriel Mountains, Aliso Canyon, E of Acton, ca. 1 mi downstream of Wagon Wheel Ranch, 3500 ft elev., 9 May 1967, *L.C. Wheeler* 9373; San Gabriel Mountains, drainage W of Little Rock Creek

Reservoir, 3900 ft elev., 5 Apr 1995, *O. Mistretta* 1604; San Gabriel Mountains, Mojave Desert slope, along Mt. Emma Road, 1.9 mi W of Little Rock Creek, below the dam, 3800 ft elev., 11 May 1973, *R.F. Thorne* 43552; San Gabriel Mountains, Big Rock Creek, N & E of Valyermo Ranger Station, off Big Pines Hwy, 3750 ft elev., 13 May 2003, *L. Gross* 874; San Gabriel Mountains, Adobe Mtn, SW extension of mountain, 3040–3200 ft elev., 28 Apr 1991; San Gabriel Mountains, Ridgeline to Mt. Emma, and canyon S of this ridge, 4052–4635 ft elev., 28 Apr 2005, *L. Gross* 2114; San Gabriel Mountains, Arraster Creek, 3000 ft elev., 10 May 1919, *F.W. Peirson* 393; San Gabriel Mountains, ca. 0.6 mi ESE of Acton, S edge of Soledad Canyon Wash, 2760–2880 ft elev., 30 Apr 1991, *T. Ross* 5023; San Gabriel Mountains, Aliso Canyon, E of Acton, ca. 1 mi downstream of Wagon Wheel Ranch, 3000 ft elev., 9 May 1967, *L.C. Wheeler* 9373. San Benito County: NE corner of Griswold Hills, Panoche Country, 2 mi S of border entrance of Hwy 180 from Fresno Co., 1375 ft elev., 29 Mar 1952, *C.H. Quibell* 906.

NEW COMBINATIONS IN *LINANTHUS CALIFORNICUS*

Recent treatments of *Linthanthus californicus* (Hook. & Arn.) J.M. Porter & L.A. Johnson (Patterson 1993; Patterson and Porter 2012) have paid little attention to infraspecific variation. This is unfortunate, as significant differences in a number of traits corresponding with geography and distribution of genetic variation have been well documented (Eastwood 1904; Gordon-Reedy 1990; Schultz and Soltis 2001). Gordon-Reedy (1990) recognized five subspecies based on a comparative study of trichome type, density and distribution. In 2001, Schultz and Soltis contrasted population genetic divergences with morphological variation in *L. californicus*. This study found great inconsistency between the patterns of genetic similarity and the subspecies delimitations of Gordon-Reedy (see also Schultz 1992), and concluded that there were three genetically-based morpho-geographic entities. We follow the subspecies delimitation of Schultz and Soltis, but differ in one aspect of nomenclature. Schultz and Soltis (2001) referred the subspecies occurring in the interior Transverse Ranges as *Leptodactylon californicum* Hook. & Arn. subsp. *leptotrichomum* P.J. Gordon-Reedy. This taxon we refer to epithet *glandulosum* which, based on the lectotypification (below), is the name of priority associated with this taxon. Below is our proposed taxonomy:

LINANTHUS CALIFORNICUS (Hook. & Arn.) J.M. Porter & L.A. Johnson subsp. *CALIFORNICUS*

Leptodactylon californicum Hook. & Arn., Bot. Beechey Voy. 369 (1839). *Gilia californica* (Hook. & Arn.) Benth., Prodr. (DC.) 9: 316 (1845). *Navarretia californica* (Hook. & Arn.) Kuntze, Revis. Gen. Pl. 2: 433 (1891). *Linthanthus californicus* (Hook. & Arn.) J.M. Porter & L.A. Johnson, *Aliso* 19: 82 (2000).—TYPE: *D. Douglas s.n.*, USA, “Nova California,” 1833 (holotype K 769129).

Leptodactylon californicum Hook. & Arn. subsp. *brevitrichomum* P.J. Gordon-Reedy, *Madroño* 37: 36 (–37) (1990).—TYPE: *P.J. Gordon* 828, USA, California, San Luis Obispo County, La Panza Range, CA Hwy, 58 ca. 7 km E of Santa Margarita, 400 m elev., 24 Apr 1981 (holotype CAS 684500; isotypes GH, MO, NY, PH, RSA, UC, US).

Linanthus californicus (Hook. & Arn.) J.M. Porter & L.A. Johnson subsp. ***glandulosus*** (Eastw.) J.M. Porter & R. Patt., comb. nov.

Gilia californica (Hook. & Arn.) Benth. var. *glandulosa* Eastw. *Bot. Gaz.* 37: 447 (1904). *Leptodactylon californicum* Hook. & Arn. var. *glandulosum* (Eastw.) Abrams, *Bull. New York Bot. Gard.* 6: 438 (1910). *Leptodactylon californicum* Hook. & Arn. forma *glandulosum* (Eastw.) Wherry, *Amer. Midl. Naturalist* 34: 383 (1945). *Leptodactylon californicum* Hook. & Arn. subsp. *glandulosum* (Eastw.) H. Mason, III. *Fl. Pacific States* [Abrams] 3: 455 (1951).—TYPE: syntypes *F. Grinnell Jr. s.n.*, USA, Los Angeles County, Mount Wilson, June 1903; *L. Forbes s.n.*, USA, Los Angeles County, La Cañada, s.d.; *M.E. Parsons s.n.*, USA, Los Angeles County, Arroyo Seco, s.d.; *J.C. Nevin s.n.*, USA, Los Angeles County, Sierra Santa Monica, s.d. (UC 101900).

Although Eastwood (1904) states that these collections were at CAS, none are there currently. We believe that all collections were destroyed in the fire that destroyed the California Academy of Sciences, following the great San Francisco earthquake of 1906. Interestingly, collections from all four of these sites were recollected by F. Grinnell in 1910 (originally at LAM, now housed at RSA). Unfortunately, these cannot serve as type material. Currently, of the syntypes only Rev. Nevin's collection can be relocated. It corresponds well with the protologue and thus can serve as lectotype. Collected in the eastern Santa Monica Mountains, this represents the same taxon found in the San Gabriel Mountains. Lectotype (here designated): *J.C. Nevin s.n.*, USA, Los Angeles County, Sierra Santa Monica, s.d. UC (101900).

Leptodactylon californicum Hook. & Arn. subsp. *leptotrichomum* P.J. Gordon-Reedy, *Madroño* 37: 38 (–39) (1990).—TYPE: *P.J. Gordon* 836, USA, California, Orange County, Santa Ana Mts., CA Hwy 74, ca. 1 km N of Ortega Oaks (Cleveland Nat. Forest), 700 m elev., 2 May 1981 (holotype CAS 684498; isotypes GH, MO, NY, PH, RSA, UC, US).

Linanthus californicus (Hook. & Arn.) J.M. Porter & L.A. Johnson subsp. ***tomentosus*** (P.J. Gordon-Reedy) J.M. Porter & R. Patt., comb. nov. *Leptodactylon californicum* Hook. & Arn. subsp. *tomentosum* P.J. Gordon-Reedy, *Madroño* 37: 40 (–41) (1990).—TYPE: *P.J. Gordon* 823, USA, California, San Luis Obispo County, Oso Flaco Lake, dunes N of end of Oso Flaco Road, 15 m elev., 20 Apr 1981 (holotype CAS 684499; isotypes RSA, UC, US).

Key to the Subspecies of *Linanthus californicus*

1. Trichomes long, (1–)5 or more celled; pubescence moderate to dense (calyx hairs number 2.4–5 trichomes per mm; stem hairs number 3–7.2 trichomes per mm; leaf hairs number 1.6–2.8 trichomes per mm).
2. Leaf lobes number 5–9, longest lobe 7.0–9.0 mm in length; corolla lobes 3.5–8.0 mm broad; flowers dark pink. Interior Transverse Range, eastern Santa Monica, San Gabriel and San Bernardino Mountains ***L. californicus*** subsp. ***glandulosus***
- 2' Leaf lobes number 3–5, longest lobe 4.0–6.0 mm in length; corolla lobes 8.0–15.0 mm broad; flowers

pale pink. Coastal stabilized sand dunes, San Luis Obispo, Santa Barbara and Ventura Counties . . .

- ***L. californicus*** subsp. ***tomentosus***
- 1' Trichomes short (1–2 cells in length) or medium (3–4 cells in length); pubescence sparse to dense (calyx hairs number 0.8–3.2 trichomes per mm; stem hairs number 2.6–5 trichomes per mm; leaf hairs number 0–2 trichomes per mm). Broadest geographic distribution, South Coast, La Panza Range and San Rafael Mountains, exterior Transverse Santa Ynez and western Santa Monica Mountains and Peninsular San Jacinto and Santa Ana Mountains *L. californicus* subsp. *californicus*

A NEW SUBSPECIES OF *LINANTHUS MACULATUS*: THE EMACULATE LINANTHUS

Field studies in Imperial County, California, have led to the discovery of an unusual series of populations of *Linanthus maculatus* (Parish) Milliken. These populations are atypical in their geographic isolation from previously known populations, being 79.5 air mi (128 km) south of the nearest known population (Patterson 1989; Fig. 17). Moreover, they are uniform in their corolla coloration, lacking the characteristic maroon spotting at the base of each lobe (Fig. 18). This trait has been one of the key diagnostic features for the species and the basis of the specific epithet. Moreover, there are differences in corolla morphology of these southern populations, which include the presence of reverse herkogamy, a consequence of the much shorter style (Fig. 19). We believe that these fixed differences are a manifestation of the genetic isolation and divergence that the southern populations have experienced. These populations are here segregated from the typical *L. maculatus* as a new subspecies.

LINANTHUS MACULATUS (Parish) Milliken subsp. ***emaculatus*** J.M. Porter, D.S. Bell & R. Patt., subsp. nov.—TYPE: *J.M. Porter & S.J. De Groot* 15086, USA, California, Imperial County, Palm Canyon Wash, 5.5 mi W of Ocotillo, N of Interstate 8 and S of Dos Cabezas Road, near abandoned railroad, at the southern margin of broad wash, 32.73637° N, 116.08879° W, ca. 1138 ft elev., 12 Apr 2012 (holotype RSA) (Fig. 20).

Ephemeral-annual herb, taprooted, spreading or erect, 0.9–3.5 cm tall, to 5 cm in diameter; cotyledons sheathing, ovate to narrowly ovate, 0.9–1.5 mm long, 0.4–0.8 mm wide, apex cuspidate. Stems openly branching, beginning at the first or second node, coarsely spreading, villous with uniseriate, multicellular (2–6 cells), eglandular trichomes, the terminal cell acute. Leaves alternate, above the first two to three opposite, more or less distant, nodes fleshy and thickened distally and abaxially, (1.7–)2.5–5 mm long, 0.7–1.8 mm wide, sessile, simple, entire, narrowly oblanceolate or oblong, mucronate, the base sheathing, marginally ciliate villous, trichomes like those of the stems. Inflorescence open and ±diffuse, compound-cymose, composed of 1–3-flowered cymes, terminating the branches, sessile or subsessile, pedicels 0.2–0.7 mm long; floral bracts similar to upper cauline leaves, simple and entire, fleshy and thickened distally and abaxially, ±sheathing the stem, 2.5–4.5 mm long, ciliate. Flowers opening in full sunlight, remaining open day and night, minute. Calyx (2–)2.3–3.4 mm long, lobes

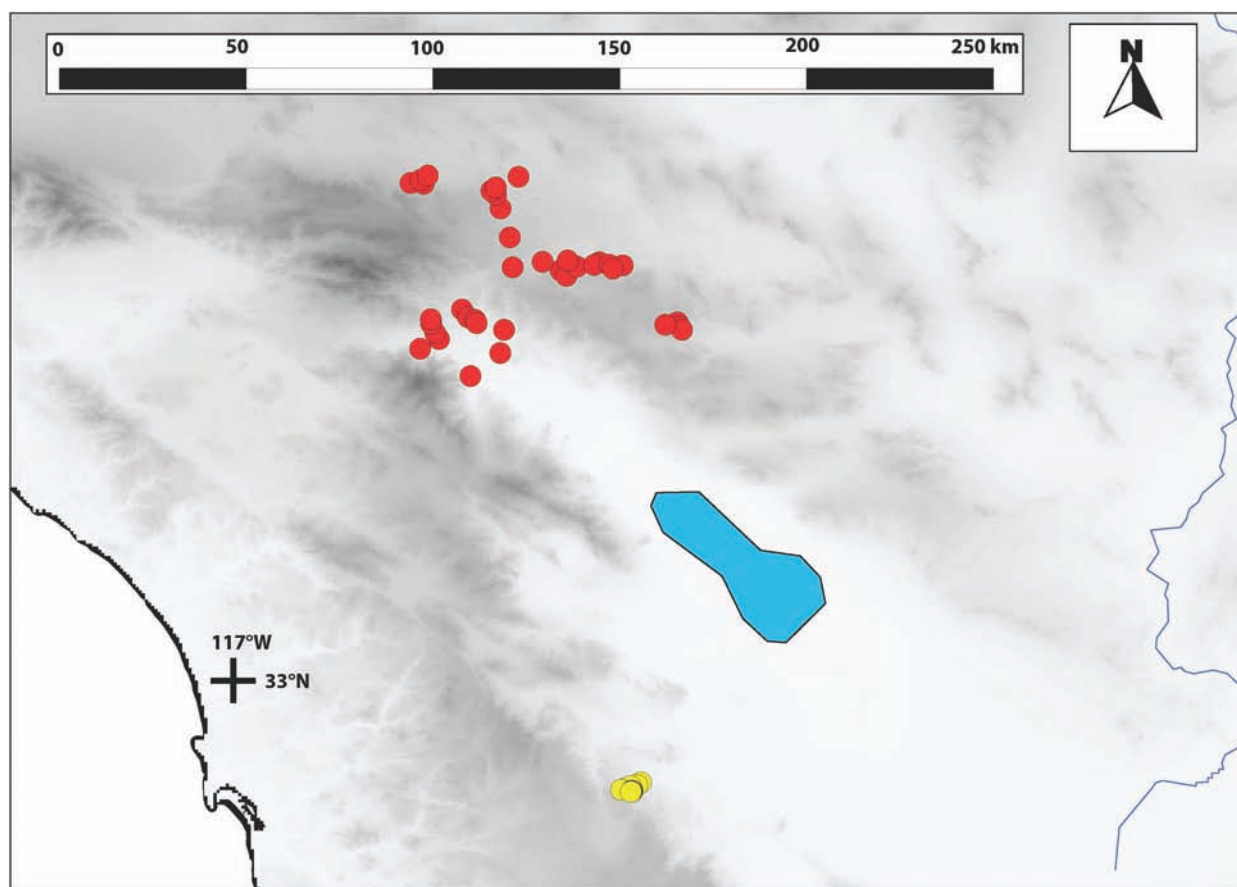


Fig. 17. Distribution of collection records of *Linanthus maculatus* (Parish) Milliken in southern California. The two subspecies are identified by color: red, subsp. *maculatus*; yellow, subsp. *emaculatus* J.M. Porter, D.S. Bell & R. Patt. An elevation model is depicted in grayscale, with light tones at low elevations and dark tones at high elevations.

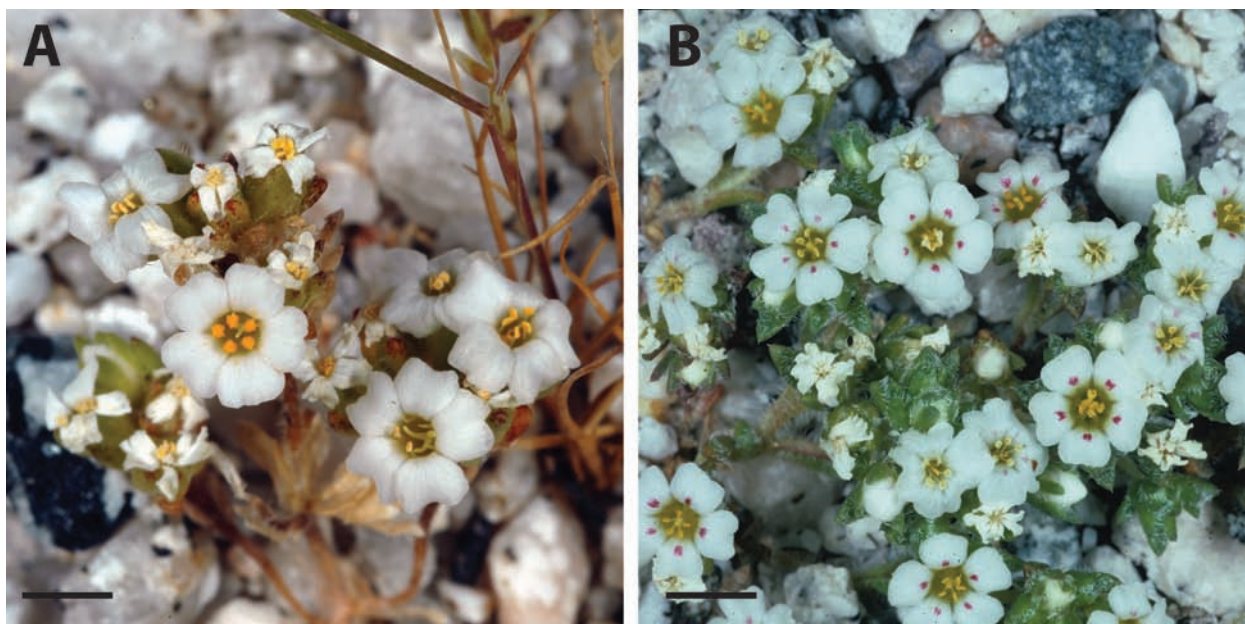


Fig. 18. Morphology of (A) *Linanthus maculatus* (Parish) Milliken subsp. *emaculatus* J.M. Porter, D.S. Bell & R. Patt. in comparison to (B) *L. maculatus* subsp. *maculatus*. Scale bar = 2.0 mm.

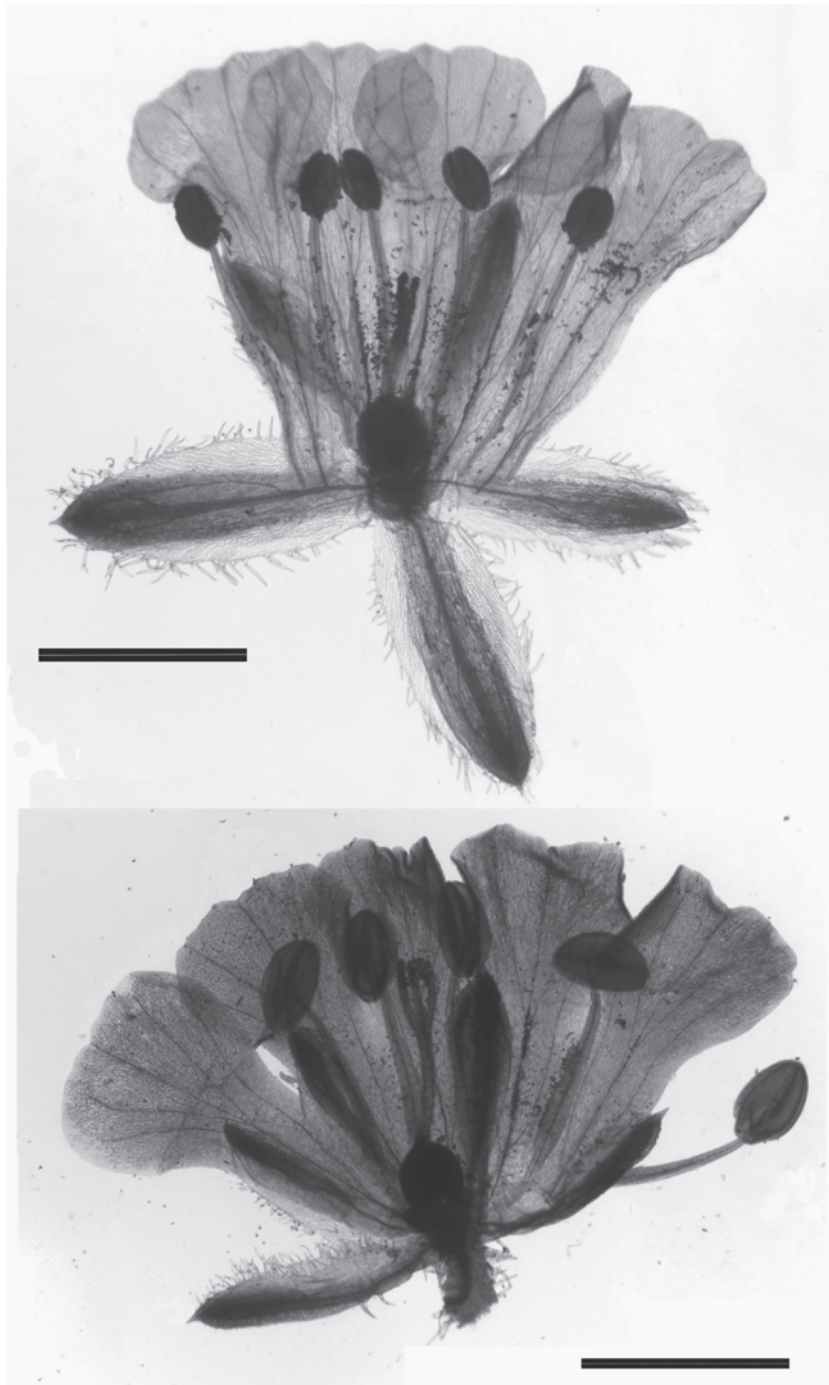


Fig. 19. Comparative floral morphology of *Linanthus maculatus* (Parish) Milliken. Dissected corollas of subsp. **emaculatus** J.M. Porter, D.S. Bell & R. Patt. (above), displaying reverse herkogamy, and of subsp. *maculatus* (below), displaying a longer style and stigma lobes adjacent to anthers. Scale bars = 2.0 mm.

narrowly oblanceolate to spatulate, obtuse but mucronate, 0.8–1.5 mm long, 0.4–0.8 mm wide, the proximal portion of the lobes with herbaceous costae, thick and fleshy distally, sparsely villous abaxially, sparsely and minutely glandular-villous adaxially (particularly proximally), with a broad hyaline margin that is ciliate villous, the calyx-tube very short (0.3–0.8 mm long). Corolla broadly and shortly funnelform or salverform, 3.5–5 mm long, white to cream; the lobes 1–2 mm long, 1.2–

2.2 mm wide, cordate to truncate-cuspidate, entire but wavy, recurved during late anthesis, glabrous; tube yellow to white, 2.3–3 mm long, glabrous. Stamens equally inserted 0.9–1.5 mm above the point of corolla insertion, free portions of filaments 0.9–2 mm long, somewhat dilated near the insertion, glabrous; anthers 0.4–1 mm long, 0.2–0.55 mm wide, slightly exserted; pollen yellow. Nectary deeply 5-lobed, the lobes obtuse-triangular, 0.1–0.22 mm thick, and 0.2–0.33 mm broad. Ovary



Fig. 20. The holotype specimen of *Linanthus maculatus* (Parish) Milliken subsp. *emaculatus* J.M. Porter, D.S. Bell & R. Patt.

triangular-ovoid to globose, 0.5–1 mm long, 0.5–0.8 mm in diameter, glabrous; style (not including stigma lobes) 0.4–0.6 mm long; stigma lobes 0.6–0.75 mm long; 5 ovules per locule. Capsule ellipsoid, 1.5–2.7 mm long, 1–1.7 mm in diameter. Seeds 3–5 per locule, 0.7–1.1 mm long, 0.45–0.6 mm wide, ovoidal-reniform, sometimes angular, constricted at the hilum, seed coat dark red-brown, unchanged when wetted, not producing mucilage.

Linanthus maculatus subsp. **emaculatus** occurs on dune margins, bases of sand ramps, sandy or coarse, opaque-white, decomposed granite soils of washes and on flats near wash margins; 900–1100 m, associated with Colorado Desert riparian vegetation in western Imperial and adjacent San Diego Counties, California. Flowering (March–)April(–May).

Etymology.—The epithet *emaculatus* (Greek = without spots) refers to the absence of the spots at the proximal end of the corolla lobes.

Selected representative specimens.—USA. CALIFORNIA. Imperial County: Palm Wash, E of Jacumba Mountains, 6.3 air mi W of intersection of Interstate 8 and Imperial Highway (S-2), 2.5 mi ENE of Dos Cabezas Spring, 0.1 mi E of San Diego County line, 1329 ft elev., 14 Apr 2010, *L. Hendrickson & W. L. Sward 4927* (SD); Palm Canyon Wash, approx. 5 air mi W of the community of Ocotillo, and approx. 0.8 air mi E of the San Diego/Imperial county border, 32.73640° N, 116.08871° W, in coarse, opaque, white decomposed granite soils at margins of wash and on flats near wash margin, 23 Mar 2012, *D. S. Bell 3266* (RSA); Palm Canyon Wash, approx. 6 air mi W of the community of Ocotillo, and approx. 0.25 air mi E of the San Diego/Imperial county border, 32.72894° N, 116.09931° W, ca. 1290 ft, on gravelly slopes of opaque, white decomposed granite above wash bottom, 24 Mar 2012, *D. S. Bell 3270* (RSA); Palm Canyon Wash, 5.5 mi W of Ocotillo, N of Interstate 8 and S of Dos Cabezas Road, near abandoned railroad, at the southern margin of broad wash, 32.73637° N, 116.08879° W, ca. 1138 ft elev., 12 Apr 2012, *J. M. Porter & S. De Groot 15086* (RSA); Palm Canyon Wash, 6.2 mi W of Ocotillo, N of Interstate 8 and S of Dos Cabezas Road, near abandoned railroad, at the eastern margin of broad wash at the foot of stabilized dune, 32.72935° N, 116.09929° W, ca. 1258 ft elev., 12 Apr 2012, *J. M. Porter & S. De Groot 15087* (RSA). San Diego County: Anza Borrego Desert State Park, southern fork of Palm Canyon Wash, ca. 1 air mi NE of Dos Cabezas Spring, 32.72055° N, 116.12936° W, ca. 1722 ft elev., 23 Mar 2013, *D. S. Bell 4589* (RSA); Anza Borrego Desert State Park, southern fork of Palm Canyon Wash, just NW of Dos Cabezas Spring, 32.71690° N, 116.14127° W, ca. 1908 ft elev., 23 Mar 2013, *D. S. Bell 4590* (RSA); Anza Borrego Desert State Park; ca. 1.75 air mi ESE of Dos Cabezas Spring and less than 0.5 mi W of State Park boundary and San Diego/Imperial County border, 32.71286° N, 116.11148° W, ca. 1485 ft elev., 24 Mar 2013, *D. S. Bell 4591* (RSA).

INTRASPECIFIC COMBINATIONS IN *LINANTHUS PUNGENS*

Similar to the situation observed in *Linanthus californicus* noted above, infraspecific variation within *Linanthus pungens* has received little attention in recent years (but see Schultz and Patterson 2012). This is remarkable given that 12 infraspecific

taxa have been recognized historically (Hooker 1837; Gray 1870; Parish 1899; Brand 1907; Rydberg 1913; Peck 1936; Jepson 1943; Meinke 1988). Variation across the wide range of *L. pungens* is profound but remains imperfectly characterized. Here we recognize four morpho-geographic taxa at the rank of subspecies. The type of *L. pungens* is from the plains at the eastern foot of the Rocky Mountains, in Colorado (see below), but the species ranges to the Pacific Northwest and to the mountains of northern Baja California, Mexico (Fig. 21). Two subspecies, as interpreted here, are more restricted in their range and two are quite widespread. *Linanthus pungens* subsp. **hookeri** is found in southern British Columbia, Canada, Washington and northeastern Oregon, USA, while *L. pungens* subsp. **hallii** is localized in the Peninsular Ranges of southern California, USA, and Baja California (one anomalous location in Sonora), Mexico. The more widespread taxa, *L. pungens* subsp. *pungens* in the Rocky Mountains and *L. pungens* subsp. **pulchriflorus** of the Sierran-Cascades and east, while amply distinct in some regions, converge in the Great Basin and Colorado Plateau, taking on forms which are difficult to classify. In addition, similar to *L. dichotomus*, which is known to have populations with flowers that either open diurnally and close at night (subsp. *meridanthus*) or open in the evening, remain open during the night, but close in the morning (viz. vespertine, subsp. *dichotomus*), flowers of some populations of *L. pungens* are diurnal while most are vespertine (pers. obs.). Additional work is greatly needed in this system, and as such, this treatment is only a preliminary assessment.

LINANTHUS PUNGENS (Torr.) J.M. Porter & L.A. Johnson.

Cantua pungens Torr., *Ann. Lyceum Nat. Hist. New York* **2**: 221 (1826). *Batanthes pungens* (Torr.) Raf., *Atl. Journ.* 145 (1832). *Aegochloa torreyi* G. Don, *Gen. Hist.* **4**: 246 (1838). *Gilia pungens* (Torr.) Benth., *nomen illegitimum*: later homonym, *Prodr. (DC.)* **9**: 316 (1845) [not *Gilia pungens* Dougl. ex Hook., *Bot. Mag.* **57**: t. 2977 (1830) = *Navarretia squarrosa* (Eschsch.) Hook. & Arn.]. *Leptodactylon pungens* (Torr.) Nutt., *J. Acad. Nat. Sci. Philadelphia*, ser. 2, vol. 1: 157 (1848). *Navarretia pungens* (Torr.) Kuntze, *Revis. Gen. Pl.* **2**: 433 (1891). *Gilia pungens* (Torr.) Benth. subsp. *eupungens* Brand, *Pflanzenr.* (Engler) **4**, *Fam.* **250**: 126 (1907). *Leptodactylon pungens* (Torr.) Nutt. var. *eupungens* Wherry, *Amer. Midl. Naturalist* **34**: 383 (1945). *Leptodactylon pungens* (Torr.) Nutt. subsp. *eupungens* Wherry, *Contr. Fl. Idaho Leaflet* (R.J. Davis) **24**: 11 (1948). *Linanthus pungens* (Torr.) J.M. Porter & L.A. Johnson, *Aliso* **19**: 82 (2000).—TYPE: *E. James* 279, according to Torrey, “valley of the Loup Fork?” Cronquist (1986) states that according to Wherry the location is actually the forks of the Platte River, in Lincoln County, Nebraska. However, both of these locations are well outside of the current range of the species. Goodman and Lawson (1995) indicate that James’s collection was made in “late June or early July along the South Platte River, anywhere from Ft Morgan, Morgan County, Colorado to Denver” (p. 272), a more reasonable location; holotype (as here interpreted) NY.

Linanthus pungens (Torr.) J.M. Porter & L.A. Johnson subsp. **hookeri** (Douglas ex Hook.) J.M. Porter & R. Patt., comb. nov.

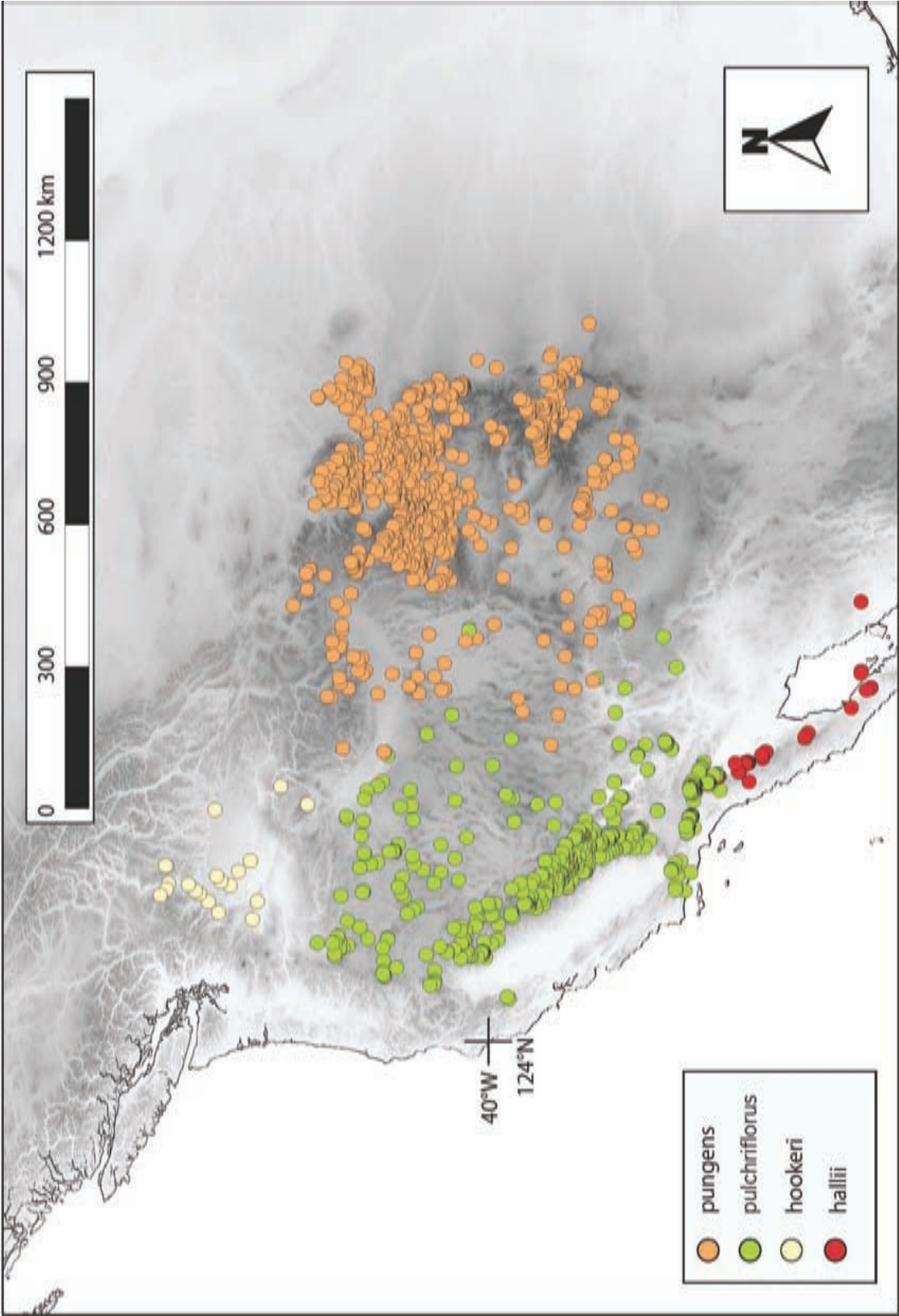


Fig. 21. The distribution of *Linthanthus pungens* (Torr.) J.M. Porter & L.A. Johnson across central western North America: *L. pungens* subsp. *pungens*, orange; *L. pungens* subsp. *pulchrriflorus* (Brand) J.M. Porter & R. Patt., green; *L. pungens* subsp. *hallii* (Pursh) J.M. Porter & R. Patt., red; and *L. pungens* subsp. *hookeri* (Douglas ex Hook.) J.M. Porter & R. Patt., cream. The background map displays an elevation model in grayscale, with light tones at low elevations and dark tones at high elevations.

Basionym: *Phlox hookeri* Douglas ex Hook., *Fl. Bor.-Amer.* (Hooker) 2: 73 (1837).

Leptodactylon hookeri (Douglas ex Hook.) Nutt., *J. Acad. Nat. Sci. Philadelphia*, ser. 2, vol. 1: 157 (1848). *Gilia pungens* (Torr.) Benth. var. *hookeri* (Douglas ex Hook.) A. Gray, *Proc. Amer. Acad. Arts* 8: 268 (1870). *Cantua pungens* Torr. var. *hookeri* (Douglas ex Hook.) T. Howell, *Fl. N.W. Amer.* 1: 453 (1901). *Leptodactylon pungens* (Torr.) Nutt. var. *hookeri* (Douglas ex Hook.) Jeps., *Man. Fl. Pl. Calif.* 807 (1925). *Leptodactylon pungens* (Torr.) Nutt. var. *hookeri* (Douglas ex Hook.) Wherry, *Amer. Midl. Naturalist* 34: 383 (1945), (later homonym).—TYPE: *D. Douglas s.n.*, “near the narrows of the Oakangan [sic] and Priest’s Rapid of the Columbia” (Grant County, Washington, USA) (holotype K).

Linanthus pungens (Torr.) J.M. Porter & L.A. Johnson subsp. ***pulchriflorus*** (Brand) J.M. Porter & R. Patt., comb. nov.

Basionym: *Gilia pungens* (Torr.) Benth. subsp. *pulchriflora* Brand, *Annuaire Conserv. Jard. Bot. Genève* 15–16: 333 (1913).

Leptodactylon lilacinum forma *pulchriflorum* (Brand) Wherry, *Amer. Midl. Naturalist* 34: 384 (1945). *Leptodactylon pungens* (Torr.) Nutt. subsp. *pulchriflorum* (Brand) H. Mason, III, *Fl. Pacific States [Abrams]* 3: 455 (1951).—TYPE: *D.J. Culbertson 4451*, USA, California, Farewell Gap (1904) (lectotype here designated: GH; isolectotype RSA).

Gilia pungens (Torr.) Benth. var. *squarrosa* A. Gray, *Proc. Amer. Acad. Arts* 8: 268 (1870). *Cantua pungens* Torr. var. *squarrosa* (A. Gray) T. Howell, *Fl. N.W. Amer.* 1: 453 (1901). *Leptodactylon patens* A. Heller, *Muhlenbergia* 1: 146 (1906). *Leptodactylon pungens* (Torr.) Nutt. var. *squarrosus* (A. Gray) Tidestr., *Proc. Biol. Soc. Wash.* 48: 42 (1935). *Leptodactylon pungens* (Torr.) Nutt. subsp. *squarrosus* (A. Gray) Tidestr., *Contr. Fl. Idaho Leaflet* (R.J. Davis) 24: 11 (1948).—TYPE: protologue states, “Anderson, Watson, etc.,” syntypes include *S. Watson s.n.*, Utah, s.d. (GH), *C. L. Anderson 85*, near Carson City, Nevada, 1865 (GH), *J. Torrey 233*, near Empire City, Nevada, 1865 (GH); lectotype here designated: *C. L. Anderson 85*, near Carson City, Nevada, 1865, GH (00078923).

Gilia tenuiloba Parish, *Erythraea* 7: 95 (1899). *Gilia pungens* (Torr.) Benth. var. *tenuiloba* (Parish) Milliken, *Univ. Calif. Publ. Bot.* 2: 43 (1904). *Leptodactylon tenuilobum* A. Heller, *Muhlenbergia* 1: 146 (1906). *Gilia pungens* (Torr.) Benth. var. *tenuiloba* (Parish) Brand, *Pflanzenr.* (Engler) 4, Fam. 250: 128 (1907). *Leptodactylon pungens* (Torr.) Nutt. var. *tenuilobum* (Parish) Jeps., *Man. Fl. Pl. Calif.* 807 (1925).—TYPE: *S. B. Parish & W. F. Parish 689*, USA, California, Riverside Co., San Jacinto Mts. (probably Taquitz Valley), July 1880 (holotype GH 78942; isotype CAS 00123838, 00123839).

Gilia pungens (Torr.) Benth. var. *devestita* Brand, *Pflanzenr.* (Engler) 4, Fam. 250: 128 (1907).—TYPE: syntypes include *T. Howell s.n.*, USA, Oregon, Harney County, Steens Mountain, 1 Jun 1885 (OSC, P, RM, RSA); *W.C. Cusick 1976*, USA, Oregon, Harney County, Steens Mountain (OSC, P); *A. Nelson & E. Nelson 5695*, USA, Wyoming, Park County, Yellowstone National Park, Mount Everts, 7 Jul 1899 (P, RM, RSA); *C.F. Baker 416*, USA, Colorado; *E. Hall & J.P. Harbour 463*, American plains flora, latitude 41°, 1862 (P).

Lectotype (here designated) *T. Howell s.n.*, USA, Oregon, Harney County, Steens Mountain, 1 Jun 1885, P (00640897); isolectotypes: OSC, P (00640898), RM, RSA.

Gilia lilacina Greene ex A. Brand, *Pflanzenr.* 4, Fam. 250: 128 (1907). *Leptodactylon lilacinum* (Greene ex Brand) Wherry, *Amer. Midl. Naturalist* 34: 384 (1945).—TYPE: *C.F. Baker 1307*, USA, Nevada, Ormsby County, Clear Creek Canyon, 2000–2615 m, 11 Jul 1902 (holotype G; isotypes CAS 37417, NY 336936, POM 65151, 0004833; US 00419482).

Leptodactylon brevifolium Rydb., *Bull. Torrey Bot. Club* 40: 474 (1913). *Leptodactylon pungens* (Torr.) Nutt. var. *brevifolium* (Rydb.) Wherry, *Amer. Midl. Naturalist* 34: 383 (1945). *Leptodactylon pungens* (Torr.) Nutt. subsp. *brevifolium* (Rydb.) Wherry, *Contr. Fl. Idaho Leaflet* (R.J. Davis) 24: 11 (1948).—TYPE: *C.A. Purpus 6306*, USA, Utah [Nevada (Pershing County), according to Purpus’s field notes], Juniper Range, May–October 1898 (holotype US 348265, 00110369; isotypes NY 336933, UC 106785).

Leptodactylon pungens (Torr.) Nutt. var. *subflavidum* Jeps., *Fl. Calif.* 3: 143 (1943). *Leptodactylon hallii* A. Heller forma *subflavidum* (Jeps.) Wherry, *Amer. Midl. Naturalist* 34: 384 (1945).—TYPE: *W. L. Jepson 19830*, USA, California, Inyo Co., Leadfield, Grapevine Mts., 3 May 1940 (holotype JEPS 2688; isotype RSA 27941, 0004835; US 02946070).

Leptodactylon pungens (Torr.) Nutt. var. *shastense* Jeps., *Fl. Calif.* 3: 143 (1943). *Leptodactylon lilacinum* Greene ex Brand forma *shastense* (Jeps.) Wherry, *Amer. Midl. Naturalist* 34: 384 (1945).—TYPE: *W. L. Jepson 19994*, USA, California, E of Mayten, Little Shasta Valley, rocky flat, 23 Jun 1940 (holotype JEPS 2687).

Linanthus pungens (Torr.) J.M. Porter & L.A. Johnson subsp. ***hallii*** (Parish) J.M. Porter & R. Patt., comb. nov.

Basionym: *Gilia hallii* Parish, *Erythraea* 7: 94 (1899).

Gilia pungens (Torr.) Benth. var. *hallii* (Parish) Milliken, *Univ. Calif. Publ. Bot.* 2: 42 (1904). *Leptodactylon hallii* (Parish) A. Heller, *Muhlenbergia* 1: 146 (1906). *Gilia pungens* (Torr.) Benth. subsp. *hallii* (Parish) Brand, *Pflanzenr.* (Engler) 4, Fam. 250: 128 (1907). *Leptodactylon pungens* (Torr.) Nutt. var. *hallii* (Parish) Jeps., *Man. Fl. Pl. Calif.* 807 (1925). *Leptodactylon pungens* (Torr.) Nutt. subsp. *hallii* (Parish) H. Mason, III, *Fl. Pacific States [Abrams]* 3: 455 (1951).—TYPE: *H. Hall s.n.*, USA, California, Riverside Co., Coyote Canyon, San Jacinto Mountains, on the desert slope of El Toro Mountain, 1524 m, May 1899 (holotype CAS 0012378 = DS 138957; isotype US 668191).

Linanthus pungens (Torr.) J.M. Porter & L.A. Johnson subsp. *hazeliae* (Peck) J.L. Schultz & R. Patt., *Madroño* 59: 163 (2012). *Leptodactylon hazeliae* Peck, *Proc. Biol. Soc. Wash.* 49: 111 (1936). *Leptodactylon pungens* (Torr.) Nutt. subsp. *hookeri* (Dougl. ex Hook.) Wherry forma *hazeliae* (Peck) Wherry, *Amer. Midl. Naturalist* 34: 383 (1945); *Leptodactylon pungens* (Torr.) Nutt. subsp. *hazeliae* (Peck) Meinke, *Madroño* 35: 107 (1988).—TYPE: *H. Barton s.n. (18415)*, USA, Oregon, Wallowa Co., dry rocky slope, Snake River Canyon near mouth of Battle Creek, 13 Apr 1934 (holotype WILLU 18415).

Key to the Subspecies of *Linanthus pungens*

1. Leaves mostly simple and entire, with only a few, distal, palmate leaves and those with highly reduced lateral lobes ($<1/3$ the length of the porrect, central lobe); floral bracts trifid; plants with only eglandular, villous trichomes; distributed along the Peninsular Ranges of southern California and Baja California, Mexico ***L. pungens* subsp. *hallii***
- 1' Leaves mostly 3–13-lobed, palmatifid (to pinnatifid) leaves, few if any proximal nodes bearing simple, linear leaves; floral bracts usually 5 or more, lobed; plant vestiture variable, often with both eglandular, villous trichomes and stipitate glands, but glandular trichomes always present; distribution mostly north and east of the Peninsular Ranges 2.
2. Calyx apparently glabrous abaxially or sparsely glandular-puberulent only at the very base; along the east slope of the Rocky Mountains and adjacent Great Plains, extending through Wyoming to Montana, eastern Idaho, and northeastern Utah ***L. pungens* subsp. *pungens***
- 2' Calyx glandular-puberulent or glandular-villous abaxially, often also with eglandular-villous trichomes; occurring in the intermountain region, Colorado Plateau, extending to western Idaho, Oregon, Washington British Columbia, Canada to California 3.
3. Flowering stems erect and woody; leaves alternate distally, leaflets 1–1.8 mm wide, linear to linear-lanceolate or subulate; the intermountain region, Colorado Plateau, extending to western Idaho, Oregon, Washington, British Columbia, Canada to California, but not the Snake River Valley 4.
- 3' Flowering stems sprawling to mounded, herbaceous; leaves opposite distally, leaflets 0.2–0.6 mm wide, soft-filiform; NW Great Basin, Snake River Drainage ***L. pungens* subsp. *hazeliae***
4. Cauline leaves with central lobe recurved and often broad and rigid; intermountain, Great Basin, Mojave Desert and adjacent mountains ***L. pungens* subsp. *pulchriflorus***
- 4' Cauline leaves with central lobe erect, in the same plane as the lateral lobes, only slightly broader than lateral lobes; apparently restricted to northern Oregon, Washington and British Columbia, Canada ***L. pungens* subsp. *hookeri***

TWO NEW SUBSPECIES OF *LINANTHUS WATSONII*

Linanthus watsonii (A. Gray) Wherry occurs as a series of disjunct populations across the Rocky Mountains and Great Basin regions. The high degree of isolation of these populations has resulted in morphological differentiation across the range. Patterson and Yoder-Williams (1984) segregated populations from the Bruneau and Little Humboldt River canyons as *Linanthus glaber* (R. Patt. & Yoder-Williams) J.M. Porter & L.A. Johnson. However, a number of other variants are equally distinct, or nearly so. Populations from eastern and central Nevada and Yavapai County, Arizona, are compact, 5-

merous and have leaves with fewer lobes (usually 3) that are very narrow. These populations have variously been identified as *L. pungens*, *L. caespitosa* and *L. watsonii* (see Wilken and Porter 2005). This morpho-geographic race appears to be restricted to limestone and dolomite. Eastern Arizona hosts another phase with small, 6-merous flowers and compact habit. This phase also appears to be edaphically restricted, in this case to basalt. Here we describe these two taxa as new subspecies.

LINANTHUS WATSONII (A. Gray) Wherry subsp. *WATSONII*

Basionym: *Gilia watsonii* A. Gray, *Proc. Amer. Acad. Arts* 8: 267 (1870).

Navarretia watsonii (A. Gray) Kuntze, *Revis. Gen. Pl.* 2: 433 (1891). *Leptodactylon watsonii* (A. Gray) Rydb., *Bull. Torrey Bot. Club* 33: 149 (1906). *Linanthus watsonii* (A. Gray) Wherry, *Aliso* 5: 10 (1961).—TYPE: *S. Watson s.n.*, USA, Utah, Wasatch Mountains, s.d. (holotype GH 00091171 [mounted on right side of sheet with non-type collections: *J. D. Hooker & A. Gray s.n.*, *S. Watson* 905]; note a specimen at US [*S. Watson* 908, USA, Utah, Bear River Canyon, 2591 m, Aug 1869; US83991, 00110367] is annotated as isotype; however, this represents a different collection locality than specified in the protologue. The specimen at US is not considered type material).

Gilia floribunda A. Gray var. *arida* M.E. Jones, *Proc. Calif. Acad. Sci.* ser. 2, 5: 713 (1895). *Leptodactylon watsonii* forma *aridum* (M.E. Jones) Wherry, *Amer. Midl. Naturalist* 34: 383 (1945).—TYPE: *M.E. Jones* 5701a, USA, Utah, Wayne County, Capitol Wash, near the Henry Mountains, 5000 ft, on sandstone rocks in very arid places, 31 Jul 1894. A mount at POM (74878) bears "*Gilia floribunda* var. *arida*, var. nov., Type," in Jones' handwriting; however, the collection number and date do not correspond to that cited in the protologue. We do not consider this specimen to represent *M.E. Jones* 5701a. The only mount of this collection known to us is at US (holotype US 00236690).

Woody-based perennial, loosely matted, sprawling or tufted subshrub, 7–28 cm tall, 6–30 cm wide. Stems (annual growth) 1.4–8.5 cm long, hirtellous-puberulent or stipitate-glandular, the leaves glabrous (eastern portion of the range) or more commonly stipitate-glandular to puberulent; nodes opposite throughout. Leaves numerous, with or without axillary fascicles (short shoots), the lowermost simple and entire, 1.2–15 mm long, 0.9–2.3 mm wide, more distal leaves 3–9-palmately lobed, 6–17(–20) mm long, the central lobe longest, 5.5–15.5 mm long, 0.5–1.3 mm wide cleft nearly to the base, linear-subulate, spinulose-tipped or somewhat acerose. Inflorescences cymose, terminating the branches, the cymes 1(–3)-flowered, subtended by a pair of bracts (rarely a solitary bract; bracts leaf-like, 5–9-palmately lobed, 8–15.5 mm long, glandular-puberulent on both the adaxial and abaxial surfaces, sometimes sparsely so. Flowers sessile, commonly with 6 calyx lobes, 6 corolla lobes, 6 stamens, and 4 carpels, less often 5-merous and with 3 carpels. Calyx 6.9–14.5 mm long, stipitate-glandular to glandular-puberulent abaxially, villous on the adaxial lobes and distal tube; lobes unequal, much shorter than the tube, 1.6–3.5 mm long; tube with a broad, white hyaline region between the narrower green and herbaceous costae. Corolla 15–28 mm long, dull white or ochroleucous, often with purple or purple streaking on the distal tube, where

the anthers are positioned; the lobes 6–13 mm long, 1.7–6 mm wide; the tube 10–18.5 mm long; glabrous throughout. Stamens equally affixed in the distal tube, 8–14 mm above the insertion of the corolla; filaments short, more or less equal in length, 0.5–0.9 mm long; anthers 1–1.6 mm long; pollen yellow. Ovary ovoid, 1.5–2 mm long, 0.7–1.3 mm in diameter, glabrous; style 2.4–4.5 mm long; stigmatic lobes usually 4, occasionally 3, 2–3.8 mm long. Capsule 3.2–4.5 mm, the valves stramineous, disarticulating completely at maturity, but often remaining in the calyx over winter. Seeds (2–)5–10 per locule, 0.8–1.6(–1.8) mm long, 0.4–0.7 mm in diameter, dark red-brown, ovoid to oblongoid, angular and sometimes narrowly winged along the angles, unchanged when wetted, not producing mucilage.

Rock crevices, canyon walls of limestone, sandstone, granite, or in sandy loam, associated with sagebrush, juniper woodland, pinyon-juniper woodland, mountain mahogany, oak, ponderosa pine, spruce-fir and riparian communities, at 1350–2591 m (4425–8500 ft) elev.; flowering May–August, fruiting June–September.

Selected representative specimens.—USA. COLORADO. Garfield County: Base rocky cliff Glenwood Canyon, E of Glenwood Springs, 1920 m elev., 2 Jun 1947, *H. D. Harrington* 3223 (CS). Mesa County: Colorado National Monument, Ute Canyon, 21 Jul 1982, *V. Siplivinsky* 4293 (CS). Moffat County: E end of Cross Mountain Canyon, S side of Yampa River, 40.4763889° N, 108.1805556° W, 1830 m elev., 26 Jul 1978, *B. Painter & S. Emrich* 169 (CS). Rio Blanco County: ca. 2 mi SW of junction of Yellow Creek and the White River, 40.157° N, 108.4332° W, 1830 m elev., 10 Jun 1982, *W. Baker* 82-182 (CS). IDAHO. Bannock County: E entrance to Garden Creek Gap, ca. 6 mi W of US 91 on Arimo Road, 42.5667° N, 112.31667° W, 3 Jun 1997, *M. E. Barkworth & M. Lloyd* 97.025 (UTC). Power County: Craters of the Moon National Monument, S edge of Wapi Lava Field, 0.2 mi W of Wapi water tower, 1357 m elev., 23 Jun 2006, *N. D. Atwood* 31599 (UCR). UTAH. Beaver County: Granite Mountain Pass, 11.5 mi E of Milford, 22 Jun 1941, *B. Maguire* 21000 (NY). Box Elder County: Golden Spike National Historic Site, Big Fill Walk, Promontory Mts., 41.6205556° N, 112.54667° W, 1433 m elev., 28 May 1994, *M. Curto, L. Allen, R. Fitts & L. Teerlink* 1112 (UTC). Cache County: Dry Canyon, 9 Jun 1938, *A. J. Cronquist s.n.* (NY). Carbon County: Desolation Canyon, Green River, Rock Creek, 39.5° N, 110° W, 7 May 1999, *N. D. Atwood* 24397 (NY). Duchesne County: 2 mi W of Neola on Whiting Farm, *A. W. Collotzi* (NY). Emery County: San Rafael Reef, side canyon of Iron Wash, 38.8° N, 110.5° W, 1387 m elev., 29 May 1980, *J. G. Harris* 793 (NY). Garfield County: Along Highway 22 to Antimony, ca. 1 mi NE of the Bryce Canyon, Highway 22–Highway 12 junction, 37.704° N, 112.139° W, 2200 m elev., 23 Jun 2000, *M. Madsen* 835 (NY). Grand County: Ryan Creek, ca. 2 air mi due W of Renegade Point, 1811 m elev., 31 May 1984, *N. D. Atwood* 9812 (NY). Kane County: on the Cockscomb, a ridge west of the Paria River, 37.2162° N, 111.9331° W, 1451 m elev., 3 Jun 1982, *J. W. Grimes* 2022 (NY). Millard County: side canyon on N side of Marjum Canyon, between Sawtooth and Middle Mountains, House River, 39.257° N, 113.413° W, 1 Jun 1999, *N. D. Atwood* 24809 (NY). Tooele County: Stansbury Mountains, Devils Gate Narrows, 40.3° N, 112.6° W, 1859 m elev., 23 Jun

1979, *A. Teye* 546 (NY). Utah County: Below Timpanogos Cave, 30 Jun 1935, *B. Maguire* 12338 (NY). Wayne County: near Capitol Reef National Monument, 10 mi SSE of Fruita, 1500 m elev., 9 Jun 1953, *R. McVaugh* 14522 (NY). WYOMING. Fremont County: Wind River Indian Reservation, 43.4247° N, 108.1923° W, 1768 m elev., 23 Jun 1980, *R. D. Dorn* 3458 (RM). Hot Springs County: Owl Creek/Bridger Mountains: Owl Creek Mountains: Wind River Canyon along U.S. Hwy 20–Wyoming Hwy 789, ca. 15 mi S of Thermopolis, 43.4681° N, 108.1726° W, 1402 m elev., 14 Jun 1984, *E. F. Evert* 6474 (RM). Sweetwater County: 41.0065° N, 109.6458° W, 1859 m elev., 28 Aug 1987, *R. D. Dorn* 4827 (RM). Washakie County: W slope of Big Horn Range, Leigh Creek watershed, ca. 0.3–1 mi E of confluence with Ten Sleep Creek, ca. 0.6 mi S of U.S. Hwy 16, ca. 9 air mi E of Ten Sleep and 3 air mi E of Fertig Draw, 44.0841° N, 107.2996° W, 1707 m elev., 23 Jul 1997, *W. Fertig* 7744 (RM).

LINANTHUS WATSONII (A. Gray) Wherry subsp. **laccolithicus** J.M. Porter & R. Patt., subsp. nov.—TYPE: *K. Heil & A. Clifford* 17893, USA, Arizona, Apache County, Navajo Nation, Carrizo Mountains, ca. 4 mi SW of Teec Nos Pos, Teec Nos Pos Canyon above waterfall (end of road), 36°51'35"N, 109°07'13"W, 6740 ft elev., 13 Sep 2001 (holotype RSA [Fig. 22], isotype SJNM).

Woody-based perennial, matted and tufted subshrub, 7–12 cm tall, 3–14 cm wide. Stems (annual growth) 1.4–2.5 cm long, hirtellous-puberulent or stipitate-glandular, generally white or ivory; nodes opposite throughout, internodes shorter than the leaves; axillary fascicles (short shoots) weakly developed. Leaves 5–17 mm long, the lowermost simple and entire, more distal leaves 3–5-palmately lobed, the central lobe longest, 4–15 mm long, 0.5–0.7 mm wide cleft nearly to the base, linear-subulate, spinulose-tipped or somewhat acerose, stipitate-glandular adaxially, more sparsely so abaxially. Inflorescences cymose, terminating the branches, the cymes 1(–3)-flowered, subtended by a pair of bracts (rarely a solitary bract; bracts leaf-like, 5-palmately lobed, 10–17 mm long, glandular-puberulent to stipitate-glandular on both the adaxial and abaxial surfaces, sometimes sparsely so abaxially. Flowers sessile, commonly with 6 calyx lobes, 6 corolla lobes, 6 stamens, and 4 carpels. Calyx 7.3–10 mm long, stipitate-glandular to glandular-puberulent abaxially, villous on the adaxial lobes and distal tube; lobes unequal, much shorter than the tube, 1.6–3.5 mm long; tube with a broad, white hyaline region between the narrower green and herbaceous costae. Corolla 12–17 mm long, dull white or ochroleucous, often with purple or purple streaking on the distal tube, where the anthers are positioned; the lobes 5–7 mm long, 1.7–3.5 mm wide; the tube 7–10.5 mm long; glabrous throughout. Stamens equally affixed in the distal tube, 8–9 mm above the insertion of the corolla; filaments short, more or less equal in length, 0.4–0.9 mm long; anthers 1–1.3 mm long; pollen yellow. Ovary ovoid, 1.5–2 mm long, 0.7–1.3 mm in diameter, glabrous; style 2.4–3.5 mm long; stigmatic lobes usually 4, 2–3 mm long. Capsule 1.7–3.5 mm, the valves stramineous, disarticulating completely at maturity, but often remaining in the calyx over winter. Seeds (2–)5–10 per locule, 0.6–1 mm long, 0.35–0.6 mm in diameter, dark red-brown, ovoid to oblongoid, angular and sometimes narrowly winged along the angles, unchanged when wetted, not producing mucilage.

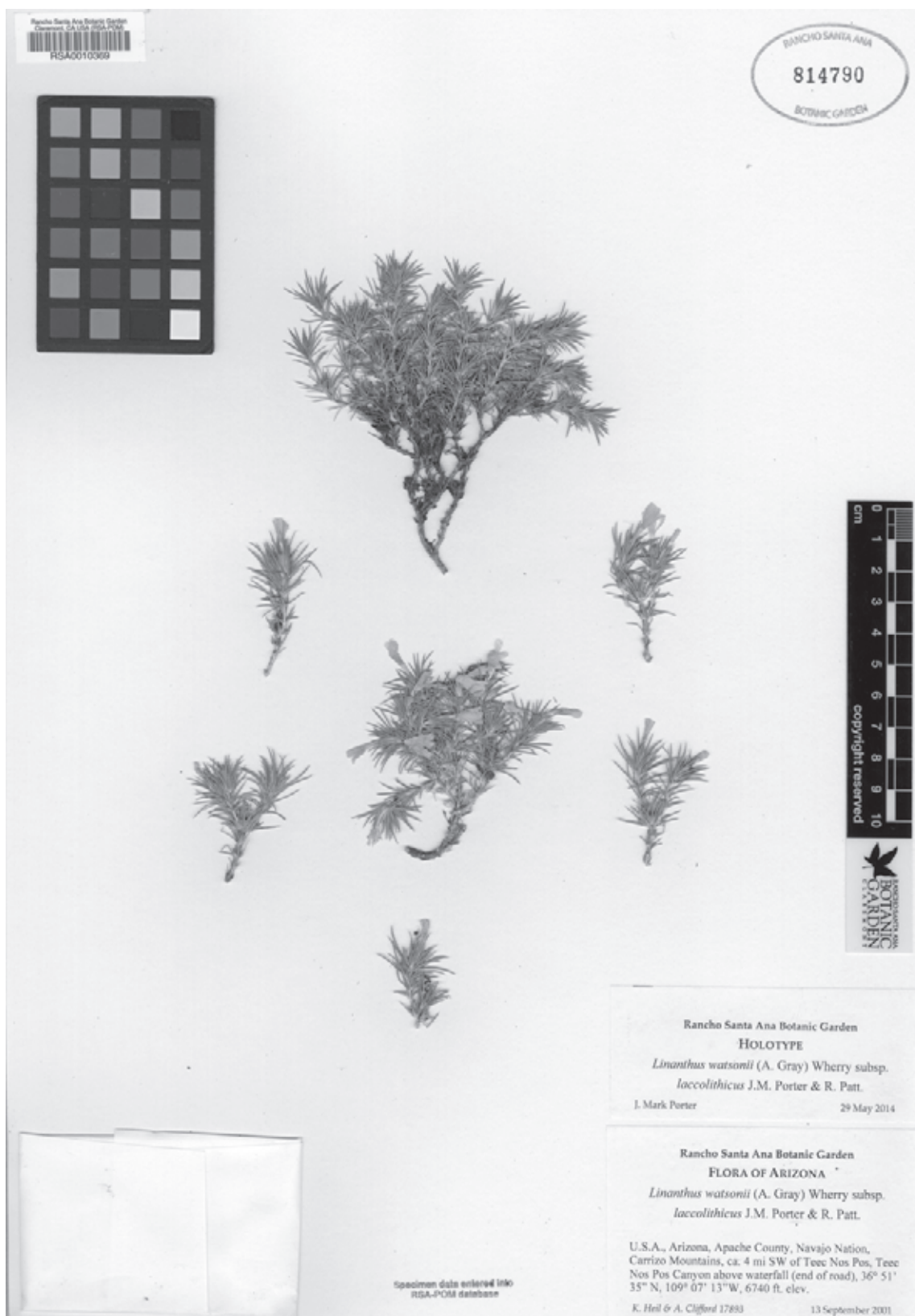


Fig. 22. The holotype specimen of *Linthus watsonii* (A. Gray) Wherry subsp. **laccolithicus** J.M. Porter & R. Patt.

Etymology.—The epithet *laccolithicus* is derived from the geologic landform at the type locality of this taxon, a basaltic laccolith (Carrizo Mountains), in Teec Nos Pos Canyon, Apache County, Arizona.

Selected representative specimens.—USA. ARIZONA. Apache County: Navajo Nation, Carrizo Mountains, Teec Nos Pos Canyon drainage, 3.5 mi SSW of Teec Nos Pos Boarding School, narrow steep-walled canyon, weathered intrusive igneous laccolithic sill, T40N, R39E, Sec. 22 NW1/4, 6500 ft elev., 4 Aug 2000, *A. Clifford 00-925* (SJNM); Carrizo Mtns, Teec Nos Pos Canyon, canyon floor, lower slopes and cliff, UTM 0667464N 4080855E, 6668–6772 ft elev., 15 Sep 2001, *T. Reeves 10455B* (SJNM).

LINANTHUS WATSONII (A. Gray) Wherry subsp. *dolomiticus* J.M. Porter & R. Patt., subsp. nov.—TYPE: *J. André 8345*, with *G.L. Clifton & R. Crawford*, Nevada. Lincoln County: Schell Creek Range, S Schell Creek Range, S of Mt. Grafton, just S of Patterson Pass, E of Cave Valley, 38.5912° N, 114.729° W, 2327 m elev., limestone slope, 17 Jun 2006 (holotype RSA [Fig. 23]; isotype UCR).

Woody-based perennial, matted and tufted subshrub, 7–12 cm tall, 3–14 cm wide. Stems (annual growth) 1.4–2.5 cm long, hirtellous-puberulent or stipitate-glandular, generally white or ivory; nodes opposite throughout, internodes shorter than the leaves; axillary fascicles (short shoots) weakly developed. Leaves 5–15 mm long, the lowermost simple and entire, more distal leaves 3-palmately lobed, the central lobe longest, 4–11 mm long, 0.4–0.7 mm wide cleft nearly to the base, narrowly linear-subulate to aciculate, spinulose-tipped, stipitate-glandular adaxially, more sparsely so abaxially. Inflorescences cymose, terminating the branches, the cymes 1(–3)-flowered, subtended by a pair of bracts (rarely a solitary bract; bracts leaf-like, 3-palmately lobed, 5–15 mm long, glandular-puberulent to stipitate-glandular on both the adaxial and abaxial surfaces, sometimes sparsely so abaxially. Flowers sessile, commonly with 5 calyx lobes, 5 corolla lobes, 5 stamens, and 4 carpels. Calyx 7–11.3 mm long, stipitate-glandular to glandular-puberulent abaxially, villous on the adaxial lobes and distal tube; lobes unequal, much shorter than the tube, 1.2–3.3 mm long; tube with a broad, white hyaline region between the narrower green and herbaceous costae. Corolla 12–17 mm long, dull white or ochroleucous, often with purple or purple streaking on the distal tube, where the anthers are positioned; the lobes 5–7 mm long, 1.7–3.5 mm wide; the tube 7–10.5 mm long; glabrous throughout. Stamens equally affixed in the distal tube, 8–9 mm above the insertion of the corolla; filaments short, more or less equal in length, 0.4–0.9 mm long; anthers 1–1.3 mm long; pollen yellow. Ovary ovoid, 1.5–2 mm long, 0.7–1.3 mm in diameter, glabrous; style 2.4–3.5 mm long; stigmatic lobes usually 4, 2–3 mm long. Capsule 1.7–3.5 mm, the valves stramineous, disarticulating completely at maturity, but often remaining in the calyx over winter. Seeds (2–)5–10 per locule, 0.6–1 mm long, 0.35–0.6 mm in diameter, dark red-brown, ovoid to oblongoid, angular and sometimes narrowly winged along the angles, unchanged when wetted, not producing mucilage.

Etymology.—The epithet *dolomiticus* is derived from the geologic substrate to which this subspecies appears to be restricted, dolomite and limestone.

Selected representative specimens.—USA. ARIZONA. Yavapai County: S of Ash Fork, N of Paulden, 1.2 km NW of Fritsche Peak, 34.6738° N, 112.585° W, 15 Jul 1994, 5780 ft, *T. Wright 1167* (ASU); S of Ash Fork, N of Paulden, 8.6 km SSW of Upper Limestone Tank, 850 m NNW of Spring Canyon Tank, 34.9906° N, 112.515° W, 13 Jun 1994, 5530 ft, *M. A. Baker 11451* (ASU); S of Ash Fork, N of Paulden, 5.6 km SW of Upper Limestone Tank, 2.6 km NE of Wineglass Tank, 34.9939° N, 112.528° W, 28 Jul 1994, 5550 ft, *M. A. Baker 11500* (ASU); Wineglass Ranch 7.5' Quad., Black Mesa, NNW of Paulden, mostly S-facing cliffs of the youngest unit of the Upper Devonian age Martin Formation consisting of thick, blocky, homogeneous ledges of weathered fine to medium, pale brown-gray crystalline dolomite, 34.9967° N, 112.507° W, 27 Aug 2001, 5500–1675 ft, *M. A. Baker 14202* (ASU); S of Ash Fork, 5.5 km SW of Upper Limestone Tank, 4 km SE Fritsche Peak, 35.0185° N, 112.558° W, 29 Aug 1994, 5630 ft, *T. Wright 1194* (ASU); Picacho Peak SE 7.5' USGS Quadrangle, Black Mesa, NNW of Paulden, mostly W-facing cliffs of the youngest unit of the Upper Devonian age Martin Formation consisting of thick, blocky, homogeneous ledges of weathered, fine to medium, pale brown-gray crystalline dolomite, 35.0367° N, 112.56° W, 22 Jun 2001, 5880 ft, *M. A. Baker 14159* (ASU); S of Ash Fork, 6.7 km NW of Upper Limestone Tank, 1.8 km NE of Fritsche Peak, limestone cliff-face, 35.0554° N, 112.57466° W, 14 Aug 1994, 5880 ft, *M. A. Baker 11506* (ASU); S of Ash Fork, 6.7 km NW of Upper Limestone Tank, 1.8 km NE of Fritsche Peak, 35.0554° N, 112.575° W, 29 May 1994, 5880 ft, *T. Wright 1110* (ASU); S of Ash Fork, 6.7 km NW of Upper Limestone Tank, 1.8 km NE of Fritsche Peak, 35.0554° N, 112.575° W, 14 Aug 1994, 5880 ft, *M. A. Baker 11506* (ASU); Picacho Peak SE 7.5' USGS Quadrangle, Black Mesa, NNW of Paulden, W and SE-facing cliffs of the youngest unit of the Upper Devonian age Martin Formation, crystalline dolomite, interspersed with thinner layers of chert, 35.0633° N, 112.565° W, 27 Jun 2001, 5900 ft, *M. A. Baker 14178* (ASU). NEVADA. Lincoln County: Schell Creek Range, Cave Valley, slopes of S Schell Creek Range, ca. 1 mi N of Sidehill Pass, 38.384° N, 114.816° W, 1951 m elev., limestone gravel W-facing slopes with *Juniperus osteosperma*, *Artemisia nova*, *Penstemon barnebyi*, *Physaria chambersii*, *Cryptantha humilis*, 5 Jun 2007, *J. André 8397* (UCR); Schell Creek Range, S Schell Creek Range, S of Mt. Grafton, just S of Patterson Pass, E of Cave Valley, 38.5912° N, 114.729° W, 2327 m elev., pinyon-juniper woodland with *Pinus monophylla*, *Juniperus osteosperma*, *Oenothera howardii*, *Castilleja linariaefolia*, *Penstemon watsonii*, on limestone slope, 17 Jun 2006, *J. André 8345* (UCR). Nye County: Cherry Creek, Quinn Canyon Range, 38.14556° N, 115.60972° W, 2012 m elev., in tight crevices of limestone cliffs, with *Petrophytum*, in the pinyon-cowania belt, 10 Jun 1966, *R. C. Barneby 14399-a* (NY); Toiyabe National Forest, Toiyabe Range, South Twin River, in the canyon near the mouth, 16 mi 325° from town of Round Mountain, 38.8875° N, 117.24444° W, 1920 m elev., in talus and on rocks, 26 Jun 1979, *S. Goodrich 12930* (NY); right hand fork near head of Cherry Creek, Quinn Canyon Range, Nevada National Forest, 2438 m elev., with pinyon-juniper, in crevices of limestone, 7 Jun 1945, *B. Maguire 25321* (NY).

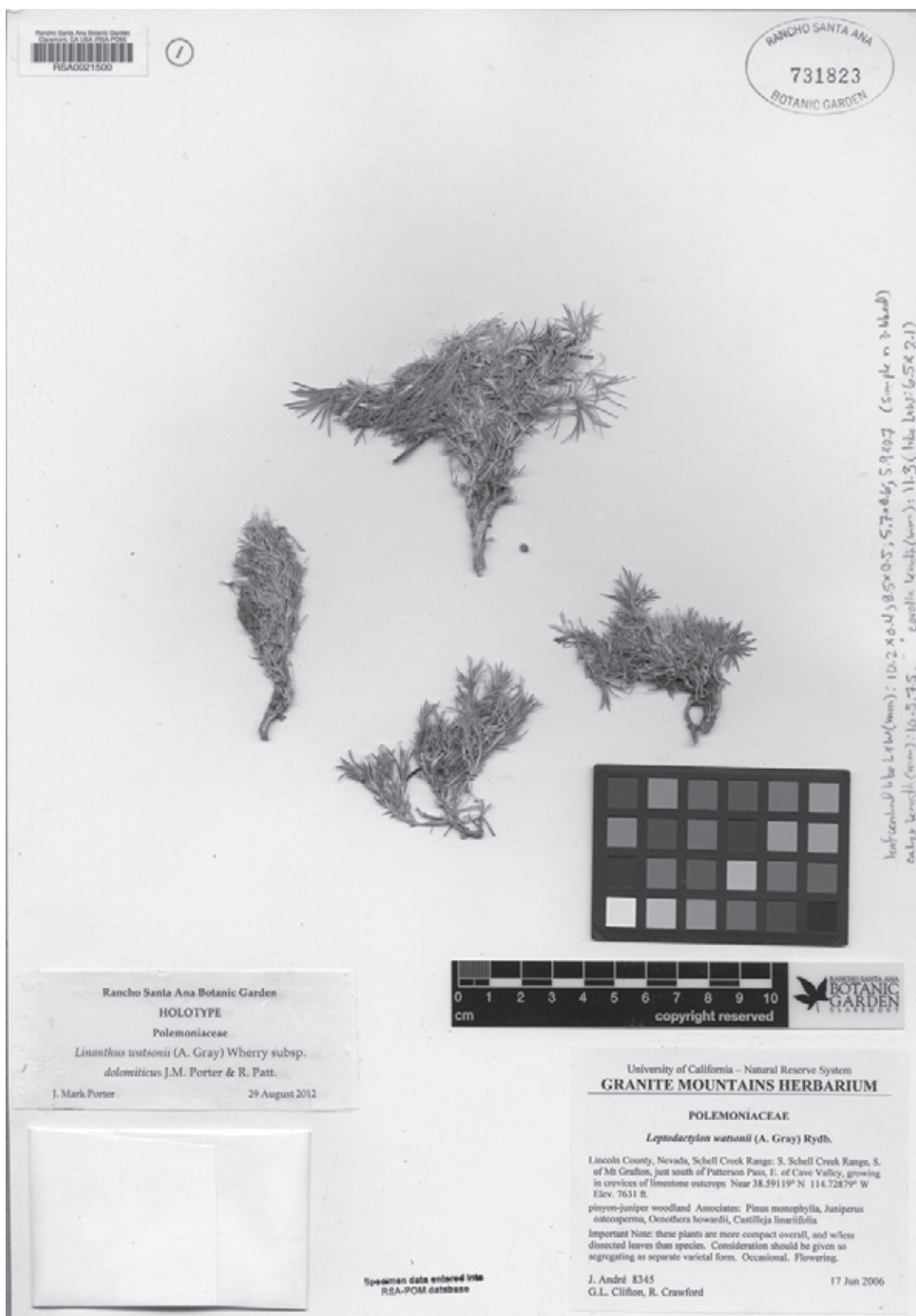


Fig. 23. The holotype specimen of *Linthus watsonii* (A. Gray) Wherry subsp. *dolomiticus* J.M. Porter & R. Patt.

Key to Subspecies of Linanthus watsonii

1. Corolla lobes usually 6; leaf lobes (3–)5–9.
 2. Corolla 15–28 mm long, lobes (6–)7–13 mm long, 1.7–6 mm wide; stems to 28 cm tall subsp. *watsonii*
 - 2' Corolla 12–17 mm long, lobes 5–7 mm long, 1.7–3.5 mm wide; stems to 12 cm tall subsp. *laccolithicus*
- 1' Corolla lobes usually 5; leaf lobes (1–)3 . . . subsp. *dolomiticus*

A NEW *LOESELIA* FROM SOUTHERN ARIZONA AND ADJACENT SONORA

Loeselia glandulosa (Cav.) G. Don is the most broadly distributed species of *Loeselia* L. It ranges from Santa Cruz County in southern Arizona, through Mexico and Central America, to Colombia and Venezuela. This distribution spans a remarkable array of habitats ranging from temperate oak woodland, to tropical pine-oak forest, cloud forest, and tropical deciduous forest. While a number of infraspecific taxa have been recognized (e.g., Porter and Johnson 2000), one phase has gone unrecognized.

In the northwestern extreme of the species range, *Loeselia glandulosa* occurs on rocky outcrops in the shade of *Quercus hypoleucoides* A. Camus, *Q. arizonica* Sargent and *Cercocarpus montanus* Raf. of interior chaparral. To the south, it occurs in a diversity of habitats, including cloud forest, lowland tropical scrub, tropical deciduous forest and tropical pine-oak woodlands. While the interior chaparral habitat has much in common with tropical pine-oak woodlands, e.g., Madrean origins, the southern climates are significantly different (J. M. Porter and S. M. Namoff, in prep.). Associated with the different environments are a suite of morphological differences that distinguish this phase from the typical form of *L. glandulosa* (from the eastern trans-volcanic belt region, in the Querétaro-Hidalgo region of central Mexico). The new taxon (a new subspecies of *L. glandulosa*, see below) differs from subsp. *glandulosa* in having linear to linear-lanceolate leaves (subsp. *glandulosa* has lanceolate to lance-ovate leaves), nectar guides composed of magenta streaking on the lower corolla lobes (subsp. *glandulosa* has magenta streaking on all lobes and varying degrees of spotting on the lower two), and a short and ramified habit (subsp. *glandulosa* is relatively tall and less branched).

The difference in leaf morphology is subtle, but significant. Examination of a sample of 31 leaves taken from herbarium collections of *Loeselia glandulosa* subsp. *sonorae* (collections with an asterisk cited under *Representative specimens* below) and subsp. *glandulosa*, analyzed using elliptical Fourier analysis followed by principal component analysis of Fourier coefficients (momocs [Bonhomme et al. 2014] and ade4 [Thioulouse et al. 1997; Dray and Dufour 2007] libraries under the R environment [R Development Core Team 2008]), shows that the leaves of subsp. *sonorae* and *glandulosa* not only differ in shape, but that there are significant differences in the centroids of each (based on 95% confidence ellipses surrounding the centroids; Fig. 24).

LOESELIA GLANDULOSA (Cav.) G. Don subsp. *sonorae* S.M. Namoff & J.M. Porter, subsp. nov.—TYPE: *J.M. Porter 14071*, USA, Arizona, Santa Cruz County, Patagonia Mtns, E side of road from Patagonia to Lochiel, 11 mi SE of Patagonia, S slope of American Peak; 31.45° N, 110.7333° W, in steep, limestone slope, with *Cercocarpus montanus*,

Rhus virens, and oak, 27 Mar 2004, (holotype: RSA [Fig. 25]; isotypes: IEB, P).

Suffrutescent perennial to 35 cm tall, usually with more than one primary axis. Stems light to dark brown or reddish, younger stems green; branches and leaves mostly alternate or occasionally with opposite nodes proximally and alternate distally; internodes 0.5–6.0 cm long, shorter in the inflorescence than below. Stems generally glabrate near base, becoming sparsely to densely puberulent to villous above with both antrorse-arcuate, eglandular trichomes, or straight, gland-tipped trichomes. Lower leaves sparsely puberulent or scabrous on upper sides and veins beneath; upper stems, peduncles, leaves and outer bracts glandular villous to glandular-puberulent and often with eglandular trichomes as well. Leaves bright green above, lighter beneath, with slightly raised, white, adaxial veins, lanceolate to linear-lanceolate, apex acute to acuminate, shortly petiolate, the blades attenuate to cuneate proximally, serrate-cuspidate except along the proximal margins where essentially entire; inflorescence leaves shorter and narrower than the primary leaves, grading into the cymule bracts. Inflorescence (synflorescences) diffuse, composed of solitary or paired, bracteate cymules borne terminally and on axillary shoots or in leaf axils of primary stems. Bracts polymorphic, mostly opposite, outermost herbaceous, flattened, linear, serrate with 3–5(–6) attenuate-aristate teeth per margin, occasionally entire, glandular-villous throughout; transitioning to innermost bracts that are entirely hyaline or green and herbaceous along the distal central vein, strongly keeled, coarsely serrate along the distal third but otherwise entire, bearing a few glandular or eglandular trichomes along the midrib. Calyx largely polysymmetric, entirely or largely hyaline, slightly herbaceous and green or anthocyanic on the distal lobes. Corolla monosymmetric (sometimes only slightly so), 16–22 mm long, corolla tube 8.5–10.5 mm long, exerted from the calyx and perceptibly bent, with the distal corolla angled geotropically, lobes 8–11 mm long, 2.3–4.2 mm wide, spatulate or narrowly oblanceolate and clawed proximally, claws somewhat conduplicate and channeled below, sinuses of lobes unequal, the three upper lobes erect and spreading, the two lower lobes spreading forward, lobe apex rounded to truncate and glandular-ciliate, midvein and lateral vascular strands branching or simple, but without anastomoses. Stamens equally inserted just below level of lowest sinus, filaments glabrous, long-exserted, arching upward, emerging together from lowest corolla sinus, becoming curled and reflexed to the corolla orifice following anthesis. Ovary oblongoid, with a small tuft of glandular trichomes at the apex; style straight, long-exserted, subequal corolla; stigmas 0.8–1.0 mm long. Capsule ellipsoid, 3.2–4.0 mm long, dehiscing between valves in upper half at maturity. Seeds 1.5–1.7 mm long, borne 2 (or 3) end to end in each locule, narrowly winged at the ends, flattish, rounded at one end, slanting-truncate at the other where seeds abut.

Occurring along the northern Sierra Madre Occidental, *Loeselia glandulosa* subsp. *sonorae* is associated with canyons, rocky slopes and crevices, of limestone, basalt, diorite and rhyolite, in oak woodlands (interior chaparral), and pine-oak forests, from 240 to 2100 m elev.

Although *Loeselia glandulosa* subsp. *sonorae* has been collected since the late 1800s, it has been treated as the typical

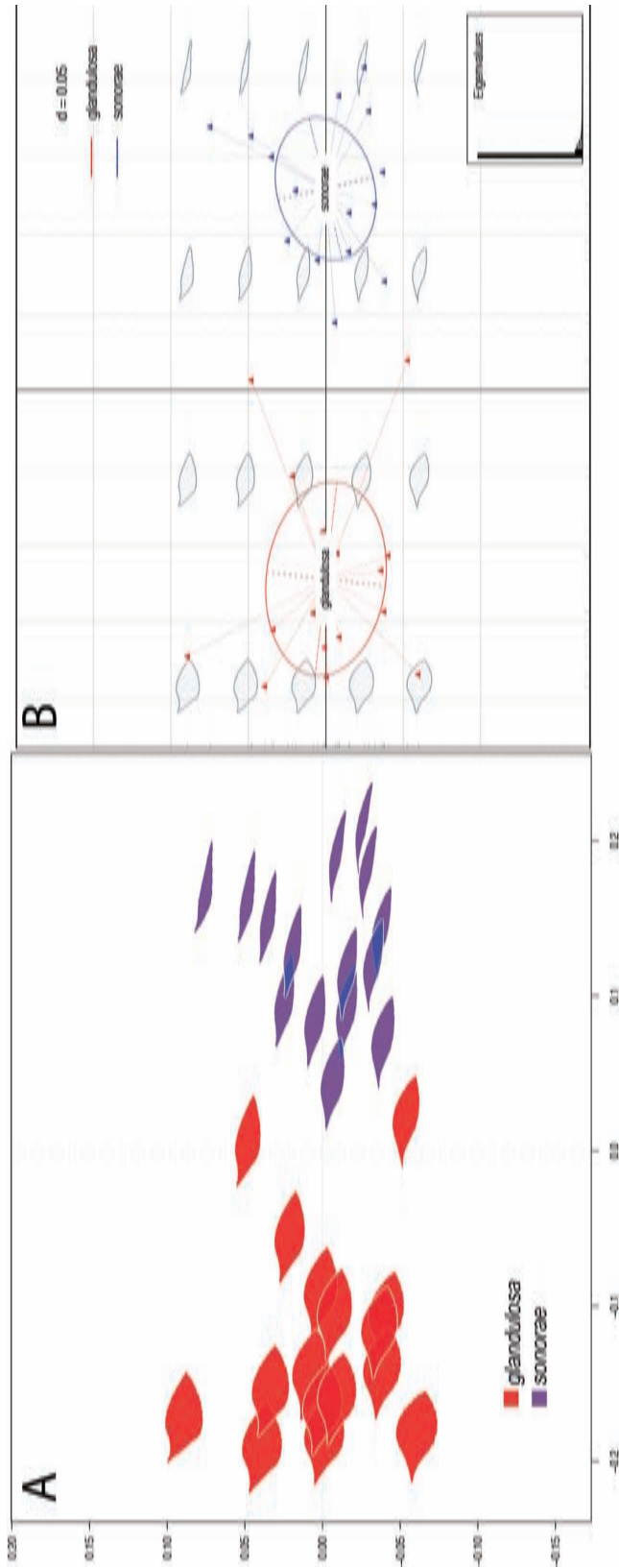


Fig. 24. Principal component analysis (PCA) of elliptical Fourier coefficients from leaf silhouettes of *Loeselia glandulosa* (Cav.) G. Don subsp. *glandulosa* (in red) and *Loeselia glandulosa* subsp. *sonorae* S.M. Namoff & J.M. Porter (in blue). (A) The reconstructed shape of each sample is presented in centered PC-space, based upon the Fourier coefficient loadings in the PCA axes. The X-axis accounts for 82.3% of the variance in the data, while the Y-axis accounts for 5.6% of the variance. (B) The 95% confidence ellipses around the centroids of subsp. *glandulosa* (red triangles) and subsp. *sonorae* (blue triangles) are portrayed. The background shapes reflect the morphospace represented in the analysis. The inset shows the Eigenvalues of PC axes.

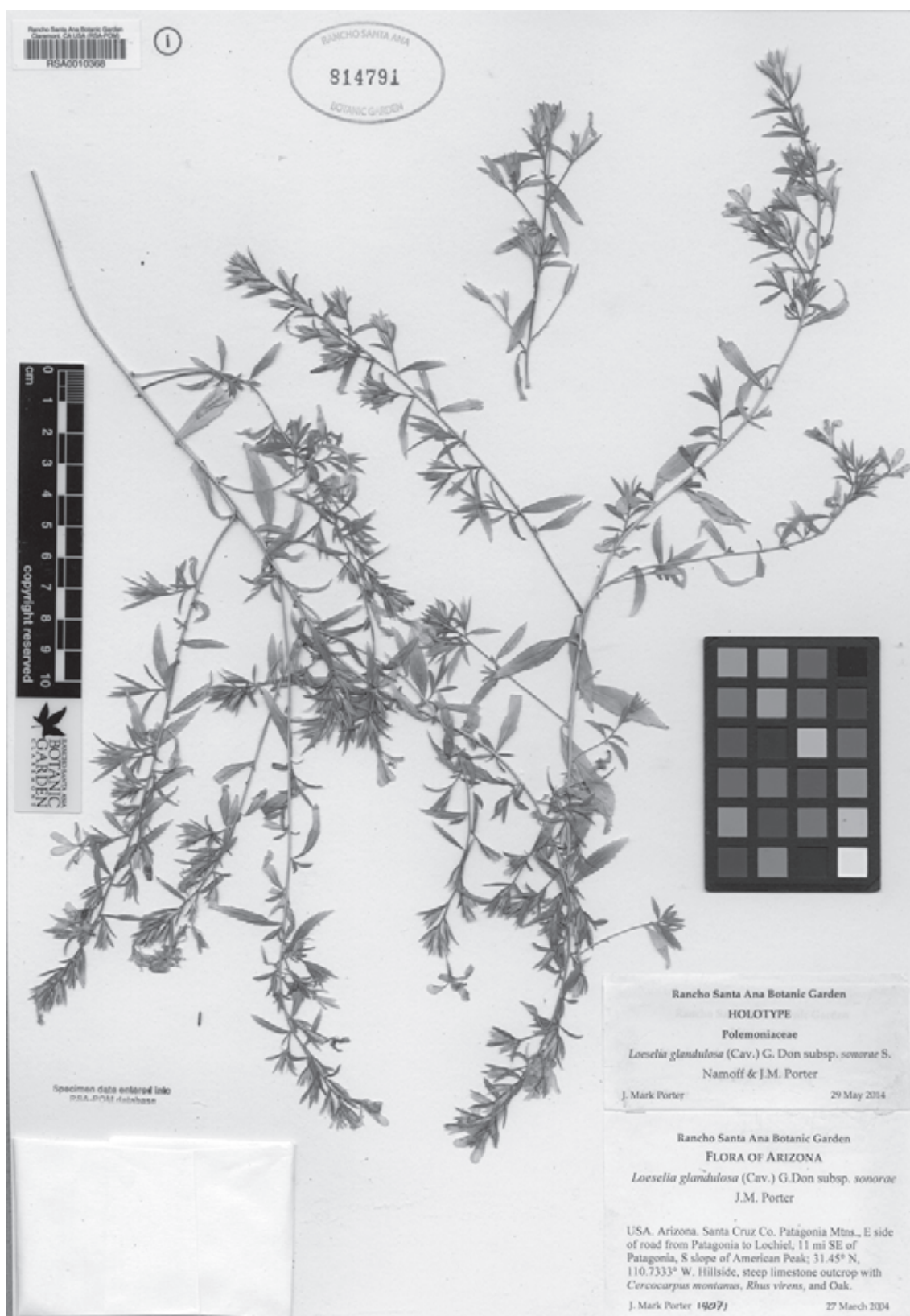


Fig. 25. The holotype specimen of *Loeselia glandulosa* (Cav.) G. Don subsp. *sonorae* S.M. Namoff & J.M. Porter.

subspecies. It is noteworthy that Asa Gray suggested a collection of this new subspecies (*G.C. Pringle 15923*) represented a “small-form” of *L. glandulosa*.

This subspecies apparently intergrades with subsp. *glandulosa* in northern Sinaloa; however, existing collections in this region are insufficient to determine if there are ecological differences between the subspecies in this region.

Representative specimens.—MEXICO, SONORA. Mpio. Alamos: Sierra de Alamos, La Huerta (abandoned), ca. 4 km SW of Chalaton, magnolia trail into sierra, 26.92167° N, 108.9767° W, 1100 m, 6 Dec 1988, *P. S. Martin et al. s.n.* [RSA]; Sierra de Alamos, ca. 3 km SW of Alamos, 1 km N of La Huerta, ca. 3 km NE of Aduana Peak, 26.9958° N, 108.975° W, 945 m, 12 Mar 1994, *T. R. Van Devender 94-126* [RSA]; Cajon of the Cucujaqui, 27.05° N, 108.7083° W, 460 m, 15 Mar 1989, *P. Jenkins 89-404* [ARIZ]; Sierra de Alamos, ca. 2 km SW of El Chalaton park, along the trail to La Huerta, 27.00° N, 108.9583° W, 800 m, 10 Mar 1993, *V. W. Steinmann 93-46* [ARIZ]; Arroyo Las Rastras, 2.6 km NE of Las Rastras, SW side of Sierra de Alamos, 26.9458° N, 109.0458° W, 400 m, 27 Feb 1995, *T. R. Van Devender 95-135a* [ARIZ]; Arroyo Guajarray, ca. 0.5 km upstream from Los Agueros, Rio Mayo region, 27.64167° N, 108.9667° W, 310 m, 16 Mar 1994, *R. S. Felger 94-88A** [ARIZ]; Mpio. Yecora: 1.5 km SW of Santa Ana, on road to Guadalupe Tatopa, 28.38167° N, 109.15833° W, 775 m, 21 Feb 1997, *T. R. Van Devender 97-216* [RSA]; 3.5 km W of Santa Ana road, on roadside, 4.8 km E of San Nicolas road on Mexico Hwy 16, 28.4258° N, 109.1472° W, 775 m, 31 Mar 1997, *T. R. Van Devender 97-467* [RSA]; El Divisidero (El Bordo), 1 km SE of El Llano, on road to Bermudez, Mesa del Campanero, 28.3281° N, 109.0438° W, 2100 m, 1 Oct 2000, *T. R. Van Devender 2000-823* [ARIZ]; Sierra des Papas, 20 Oct 1933, *H. Gentry 605M* [POM]; Canyon de Tejas, Sierra Charuco, 1350 m, 24 Apr 1948, *H. S. Gentry 8118* [ARIZ, POM]; mountain ridge ca. 39 mi NE of junction of roads to Cananea & Moctezuma from Ures (toward Ures), 1000 m, 18 Sep 1962, *R. Straw 2128* [RSA]; Rio Mayo Region, Arroyo Tepopa, 27.3333° N, 108.7333° W, 940 m, 15 Mar 1993, *M. Fishbein 963a* [ARIZ]; Rio Mayo Region, Arroyo Santa Barbara, 27.1167° N, 108.72167° W, 1250 m, 15 May 1990, *P. S. Martin s.n.* [ARIZ]; Rio Mayo Region, Cerro Blanco, 27.9583° N, 109.1833° W, 1100–1200 m, 5 Nov 1989, *D. Howell et al. s.n.** [ARIZ]; Arroyo El Mentidero at the crossing of the El Chimal road, 11.5 km (air) S of Alamos, 26.915278° N, 108.918056° W, 240 m, 10 Mar 1993, *T. R. Van Devender & R. K. Van Devender 93-78* [ARIZ]; Rio Mayo region, Sahuarivo to Corogui, 27.37167° N, 108.6633° W, 900 m, 18 Mar 1992, *D. Yetman et al. s.n.* [ARIZ]; Rio Mayo region, camp near Los Llanitos, Barranca Huicoche, 27.32167° N, 108.65° W, 1500 m, 18 Mar 1992, *P. S. Martin et al. s.n.** [ARIZ]; Las Piedras Canyon, E side of Sierra Alamos, 26.9833° N, 108.9583° W, 650 m, 14 Mar 1983, *G. Starr 360* [ARIZ]; Arroyo el Guirotal (Guaje), parallel to Arroyo El Mentidero, Rancho Uvalama, SE slopes of Sierra de Alamos, 11 km WSW of Alamos, 26.9167° N, 108.9167° W, 600 m, 2 Jan 1992, *P. S. Martin et al. s.n.* [ARIZ]; Rio Mayo Region, first pines, 3 km W of Las Chinacas at Cerra las Tinajas, 27.24167° N, 108.6778° W, 1400 m, 13 Oct 1988, *P. S. Martin et al. s.n.** [ARIZ]; Rio Mayo Region, Sierra de Alamos: La Huerta (abandoned) on magnolia trail into sierra,

ca. 4 km SW of Chalaton, 26.92167° N, 108.9767° W, 1100 m, 6 Dec 1988, *P. S. Martin et al. s.n.* [ARIZ]; 7.0 mi (road) N of Guirocoba, 26.9833° N, 108.6833° W, 560 m, 27 Dec 1988, *J. V. Salmon s.n.** [ARIZ]; Rio Mayo Region, Rancho Palo Injierto, 27.045° N, 108.7283° W, 550 m, 31 Dec 1988, *P. S. Martin & M. K. O'Rourke s.n.** [ARIZ]; Rio Mayo Region, gate of Sabinito Sur, 20 Dec 1989, *P. S. Martin & P. Jenkins s.n.** [ARIZ]; Saucito Canyon, Rancho la Sierrita (= Rancho El Negrito), E slopes of Sierra de Alamos, 6 km (air) SSW of Alamos, 26.975° N, 108.9681° W, 925 m, 26 Nov 1993, *T. R. Van Devender 93-1347** [ARIZ]; E of Tesopaco to Rio El Tigre on Chihuahua state line, 27.9556° N, 109.15° W, 1400 m, 25 Mar 1985, *P. S. Martin s.n.** [ARIZ]; Canyon las Piedras, Sierra de Alamos, 3.5 km (air) S of Alamos, 26.98472° N, 108.9556° W, 640 m, 5 Jul 1992, *T. R. Van Devender 92-727** [ARIZ]; Tepopa, between San Bernardo and Chinipas, 27.32167° N, 108.7333° W, 1250 m, 18 Mar 1992, *P. S. Martin et al. s.n.** [ARIZ]; Sierra Sahuaribo, 3 km (road) W of Las Chinacas, on road to Taymuco, 27.24583° N, 108.6875° W, 1350 m, 28 Apr 1994, *V. W. Steinmann 94-27** [ARIZ]; Tepopa, Rio Mayo, 7 Mar 1935, *H. S. Gentry 1395** [ARIZ]; 8.0 mi by Milpillas Road SW of Milpillas, 28 Nov 1969, *R. D. Krizman s.n.** [ARIZ]; Aroyo Cucujaqui, E of Alamos, 13 Mar 1977, *M. Ames 77-75* [ARIZ]; Rancho San Pedro eastern entry to the Cajon along the Rio Cucujaqui, owned by Bill Alcorn, 10 Nov 1988, *P. S. Martin & P. Jenkins 88-288* [ARIZ]; waterfall at Sahuarivo, 1550 m, 17 Mar 1992, *P. S. Martin et al. s.n.* [ARIZ]; Las Chinacas and vicinity on road to Chinipas, 27.24° N, 108.65° W, 1450 m, 15 Mar 1992, *P. S. Martin et al. s.n.* [ARIZ]; Palm Canyon, 17.7 mi SE of Magdalena, Cerro Cinta de Plata, 2 Oct 1976, *T. R. Van Devender et al. s.n.* [ARIZ]; upper tributary of Arroyo La Cieneguita, 1 km SE of Cerro Penas Blancas, about 5 mi N of Rancho La Volanta, 30.875° N, 109.9083° W, 1850 m, 23 Apr 1995, *M. Fishbein 2319* [ARIZ]; road bend beyond El Reparo, S of Peña Blanca on Mexico Hwy 16, 28.3833° N, 109.0667° W, 1400 m, 3 Dec 1990, *P. S. Martin & G. Ferguson s.n.* [ARIZ]; Cerro Verde, SW of San Javier, 28.5667° N, 109.76389° W, 550 m, 8 Oct 1988, *P. S. Martin et al. s.n.* [ARIZ]; El Reparo; upper old road to Bermudez, 28.3444° N, 109.0833° W, 1000 m, 15 Mar 1988, *P. S. Martin et al. s.n.* [ARIZ]; 3.5 km (road) SW of Santa Barbara; Rio Mayo region, 27.0967° N, 108.74° W, 1200 m, 15 Mar 1990, *P. S. Martin & G. Ferguson s.n.** [ARIZ]; Rio de Bavispe region, Canayon de la Bellota, Sierra de la Cabellera, 4300 ft, 7 Oct 1941, *S. S. White 4669** [ARIZ]; Palm Canyon, 17 mi SE of Magdalena, Cerro Cinta de Plata (Sierra Babiso), 30.350° N, 110.800° W, 7 Oct 1984, *T. R. Van Devender & R. K. Van Devender 84-480* [ARIZ]; Palm Canyon, Magdalena Palm Canyon, Sierra Babiso, 1100 m, 11 Oct 1987, *M. B. Johnson 87-001* [ARIZ]; Palm Canyon, 17 mi SE of Magdalena, road to Cucurpe, Cerro Cinta de Plata, 1100 m, 3 Oct 1982, *G. Starr 172** [ARIZ]; Palm Canyon, SE of Magdalena, Cerro Cinta de la Plata, 1100 m, 14 May 1979, *L. J. Toolin 370** [ARIZ]; trail from Arroyo Los Lavadores to Cajon Infierno headwaters, N of Sierra Aconchi, 7.0 mi by dirt road, W of San Felipe, and ca. 0.5 mi, by footpath, S of Arroyo Los Lavadores, 29.850° N, 110.350° W, 4200 ft, 19 Sep 1982, *F. W. Reichenbacher 1168* [ARIZ]; 17 mi SE of Magdalena, road to Cucurpe, Cerro Cinta de Plata (Cerro del Yeso), Palm Canyon, 5 Jun 1978, *T. R. Van Devender s.n.* [ARIZ]. USA. ARIZONA. Santa Cruz County:

Santa Rita Mountains, 20 May 1884, *C. G. Pringle 15923* [MO]; ca. 17.5 km (by road) SE of Patagonia, along road to Lochiel, 31.44583° N, 110.72361° W, 1750 m, 8 Oct 1995, *V. W. Steinmann 803* [ARIZ. RSA]; S slope of Santa Rita Mountains, 26 Sep 1941, *L. N. Goodding 442-41* [ARIZ]; The Bathub, N fork of Big Casa Blanca Canyon, Santa Rita Mountains, 5200 ft (1485 m), 18 May 1975, *T. R. Van Devender s.n.* [ARIZ]; Sycamore Canyon, 24 Nov 1936, *E. W. Hardies & C. R. Proctor 6093* [ARIZ]; Sycamore Canyon, near Ruby, 3900 ft (1188 m), 30 Sep 1944, *R. A. Darrow 2055* [ARIZ]; Comoro Canyon, W side of Patagonia Mtns, 18 Sep 1977, *J. Kaiser 1115* [ARIZ]; Atascosa Mountains, Upper Sycamore Canyon, above Agua Cercada Spring; T23S, R11E, S7 NW quarter of NE quarter, 4600 ft (1402 m), 24 May 1992, *M. Fishbein 369* [ARIZ]; Patagonia Mtns, E side of road from Patagonia to Lochiel, 11 mi SE of Patagonia, S slope of American Peak; 31.45° N, 110.7333° W, 12 Sep 1990, *J. M. Porter & C. Campbell 9231* [RSA]; Patagonia Mtns, E side of road from Patagonia to Lochiel, 11 mi SE of Patagonia, S slope of American Peak; 31.45° N, 110.7333° W, 27 Mar 2004, *J. M. Porter 14071** [RSA].

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