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SALTUGILIA LATIMERI: A NEW SPECIES OF POLEMONIACEAE

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Abstract

Saltugilia latimeri, a new species of Polemoniaceae, is endemic to dry, rocky to sandy slopes and foothills, primarily in San Bernardino and Riverside Counties, California. *Saltugilia latimeri* superficially resembles *S. australis* and has, until now, been considered conspecific with this taxon based on the small corolla size shared by both species. The two species differ in several morphological characters including stature, corolla throat coloration and exertion, and degree of glandularity.

Saltugilia latimeri, species, Polemoniaceae, taxonomy

Gilia is the historical catchall genus within Polemoniaceae for species of uncertain phylogenetic affinity (Wherry 1940, Mason and Grant 1948). Within this polyphyletic genus, Mason and Grant (1948) described a new taxon, *Gilia splendens* ssp. *australis* H. Mason & A. D. Grant, with stamen insertion and corolla throat and tube proportions similar to those of *Gilia splendens* H. Mason & A. D. Grant, but with a smaller corolla and a proportionally longer limb, similar in these respects to *Gilia caruifolia* Abrams.

As characters delimiting putative natural groups within *Gilia* were identified, such groups have been recognized with sectional or generic status. In one such case, Grant and Grant (1954) constructed *Gilia* section *Saltugilia* and included therein five species divided into two species groups. The section was considered to be natural from observations of corolla morphology and ecology of the members. Within their newly erected section *Saltugilia,* Grant and Grant (1954) elevated *G. splendens* ssp. *australis* to the species level, as *Gilia australis* (H. Mason & A. D. Grant) V. E. Grant & A. D. Grant. Grant and Grant (1954) distinguished *G. australis* from *G. splendens* and *G. caruifolia* by its smaller stature, whitish flowers (pale violet to white), and simpler leaves. The authors also noted minimal geographic overlap, partial to full breeding barriers, and apparent ecological isolation between *G. australis* and these other species.

Johnson (in Porter and Johnson 2000) elevated *Saltugilia* to generic status within Polemoniaceae. Following rules of priority, Porter and Johnson also restored Brand's (1907) epithet, *grinnellii,* in place of the more recently used epithet, *splendens,* for the largest-flowered species. As circumscribed by Porter and Johnson (2000), the genus *Saltugilia* comprises four closely related taxa: *Saltugilia australis* (H. Mason & A. D. Grant) L. A. Johnson, *S. caruifolia* (Abrams) L. A. Johnson, *S. grinnellii* (Brand) L. A. Johnson subspecies *grinnellii* and *S. grinnellii* subspecies *grantii* (Brand) L. A. Johnson.

A fifth taxon in *Saltugilia* has been identified. Our observations of greenhouse-grown plants and herbarium specimens indicate that two distinct forms have been referred to *S. australis* (as *Gilia australis*). Herbarium collections at RSA indicate that Latimer (1958) recognized, in his unpublished dissertation, these two forms as distinct subspecies within *G. australis*: a typical subspecies *australis,* and a geographically restricted subspecies *desertorum.* Based on observations of additional distinguishing characters, we here describe this geographically restricted taxon as a new species in the genus *Saltugilia.*

Saltugilia latimeri T. L. Weese & L. A. Johnson, sp. nov. (Fig. 1)—TYPE HERE DESIGNATED: USA, California, Riverside County, canyon in pass between Whitewater and Morongo Valley, 0.4 miles south of the San Bernardino county line, 9 April 1950, Verne & Alva Grant 8840 (holotype, RSA!).

Species nova ab *Saltugilia australis* (H. Mason & A.D. Grant) L.A. Johnson differt tubo corollae violaceo et exserto (nec albo et incluso), lobi corollae acutis (nec cuspidatis), et calyce dense glanduloso (nec glabro, glabrescenti, vel sparse glanduloso).

Annual herbs, to 30 cm in height, scapiform with a central stem and several basally branching axes subequal to equal with the main axis. Lower stems with long, uniserriate transparent trichomes commonly terminating in transparent glands (Fig. 1I; stalk cells becoming flattened and chain-like upon drying). Mid to upper stems densely glandular with the glands multicellular, flat-topped, and translucent (Fig. 1J; chloroplasts present in glands, but these neither darken beyond amber nor appear anthocyanic, as is common in *Gilia*). Lower leaves persistent, 5–many, forming a loose to dense basal rosette. Basal and lower cauline leaves generally 2×–3× pinnately divided with 3–10 sub-opposite lobes; leaf blade 20–45 mm long (–70 mm on greenhouse grown plants), 6–16 mm wide (–40 mm on greenhouse grown plants; Fig. 1C). Rosette and lower cauline leaves

with transparent, glandular trichomes of varying lengths (Fig. 1H). Upper cauline leaves glandular (Fig. 1K), reduced, bract-like, entire or occasionally pinnately divided, 1.5–14 mm long (–30 mm on greenhouse grown plants) and 0.2–6 mm wide (–17 mm on greenhouse grown plants; Fig. 1D). Inflorescence cymose, with flowers borne singly, or paired on ultimate stem extensions. Pedicels 2–16 mm long, occasionally longer, densely glandular (cf. Fig. 1L). When paired, pedicel of terminal (first maturing) flower usually shorter than pedicel of lateral (second maturing) flower (Fig. 1E). Calyx 2.6–3.5 mm long in flower, densely glandular (Fig. 1L–N), with an average of 20 glands per calyx lobe on herbarium sheets (range from 6 to 35 glands per calyx lobe). Calyx lobes dull green, sometimes purple spotted, 0.8 mm wide, united 3/5 length of calyx by an hyline membrane. Corolla 7.5–10 mm long, the fused portion 3–6.5 mm long, tube (=unexpanded portion of the fused corolla) exserted from the calyx. Tube dark lavender-purple, fading to blue (or yellow with extreme age) when dried. Lower throat (=expanded portion of fused corolla) yellow spotted; upper throat and lobes pinkish-lavender, but also fading to pale blue or yellowish on herbarium sheets. Corolla lobes 2.0–3.5 mm long and 1–3.5 mm wide, acute. Stamens inserted equally in the sinuses of the corolla lobes. Filaments 0.5–1.1 mm long to point of insertion, anthers 0.65–0.85 mm long and 0.35–0.50 mm wide. One stamen frequently extends at right angle to the throat. Style 7–8 mm long, extending slightly beyond the orifice. The three lobes of the stigma 0.8–1.0 mm long with tips curling downward. Capsule 3.5–5.0 mm long and 2.0–3.5 mm wide, typically 1.4–1.8 times as long as wide, more or less equaling the length of the calyx. Capsule dehiscent in three sections from the top to the base, 6–9 ovules per locule. Seeds ± 0.85 mm long, honey gold in color. Testa verrucate with anticlinal epidermal cell walls defined as low ridges, the ridges lost and cell wall boundaries obscure when this outer epidermal layer is shed upon wetting. Seeds mucilaginous via expansion of spiricals when wet. Pollen grains blue, ±40 μm in diameter, 5–6 zonocolpate, with lirae radiating from the apertures in magnetic-field fashion. $n = 9$.

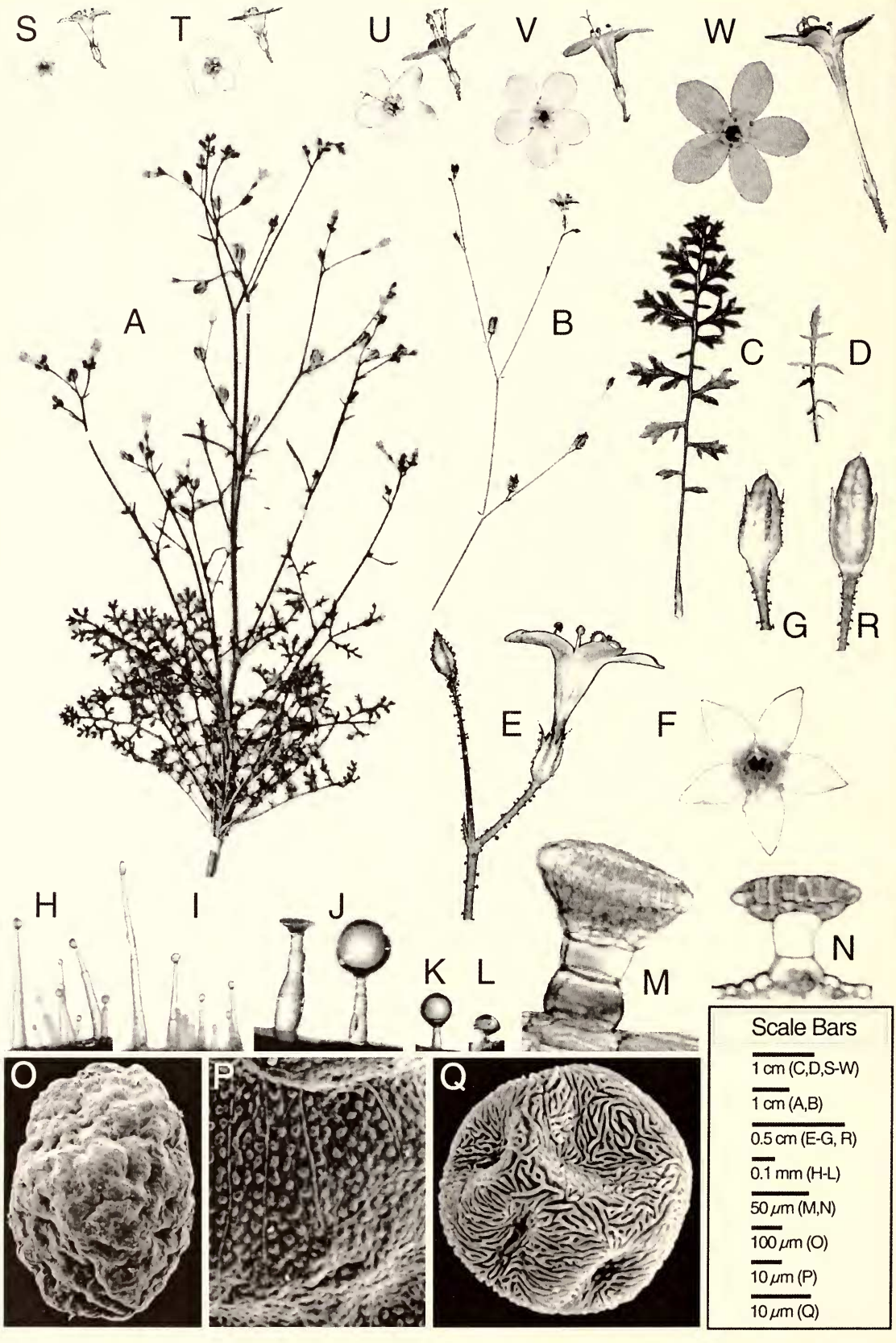
Paratypes. U.S.A. California, Inyo County: Hanaupah Cañon, Panamint Mountains, 16 May 1917, *Jepson 7091* (JEPS). Riverside County: Box Canyon, 16 Mar 1937, *Winblad s.n.* (CAS); Palms to Pines Hwy, Mount San Jacinto, 23 Apr 1937, *Winblad s.n.* (CAS); Palm Springs, 11 Apr. 1920, *Spencer 1569* (POM); Pinyon Flat, 1/2 way between Palm Canyon Drive and Jeraboa Road, 15 May 1992, *Johnson 92-021* (BRY, RSA, WS). San Bernardino County: Sandy-rocky place at base of foothills of Little San Bernardino Mountains, south of Yucca Valley, 6 May 1957, *Grant & Latimer 9986* (RSA); Cactus Flat, San Bernardino Mountains, 25 Jun 1926, *Munz 10514* (POM 96484 in part); Granite Mountains, Mojave Desert, 13 May 1939, *Jaeger s.n.* (CAS, POM); About 3 miles East of Joshua Tree off road to Twentynine Palms, 3 May 1964, *Thorne 33975* (RSA).

Comparative morphology and relationships. Until now, *Saltugilia latimeri* has been regarded as conspecific with *S. australis*. Both species possess small flowers, tend toward a smaller stature, and are ecologically disposed to drier habitats relative to *S. grinnellii* and *S. caruifolia*. Because convergence in these features may result from selection imposed by similar habitat types and available pollinators, they are not necessarily useful indicators of phylogenetic affinities or taxonomic boundaries. Flower size, in particular, has received disproportionate emphasis as an identification tool in *Saltugilia* (Day 1993). As a result, small flowered representatives of *S. caruifolia* and *S. grinnellii* have been misidentified as *S. australis* (e.g., CAS 627511, POM 48851). Similarly, it seems likely that *S. latimeri* has escaped previous delimitation by over reliance on flower size, to the exclusion of other characters that clearly distinguish *S. latimeri* from *S. australis*.

Beyond flower size, *S. latimeri* differs from *S. australis* in other floral features (Table 1). The corolla of *S. australis* is whitish overall. The lobes are cusped at the apex and may be suffused with pink or bluish-lavender, but the tube and throat (exclusive of the yellow spots, characteristic of *Saltugilia*) remain white. Furthermore, the tube is more or less included within the calyx, the throat flares widely, and the calyx is mostly glabrescent at maturity. These features are consistent with the type (UC!) and populations examined from throughout *S. australis*' range. In contrast, *S. latimeri* has saturated pink to lavender, tapering acute corolla lobes, a colored and more narrowly funnelform throat, a purple, exserted tube, and a more intensely glandular calyx, with the glands large and as abundant as on the pedicel.

Although corolla coloration provides a definitive means of distinguishing *S. latimeri* from *S. australis* on fresh and most herbarium specimens, color may fade from *Saltugilia* flowers over time and can be a less reliable diagnostic character on some herbarium specimens of extreme age. On living plants, flowers senesce quickly (1–2 days after opening, personal observation), and there is insufficient time for the distinctive coloration to fade while the flowers remain on the plant, thus identification of *S. latimeri* relative to *S. australis* is straightforward. When color has faded on herbarium specimens, the exserted tube, narrower throat, and glandular calyx are useful secondary characteristics for distinguishing between *S. latimeri* and *S. australis*.

Relative to other *Saltugilia, S. latimeri* is readily distinguished from *S. caruifolia* in stamen features (short filaments inserted in the sinus of the corolla lobes vs. long exserted stamens inserted mid-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Scale Bars
1 cm (C,D,S-W)
1 cm (A,B)
0.5 cm (E-G, R)
0.1 mm (H-L)
50 μm (M,N)
100 μm (O)
10 μm (P)
10 μm (Q)

TABLE 1. MORPHOLOGICAL CHARACTERS OF *SALTUGILIA* SPECIES.

	Saltugilia australis	*Saltugilia caruifolia*	*Saltugilia grinnellii*	*Saltugilia latimeri*
corolla lobe color	white/pale pink	lavender/blue	lavender/bright pink	pink/lavender
throat color	white	white/lavender	lavender/pink	pink/lavender
tube color	white	purple	purple/pink	purple
petal lobe shape	cusped	obtuse/rounded	obtuse	acute, tapering
tube position relative to calyx	included	exserted	exserted	exserted
expansion of throat outside calyx	flares widely	wide flare/campanulate	narrow flare	narrow flare
stamen insertion	sinus of corolla lobes	mid throat	sinus of corolla lobes	sinus of corolla lobes
average number of glands per calyx lobe (min.–max. observed)	3 (0–7)	4 (0–11)	7 (0–27)	21 (6–35)
habit	one main central leader	one main central leader	one main central leader	branches near base

throat), and from *S. grinnellii* that tends to have rounder corolla lobe apices and a minutely glandular exterior corolla (Table 1). *Saltugilia latimeri* corollas most nearly approach the relative proportions of *S. grinnellii* corollas, although without the minute glands mentioned above.

As implied by morphology, *Saltugilia* are closely allied species differing primarily in corolla features. In addition to these floral characters, the capsule in *S. latimeri* is more or less equal to the calyx, whereas it frequently (but not always) greatly exceeds the calyx in *S. australis.* Differing from all other *Saltugilia, S. latimeri* also typically branches near the base so that several sub-equal lateral branches soon approach the central stem in length and diameter. In contrast, other *Saltugilia* usually have dominant central axes. Although the basal leaves of *S. latimeri* have broader, and fewer, lobe segments than typical *S. australis,* the leaves of *S. australis* show considerable variation across its range with some specimens possessing broader lobes.

Close relationships among *Saltugilia* species are also evidenced by hybridization studies. Grant and Grant (1954) concluded that species now placed in *Saltugilia* are interfertile, although these studies revealed that sterility to partial sterility exists between some populations (from 5 to 28% inviable individuals following interspecific crosses), leading Grant and Grant to hypothesize the presence of semi-lethal gene combinations (see also Latimer 1958). Of relevance here, a cross between S. *latimeri* and *S. australis* produced viable F1 with pollen viability of 11% (Latimer 1958), compared to 58% viable pollen in F1 progeny of a cross between two populations of *S. latimeri.* This reduced fertility in interspecific crosses of *S. latimeri* × *S. australis* parallels our own results. A cross of *S. latimeri* (*Johnson 92-021*) with *S. australis* (*Johnson 92-011,* BRY) produced vigorous F1 offspring, but even hand pollination of the F1 produced only 1 to 7 seeds per capsule (average = 2.7; average number of ovules per capsule = 25) compared to an average of 23 seeds (24 ovules) and 19 seeds (21 ovules) in self pollinated capsules of the parental *S. latimeri* and *S. australis,* respectively. Pollen viability in hybrid progeny from other crosses reported by Grant and Grant (1954) averaged 14% between *S. caruifolia* and both subspecies of *S. grinnellii,* and 12% between extreme forms of the *S. grinnellii.* The ability of *S. latimeri* and *S. australis* to cross with *S. grinnellii* differed substantially (Latimer 1958). These hybridization studies provide inconclusive evidence regarding species boundaries and sister relationships within *Saltugilia,* but they do indicate levels of differentiation between *S. latimeri* and *S. australis* at least as great as between pair-wise combinations of other *Saltugilia* species.

Were *Saltugilia latimeri* itself the product of hy-

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FIG. 1. Features of *Saltugilia latimeri* alone and in comparison with selected features of other *Saltugilia.* A. habit in early flower. B. inflorescence branch in mid flower. C. basal leaf. D. cauline leaf. E, F. flower. G. capsule. H–L. trichomes from living plant. H. basal leaf. I. Lower stem. J. mid stem (gland on right with secretion present). K. flower bract (secretion present). L. calyx (secretion present). M. calyx gland cleared in choral hydrate. N. paraffin section of calyx gland. O. scanning electron micrograph of unhydrated seed. P. scanning electron micrograph of unhydrated seed surface showing verrucae and ridges formed from anticlinal walls. Q. scanning electron micrograph of untreated pollen grain. R. capsule of *S. australis.* S–W. relative size and shape of *Saltugilia* flowers. S. *S. latimeri.* T. *S. australis* (*Johnson 97-049,* BRY). U. *S. caruifolia* (*Johnson 97-099,* BRY). V. *S. grinnellii* subspecies *grinnellii* (*Johnson 93-098,* BRY). W. *S. grinnellii* subspecies *grantii* (Johnson 94-057, BRY). A, Q. *Grant & Grant 8840,* RSA. B-P. S. progeny of *Johnson 92-021,* BRY.

bridization, progeny of self-pollinated plants should demonstrate character segregation. In each generation, less intermediacy and more individuals with parental phenotypes would be observed. Four generations of greenhouse grown progeny from a single population have produced no segregation of morphological characters, supporting the autonomy of this species. Additionally, greenhouse grown plants readily set full capsules of seeds upon selfing, suggesting that *Saltugilia latimeri* is autogamous. Further evidence for autogamy is provided by allozyme analyses (26 individuals; *Johnson 92-021*) that reveal complete homozygosity at 28 surveyed putative loci representing 19 enzyme systems: AAT, ACN, ACPH, ALD, BGAL, CAT, EST, GDH, G3PDH-1, G3PDH-2, IDH, MDH-1, MDH-2, MDH-3, ME-1, ME-2, MNR-1, MNR-2, 6PGD-1, 6PGD-2, PGI−1, PGM-1, PGM-2, PGI-2, SKDH, SOD, TPI-1, TPI-2 (Following methods of Soltis et al. 1983 with or without minor modifications). Six of these 28 loci showed polymorphism with at most two alleles.

Sequences of the chloroplast *matK* region from *S. latimeri* (*Johnson 92-021*) have been included in molecular studies (as *Gilia australis*; Johnson and Soltis 1995, Johnson et al. 1996) and analyses of these data provide strong support for placing *S. latimeri* with other sampled representatives of *Saltugilia.* Additional sampling of multiple populations of all *Saltugilia* taxa (Weese and Johnson unpublished data) with sequences of the chloroplast *trnL* intron–*trnF* spacer and nuclear ITS regions strongly support the monophyly of *Saltugilia,* but provide insufficient resolution of taxa within the genus to use these markers alone as the basis of species recognition.

Grant and Grant (1954) proposed that species now included in *Saltugilia* evolved from an ancestral type, represented by *S. grinnellii* or a similar large flowered ancestor, occupying mild climatic conditions similar to those found along the California coast. Arising from this ancestral type were taxa adapted to extreme conditions, including the dry, arid habitats occupied by *S. australis.* This implies that *S. australis* represents an autogamous derivative from *S. grinnellii* or another similar large flowered ancestor. This hypothesis applies equally well to *S. latimeri.* We suggest *S. latimeri* represents a second, independent lineage of small-flowered, autogamous desert annuals derived from an ancestral *Saltugilia* species with features generally approaching those of *S. grinnellii.*

Ecology and distribution. Saltugilia latimeri grows in dry, desert slopes of coarse sandy to rocky soils at elevations of 400–1900 m. Flowering times typically range from mid April to early June, although collections have been made as early as mid March and as late as the end of June. Our survey of herbaria (CAS, JEPS, POM, RSA, SD, UCR, UC) reveals that fewer than 20 independent collections of *S. latimeri* exist. These were obtained from the Joshua Tree Wilderness Area at the border between San Bernardino and Riverside Counties, in the foothills of the Little San Bernardino, San Bernardino, and Santa Rosa Mountains, in the Granite Mountains of central San Bernardino County, and one disjunct collection in the Panamint Mountains of Inyo County (Fig. 2). This latter population is approximately 120 miles from other known *S. latimeri* populations.

Several collections of *S. latimeri* from the Granite Mountain range pose some taxonomic difficulty because they possess a central leader habit and cuspidate corolla lobes—two features typical of *S. australis,* but not characteristic of the holotype and paratypes listed above for *S. latimeri.* However, these collections fall within the limits of *S. latimeri* and can be identified based on their exserted, purple corolla tube, narrow corolla throat, capsule that is subequal to the calyx, and propensity for glandular calyces. The Granite and adjacent Old Dad Mountains (Fig. 2) represent a locality for *Saltugilia* separated by 50 miles from the nearest portion of *Saltugilia's* range in the desert slopes of the San Bernardino and Santa Rosa Mountains. Specimens referred to as *S. grinnellii, S. australis,* and *S. latimeri* have all been collected in the Granite Mountains, but only infrequently. Further study of this material, including new accessions, is warranted. The presence of these minimally intermediate *S. latimeri* collections in a geographically restricted location in no way interferes with the ability to differentiate *S. latimeri* from *S. australis* in other portions of these species' ranges. In addition to the Granite Mountain area, *S. latimeri* is in close proximity to *S. australis* in the Santa Ana and Little San Bernardino Mountains, and with *S. grinnellii* in the Morongo Canyon area of the Little San Bernardino Mountains (Fig. 2). Mixed collections of *S. latimeri* with other *Saltugilia* on herbarium sheets have not been observed.

Inferred from the small number of specimens present among *Saltugilia* collections acquired from seven herbaria (CAS, JEPS, POM, RSA, SD, UCR, UC), *S. latimeri* may merit conservation concern. Though almost certainly restricted in distribution, it is not known whether this species is truly rare or simply overlooked by collectors because of its small stature, inconspicuous habit, and short flowering duration. The habitat of *S. latimeri* includes desert scrub and chaparral communities that can be dense and difficult to navigate, perhaps leading to under-representation of this species in herbaria. However, more extensive collections of *S. australis* are available in several of these same areas, suggesting that *S. latimeri* is less abundant in nature. With human development encroaching in some of the known locations for this species, further study is warranted to establish the rarity of *S. latimeri.*

Whereas *S. australis* is frequently collected on first year burns within its range and its seeds re-

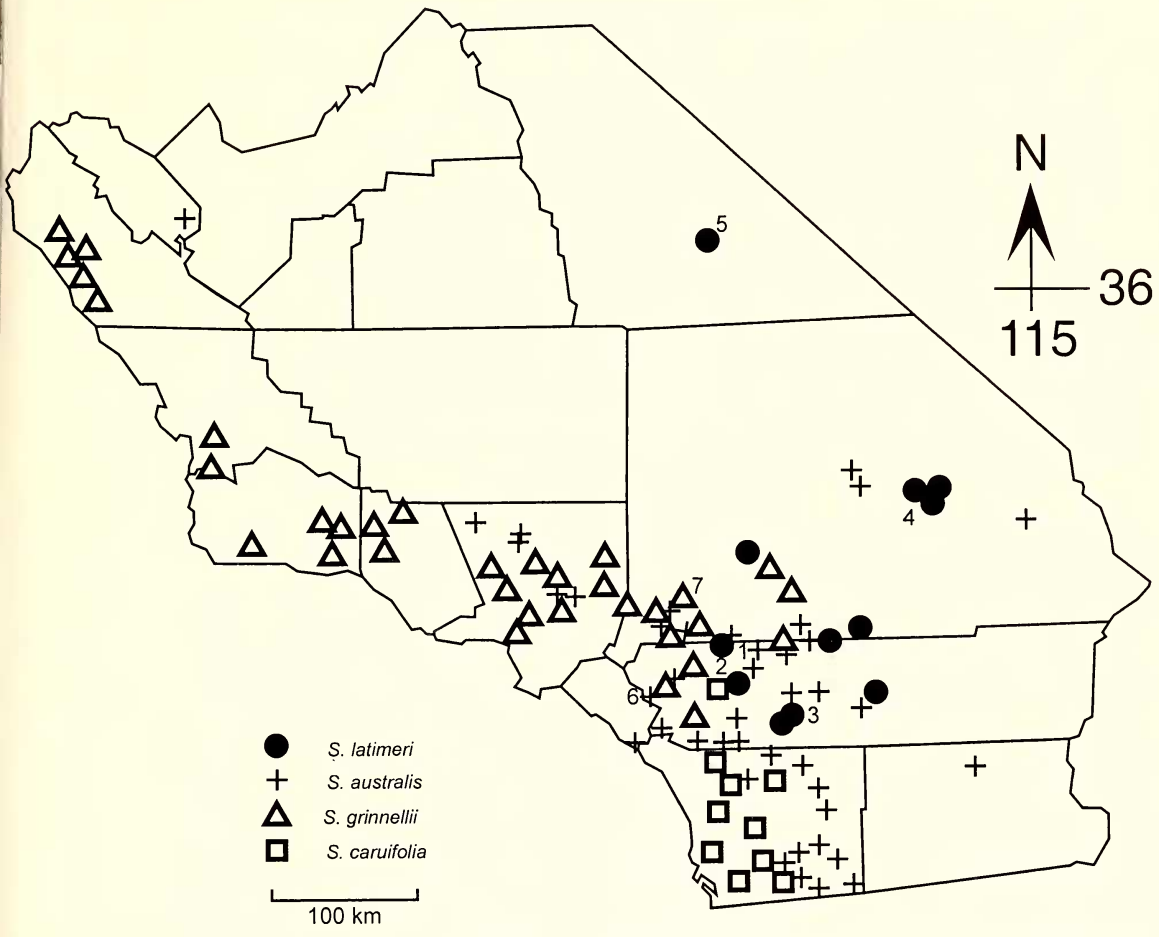

FIG. 2. Distribution of *Saltugilia* species in California, USA. The ranges of *Saltugilia australis* and *S. caruifolia* extend into Baja Mexico, but these populations are not shown. Populations are represented by symbols: ● *Saltugilia latimeri.* + *Saltugilia australis.* △ *Saltugilia grinnellii.* □ *Saltugilia caruifolia.* Locations mentioned in the text are indicated by numbers: 1. Little San Bernardino Mountains. 2. San Bernardino Mountains. 3. Santa Rosa Mountains. 4. Old Dad/Granite Mountains. 5. Panamint Mountains. 6. Santa Ana Mountains. 7. Cushenbury Grade.

spond positively to charcoal as a germination cue (Keeley and Keeley 1987), no mention of fire is made on any specimen labels for *S. latimeri.* We routinely add charcoal when germinating seeds of all *Saltugilia* with great success, but have not rigorously determined whether *S. latimeri* responds more positively to this treatment than it would without the addition of charcoal.

Taxonomic evaluation of earlier studies. Because *Saltugilia latimeri* previously has not been distinguished from *S. australis,* earlier literature may include either of these species under the name "*Gilia australis*". Johnson and Soltis (1995) and Johnson et al. (1996) both include, as *Gilia australis* (*Johnson 92-021*), a population of *S. latimeri* in comparative DNA sequencing studies of the chloroplast *matK* gene. In both studies, *Saltugilia* is incompletely sampled (represented by *S. latimeri, S. caruifolia* and *S. grinnellii* ssp. *grantii* in Johnson and Soltis 1995 and *S. latimeri* and S. *grinnellii* ssp. *grantii* in Johnson et al. 1996), yet forms a well-supported clade distinct from *Gilia.*

In their initial circumscription of *Gilia* section *Saltugilia,* Grant and Grant (1954) performed chromosome counts as well as extensive crossing studies within and among species of *Saltugilia.* The population of *G. australis* collected by Grant from Morongo Canyon in the San Bernardino Mountains (Fig. 2) used for these studies, and cited by Grant (1956), is *S. latimeri.* Additionally, specimens cited under the description of *G. australis* by Grant and Grant (1954) include both *S. australis* and *S. latimeri.* This is significant because the "desert race" of *Gilia splendens* discussed by Grant and Grant (1965) could be misconstrued to be our *S. latimeri.* This clearly is not the case, however, because this desert race of *G. splendens* is also discussed in Grant and Grant (1954), Latimer (1958) and Grant (1966).

Latimer's (1958) unpublished thesis recognized

S. latimeri at the subspecies level (as *G. australis* ssp. *desertorum*). In Grant's (1966) citation of Latimer's work, the populations of *Gilia australis* considered sympatric with *G. splendens* (collected in the Morongo Valley and Cushenbury Grade of the San Bernardino Mountains) are in fact *S. latimeri,* while those populations considered allopatric with *G. splendens* (collected inthe Santa Ana Mountains and Cajon Pass) are *S. australis* (Fig. 2).

Based on these observations, the recognition of *Saltugilia latimeri* as a new species in Polemoniaceae is warranted. This recognition is a starting point for further species level studies of *Saltugilia latimeri* and larger scale investigations both within *Saltugilia* and Polemoniaceae. To facilitate the correct identification and incorporation of *S. latimeri* in future works, the following key is provided.

Key to Genus *Saltugilia* (beginning with couplet 55 of Porter and Johnson 2000)

1. Trichomes on basal leaves eglandular white arachniod (present at least in axils), or white geniculate, or translucent; if translucent, inflorescence glands long stalked, diameter of gland less than length of stalk and generally equally abundant on pedicel and calyx, or inflorescence trichomes including long hairs . . . . . *Gilia*
1.′ Trichomes on basal leaves translucent, minutely gland tipped; inflorescence glands subsessile, diameter of gland > length of stalk, more abundant on pedicel than calyx; pedicels and calyx without long stalked hairs . . . . . 2 *(Saltugilia)*
2. Corolla tube and throat white (throat yellow spotted), adaxial lobe surface white to white suffused with blue, lavender, or pink; corolla tube included in calyx, corolla lobes cuspidate . . . . . *S. australis*
2.′ Corolla tube and throat pigmented (magenta to pink to purple and throat yellow spotted), adaxial lobe surface saturated blue, lavender, or pink; corolla tube exserted from calyx, corolla lobes rounded to acute (cuspidate only in Granite Mountains of San Bernardino County, California, but then possessing pigmented and exserted corolla tube) 3
3. Stamens exserted well beyond the corolla lobes, inserted equally mid throat; corolla lobes often reflexed, throat widely flaring, nearly campanulate, with purple marks visible on the interior of the throat at the base of each corolla lobe *S. caruifolia*
3.′ Stamens less than or equal to corolla lobes, inserted equally in the sinus of the corolla lobes; corolla lobes not reflexed, throat narrowly flaring, lacking purple marks on interior of throat 4
4. Corolla less than 11 mm long, corolla lobes pale pink to lavendar, tube purple; corolla tube eglandular and calyx glandular . . . . . .*S. latimeri*
4.′ Corolla generally more than 11 mm long, corolla lobes pale to bright pink, tube pink to magenta; corolla tube minutely glandular, calyx eglandular to glabrescent . . . . . 5 (*S. grinnellii*)
5. Corolla tube 4–10 mm long, 1–2 × calyx . . . . . subspecies *grinnellii*
5.′ Corolla tube 7–18 mm long, 2–5 × calyx . . . . . subspecies *grantii*

Acknowledgements

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