Transfer of the Western North American Species *Gilia splendens* to *Saltugilia* (Polemoniaceae), and the Taxonomic Affinities of *Gilia scopulorum*, *Gilia stellata*, and *Gilia yorkii*

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ABSTRACT. Two new combinations, *Saltugilia splendens* (Douglas ex H. Mason & A. D. Grant) L. A. Johnson and *S. splendens* subsp. *grantii* (Brand) L. A. Johnson, are proposed for taxa transferred from *Gilia* Ruiz & Pavón on the basis of phylogenetic relationship. The affinities of *G. scopulorum* M. E. Jones, *G. stellata* A. Heller, and *G. yorkii* Shevock & A. G. Day, three species that have been allied with *Saltugilia* V. E. Grant & A. D. Grant when treated as a section of *Gilia*, are reevaluated.

Key words: Classification, *Gilia*, Polemoniaceae, *Saltugilia*, taxonomy.

In elevating *Gilia* Ruiz & Pavón sect. *Saltugilia* V. E. Grant & A. D. Grant to genus rank (Porter & Johnson, 2000), a nomenclatural error was introduced that resulted in the unintentional exclusion of taxa intended to be circumscribed within *Saltugilia* (V. E. Grant & A. D. Grant) L. A. Johnson, as well as a concomitant bibliographic error that merits correction. Background regarding the nomenclatural problem can be found in Grant and Wendt (2003, 2004). In essence, recognizing the illegitimacy of the name *G. splendens* Douglas ex H. Mason & A. D. Grant, Johnson (in Porter & Johnson, 2000) accepted the neotypification of *G. grinnellii* Brand by Grant and Grant (1954), thereby equating *G. grinnellii* with the taxon commonly known as *G. splendens* (Grant & Grant, 1954; Grant & Wendt, 2003). Recognizing the neotypification of *G. grinnellii* by Grant and Grant (1954) was contrary to the code, Grant and Wendt (2003) proposed rejection of this name in order to eliminate confusion and preserve the use of *G. cana* (M. E. Jones) A. Heller, the taxon to which the name *G. grinnellii* correctly applies. This rejection was approved by the General Committee (Barrie, 2006), making *S. grinnellii* (Brand) L. A. Johnson a rejected name also. Grant and Wendt (2004) further proposed to conserve the name *G. splendens* Douglas ex H. Mason & A. D. Grant, and this proposal was likewise approved by the General Committee (Barrie, 2006). Consequently, the transfer of *G. splendens* to the genus *Saltugilia* remains necessary. Furthermore, although *G. splendens*, indicated as type for *Saltugilia* when originally proposed by Grant and Grant (1954) as a section of *Gilia*, was recognized as unavailable for this use by Porter and Johnson (2000), the above committee actions now make *G. splendens* available for use as type for both *Gilia* sect. *Saltugilia* and the genus *Saltugilia*. The bibliographic citation for *Saltugilia* is corrected below (relative to Porter & Johnson, 2000) for accuracy in future reference.

The circumscription of *Saltugilia* as a genus has also changed since Porter and Johnson (2000), with the addition of a newly described species. The broader circumscription of *Saltugilia*, however, when treated as a section of *Gilia* (i.e., Grant, 2004), continues to include species that have no demonstrated affinity with the core elements of this group, although they do show affinity with core *Gilia* in both morphological and molecular characters. Evidence bearing on the classification of these species is reexamined.

Saltugilia (V. E. Grant & A. D. Grant) L. A. Johnson, Aliso 19: 69. 2000, em. *Gilia* sect. *Saltugilia* V. E. Grant & A. D. Grant, Aliso 3: 84. 1954, p.p. TYPE: *Gilia splendens* Douglas ex H. Mason & A. D. Grant.

Saltugilia splendens (Douglas ex H. Mason & A. D. Grant) L. A. Johnson, comb. nov. Basionym: *Gilia splendens* Douglas ex H. Mason & A. D. Grant, nom. cons., Madroño 9: 212. 1948. TYPE: U.S.A. California: Monterey Co., Santa Lucia Mtns., Tassajara Hot Springs, 1530 ft., 26 Apr. 1933, *R. S. Ferris 8317* (holotype, designated by Grant & Wendt, 2004: 842, UC).

Saltugilia splendens (Douglas ex H. Mason & A. D. Grant) L. A. Johnson subsp. **grantii** (Brand) L. A. Johnson, comb. nov. Basionym: *Gilia collina* Eastwood var. *grantii* Brand, Pflanzenr. IV, 250: 101. 1907. TYPE: U.S.A. California: Los Angeles Co., Mt. Wilson, 2000 m, June 1902, *G. B. Grant 503* (holotype, CAS).

Circumscription of *Saltugilia*

Saltugilia includes four closely related species: *S. australis* (H. Mason & A. D. Grant) L. A. Johnson, *S. caruifolia* (Abrams) L. A. Johnson, *S. latimeri* T. L. Weese & L. A. Johnson, and *S. splendens*. These differ morphologically from one another primarily in floral characteristics (Porter & Johnson, 2000; Weese & Johnson, 2001). Grant (2004: 538) treats *Saltugilia* as a section of *Gilia*, recognizing within this section the four species above as one group, and a second group of three additional species (*G. scopulorum* M. E. Jones, *G. stellata* A. Heller, and *G. yorkii* Shevock & A. G. Day) with a note that "…there is a problem concerning the closeness of the relationships between the two groups and within the second group itself…the species of the second group are retained in the sect. *Saltugilia* until we know better what to do with them."

Publications that address the composition of *Saltugilia* at any rank, in all or in part, include Grant and Grant (1954, 1956), Grant (1959), Day (1993a, b), Johnson et al. (1996), Porter (1996), Shevock and Day (1998), Grant (1998), Porter and Johnson (2000), Weese and Johnson (2001), Grant (2004), and Weese and Johnson (2005). A close examination of these publications reveals that most lack discriminating detail in the presentation of morphological characters. For example, an affinity between *Gilia scopulorum* and *G. stellata* with core *Saltugilia* was suggested by Grant and Grant (1956) and the transfer of these species into *Saltugilia* made by Grant (1959), but neither publication presents explicit evidence for such a relationship beyond a general list of characters for the taxon *Saltugilia*. Importantly, section *Saltugilia* in both publications included species now excluded entirely from *Gilia* by both Porter and Johnson (2000) and Grant (2004), thus diluting the current significance of the character lists earlier presented as diagnostic. Subsequent circumscriptions of *Gilia* sect. *Saltugilia* by Day (1993b) and Grant (1998) have taken the affinity between *G. scopulorum* and *G. stellata* with core *Saltugilia* as res ipsa loquitur (i.e., the thing speaks for itself). The placement of *G. yorkii* in *Saltugilia* (Shevock & Day, 1998) included explicit comparative data, which are revisited below.

As a framework for discussing the affinities of *Gilia scopulorum*, *G. stellata*, and *G. yorkii*, a phylogenetic hypothesis for these species derived from a combined analysis of the nuclear ITS-1 and ITS-2 regions and the chloroplast *trnD-trnT* and *psbM-trnD* spacers (Shaw et al., 2005) is presented here. In addition to these three species, the sampling incorporated representatives of all genera of Gilieae (Porter & Johnson, 2000), including four species from each of the two sections of *Gilia* and each taxon in the genus *Saltugilia* (Appendix 1). Two species of *Aliciella* Brand, which fall outside of tribe Gilieae (Porter & Johnson, 2000), were used as outgroups. Sequences were obtained following the methods of Johnson and Weese (2000) and have been deposited in GenBank (Appendix 1). Parsimony analyses were conducted using PAUP* (Swofford, 1998). Analyses recovered four most parsimonious trees of 746 steps that differ only in the placement of *Lathrocasis* L. A. Johnson and in the relationship of *S. caruifolia* and *S. splendens* subsp. *splendens* relative to other *Saltugilia* (Fig. 1). With respect to *G. scopulorum*, *G. stellata*, and *G. yorkii* relative to their relationship to core *Saltugilia*, the same pattern of relationships shown in Figure 1 is recovered by analyses of the nuclear and chloroplast data separately. It is clear from these data that the chloroplast and ITS regions of *G. scopulorum*, *G. stellata*, and *G. yorkii* are genealogically close to *Gilia* s. str. and substantially divergent from *Saltugilia*. An analysis of partial sequences from a nuclear *idh* gene shows a similar pattern of affinities, though *G. yorkii* was not included in that analysis (Weese & Johnson, 2005).

The most thorough discussion of the relationship between *Gilia scopulorum*, *G. stellata*, and species now recognized as *Saltugilia* suggests similarity between *G. stellata* and *S. australis* (Mason & Grant, 1948: their *G. splendens* subsp. *australis*) in lower leaf form and flower size and color. However, leaf form in *G. stellata* cannot be distinguished from many members of *Gilia* sect. *Arachnion* A. D. Grant & V. E. Grant (e.g., *G. cana* and *G. leptantha* Parish), and neither flower size nor color is uniquely shared by these two species. Instead, in addition to DNA sequences (Fig. 1), *G. scopulorum* and *G. stellata* are distinguished from *Saltugilia* by rounded, rather than cylindrical capsules enclosed by a calyx that tends to be accrescent, rather than rupturing with age (Mason & Grant, 1948). They differ also in their calyx and pedicel glands: those in *Saltugilia* are short stalked, with a head that is generally wider than the gland is tall, whereas *G. scopulorum* and *G. stellata* have glands that are longer than broad (Porter & Johnson, 2000; Weese & Johnson, 2001). Furthermore, whereas these glands extend the entire length of the pedicel in *Saltugilia*, they are clustered most densely just below the calyx in *G. scopulorum* and in *G. stellata* such that the lower portion of long pedicels is frequently glabrous. Such clustering of pedicel glands is not uncommon in *Gilia* sect. *Arachnion*. Section *Arachnion* are diverse in their bearing and distribution of inflorescence glands, but when glands are present, they are longer than broad. Johnson et al. (2004) demonstrated that seed coat ornamentation parallels the trends above. *Saltugilia* have verrucate seed coats

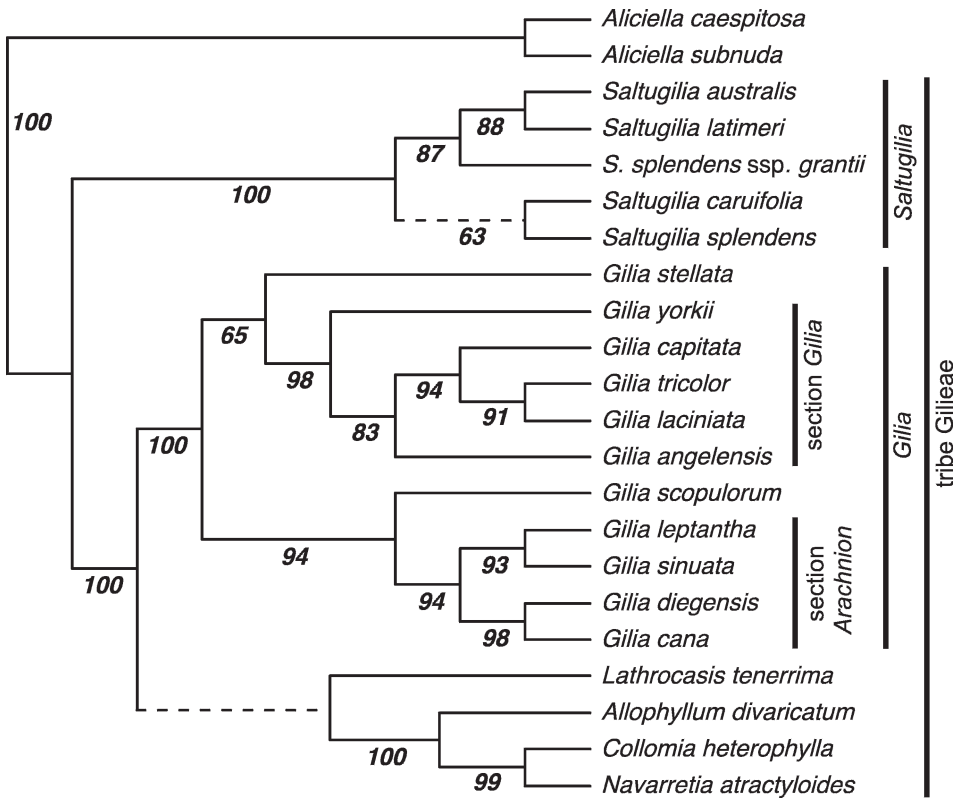

Figure 1. One of four most parsimonious trees recovered from a combined parsimony analysis of nuclear ITS-1 and -2 sequences, and chloroplast *trnD-trnT* and *psbM-trnD* regions (consistency index = 0.87; retention index = 0.92). The topology shown matches the single most parsimonious tree recovered by analyses of these same data with the outgroup excluded. Branches that collapse on the strict consensus of the four most parsimonious trees are indicated with a dashed line. Numbers below branches are bootstrap values from 1000 replications of full heuristic searches.

with caulifloriform verrucae, whereas *G. scopulorum* and *G. stellata*, like other *Gilia* s. str. (as well as *Allophyllum* (Nuttall) A. D. Grant & V. E. Grant, *Navarretia* Ruiz & Pavón, and *Collomia* Nuttall), lack these features of ornamentation.

Relatively recently described, *Gilia yorkii* was placed in section *Saltugilia* based on suggested similarity between it and *G. scopulorum*, not due to similarity with core *Saltugilia* (Shevock & Day, 1998). Like *G. scopulorum*, *G. yorkii* lacks caulifloriform verrucae on its seed coats (Johnson et al., 2004) and is widely divergent in DNA sequence from the genus *Saltugilia* (Fig. 1). However, comparative DNA sequencing indicates a closer relationship between *G. yorkii* and *Gilia* sect. *Gilia* than with *G. scopulorum* (Fig. 1). Significantly, there was no comparative evaluation made between *G. yorkii* and *Gilia* sect. *Gilia* by Shevock and Day (1998), yet I can find no morphological feature that unambiguously excludes *G. yorkii* from this section. For example, although *Gilia* sect. *Gilia* tend to have linear leaf segments, many collections of *G. capitata* Sims have broad leaf lobes like *G. yorkii*. Similarly, whereas *Gilia* sect. *Gilia* tend to have flowers in heads or clusters, *G. tricolor* Bentham, like *G. yorkii*, does not. The pedicel glands of *G. yorkii* are also minute, spheric (with four terminal cells), stalked, and studded along the entire length of the pedicels as in *G. tricolor* and *G. laciniata* Ruiz & Pavón. *Gilia scopulorum*, in contrast, has stout pedicels with large, stalked, flat-topped glands (composed of many terminal cells) clustered along the pedicel predominantly just beneath the calyx.

Available evidence suggests that *Gilia stellata*, *G. scopulorum*, and *G. yorkii* be removed from *Saltugilia* at any rank. Affinities with *Gilia* s. str. are clear. Within *Gilia*, this author suggests *G. scopulorum* and *G. stellata* be placed, at present, without sectional affiliation. *Gilia stellata* and *G. scopulorum* represent early diverging lineages of *Gilia*—lineages that diverged before the synapomorphies currently recognized as circumscribing sections *Arachnion* and *Gilia* evolved in other lineages that subsequently diversified into the specious complexes we recognize by these names today. This treatment allies *G. stellata* and *G.*

scopulorum in a natural group, *Gilia*, in agreement with all present evidence, yet avoids the naming of redundant taxa (i.e., two monotypic sections) or the placement of both species into a single section when there are no demonstrated synapomorphies for these taxa exclusive of other *Gilia*. *Gilia yorkii* should be placed within section *Gilia*, where it shares DNA synapomorphies, features of glandular and eglandular trichome kind and distribution, and where characters that exclude its circumscription are lacking.

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Appendix 1

Vouchers for samples used in DNA sequence analysis (Fig. 1). Taxa are listed alphabetically with collector, herbarium where voucher is deposited, and corresponding GenBank accession numbers given in the order: ITS, *trnD-trnT*, *psbM-trnD*.

Aliciella caespitosa (A. Gray) J. M. Porter, *Anderson & Armstrong 447* (BRY), EF199698, EF199676, EF199654; *Aliciella subnuda* (Torrey ex A. Gray) J. M. Porter, *Clark 05-113* (BRY), EF199699, EF199677, EF199655; *Allophyllum divaricatum* (Nuttall) A. D. Grant & V. E. Grant, *Johnson 04-128* (BRY), EF199700, EF199695, EF199673; *Collomia heterophylla* Hooker, *Johnson 94-076* (BRY), AY997922, EF199696, EF199674; *Gilia angelensis* V. E. Grant, *Johnson 93-029* (BRY), AF208202, EF199686, EF199664; *Gilia cana* (M. E. Jones) A. Heller, *Johnson 93-016* (WS), AF208204, EF199692, EF199670; *Gilia capitata* Sims, *Johnson 92-015* (WS), AF208206, EF199685, EF199663; *Gilia diegensis* (Munz) A. D. Grant & V. E. Grant, *Johnson 93-030* (BRY), EF199706, EF199691, EF199669; *Gilia laciniata* Ruiz & Pavón, *Morrell 403* (RSA), AF208208, EF199688, EF199666; *Gilia leptantha* Parish, *Johnson 93-045* (CAS), EF199705, EF199690, EF199668; *Gilia scopulorum* M. E. Jones, *R. Johnson 304* (BRY), AF208209, EF199689, EF199667; *Gilia sinuata* Douglas ex Bentham, *Johnson 92-004* (WS), EF199707, EF199693, EF199671; *Gilia stellata* A. Heller, *Johnson 93-059* (WS), AF208212, EF199683, EF199661; *Gilia tricolor* Bentham, *Schultz 93-029* (WS), EF199704, EF199687, EF199665; *Gilia yorkii* Shevock & A. G. Day, *Johnson s.n.* (BRY-484805), EF199703, EF199684, EF199662; *Lathrocasis tenerrima* (A. Gray) L. A. Johnson, *Johnson 93-103* (WS), AF208213, EF199694, EF199672; *Navarretia atractyloides* (Bentham) Hooker & Arnott, *Johnson 04-019* (BRY), EF199708, EF199697, EF199675; *Saltugilia australis* (H. Mason & A.

D. Grant) L. A. Johnson, *Johnson 97-004* (BRY), EF199701, EF199678, EF199656; *Saltugilia caruifolia* (Abrams) L. A. Johnson, *Johnson 93-092* (BRY), AY997940, EF199680, EF199658; *Saltugilia latimeri* T. L. Weese & L. A. Johnson, *Johnson 92-021* (BRY), AY997945, EF199679, EF199657; *Saltugilia splendens* (Douglas ex H. Mason & A. D. Grant) L. A. Johnson, *Johnson 94-035* (BRY), EF199702, EF199681, EF199659; *Saltugilia splendens* (Douglas ex H. Mason & A. D. Grant) subsp. *grantii* (Brand) L. A. Johnson, *Johnson 96-008* (BRY), AY997955, EF199682, EF199660.