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A SYNOPSIS OF IPOMOPSIS

VERNE GRANT

HISTORY OF THE GENUS

The genus *Ipomopsis* was originally established by Michaux in 1803 for a species of Polemoniaceae of the southeastern United States now known as *I. rubra*. Nuttall (1818) subsequently transferred a western species, *aggregata*, to the same genus. Although the assignments made by Michaux and Nuttall were, in the judgment of several students including myself, correct in principle, they were improperly implemented from the nomenclatural point of view. Wherry accordingly published the combination *Ipomopsis rubra* in 1936, and a number of other transfers to *Ipomopsis* are made in the present paper.

Behind these name changes lies a long history of dissatisfaction with the classification of *I. rubra* and the *I. aggregata* group in other genera, such as *Pblox*, *Cantua*, *Loeselia*, and particularly *Gilia*, in which they do not fit. Among the botanists who have disagreed expressly or implicitly with assignment of this *rubra-aggregata* assemblage to *Gilia* have been Pursh (1814), Nuttall (1818), Michaux (1820), Lindley (1829), Rafinesque (1832), Greene (1905), Flory (1937), and Wherry (1936, 1938, 1946). My own study of the genus problem in the Polemoniaceae has convinced me also that the *I. aggregata* group should be separated generically from *Gilia*, and has prompted the following synopsis of *Ipomopsis*.

The discovery some years ago of cytological resemblances between *Ipomopsis aggregata* and the plant currently known as *Gilia congesta* led to a search for other morphological similarities between these superficially very different forms. This search was rewarded by the finding of a number of common characteristics, which suggested that the two species were more closely related than had formerly been supposed. A reinvestigation of *Loeselia tenuifolia*, *Gilia multiflora*, *Leptodactylon gloriosum*, and some of the small annual desert *Gilias* (*G. polycladon*, *G. pumila*, etc.) indicated that they too belong to the *Ipomopsis alliance*. Continued study in the field, herbarium and garden with these ideas in mind has resulted in an amplified concept of *Ipomopsis* as a genus.

The common features of the various species groups now proposed for inclusion in *Ipomopsis*, together with their collective differences from *Gilia* proper, are summarized in the following tabulation.

Character	<i>Gilia</i>	<i>Ipomopsis</i>
1. Center of distribution	California	Rocky Mountains and adjacent plains.
2. Duration	Mostly annuals, some biennials and perennials.	Biennials and perennials, some annuals.
3. General aspect	Upper cauline leaves usually much reduced, the flowering stems in consequence usually naked. Herbage gray green to yellowish green.	Upper parts of stem clothed with well developed leaves. Herbage gray green to dark bluish green.
4. Leaves	Usually soft-textured but sometimes leathery. Dissection usually complex and the arrangement of lobes irregular. Tips of lobes usually not conspicuously mucronate.	Leathery to stiffish. Once pinnate with a regular arrangement of simple segments. Tips of lobes bearing horny mucros.

5. Inflorescence	More or less determinate. Bracts subtending groups of flowers or the whole inflorescence.	Indeterminate. Bracts subtending the individual flowers.
6. Corolla	Funnelform, usually with an expanded throat, tube relatively narrow. Marked by spots or streaks, but not flecked. Veins usually anastomosing so as to enclose regular areas in the throat.	Salverform, without a throat, tube relatively broad. Flecked with red or violet. Veins usually not anastomosing.
7. Seeds	Small, spheroidal, brown.	Usually long, slender, gently curved, pale waxy; rarely small and spheroidal.
8. Chromosome number	$x = 9$, rarely $x = 8$; polyploidy fairly common.	$x = 7$; polyploidy quite rare.
9. Breeding behavior	Predominantly self-compatible.	Predominantly self-incompatible.

The foregoing comparison shows that there are a number of fairly constant character differences between the two phylads in all parts of the plants. *Ipomopsis* seems to be as distinct from *Gilia* as is *Eriastrum* or *Langloisia* or *Navarretia*. If the system of classification is to be internally consistent, therefore, the only alternative to recognizing *Ipomopsis* as a genus is to treat it and *Eriastrum*, *Langloisia*, etc. as subgenera of *Gilia*. Phylogenetically it does not matter whether we recognize a tribe *Gilieae* composed of the genera *Gilia*, *Ipomopsis*, *Eriastrum*, *Linanthus*, etc., or one inclusive genus with subgenera. The main criterion for deciding between the alternative dispositions is convenience in practical classification.

An inclusive genus *Gilia* was tried out in the era of Bentham and Gray and was found to be inconvenient and unworkable. There is a good deal of truth mixed with exaggeration in Greene's statement (1896) that "the *Gilia* of the Synoptical Flora . . . would not have been much worse, as a pretended genus, if the author had put into it the entire family of the Polemoniaceae." Gray's (1886) attempt to reduce most of the family to *Gilia* was no more successful than Kuntze's later (1898) attempt to reduce it to *Polemonium*. In either case the genus came to include too many diverse groups to be meaningful as a generic name. A retreat from Gray's inclusive concept of *Gilia* and a breakup of this assemblage into several segregate genera has been forced upon several generations of students of Polemoniaceae by practical considerations. Even after the recent removal of *Allophyllum* by Grant and Grant (1955) and the proposed segregation of *Ipomopsis*, *Gilia* remains second only to *Pbiox* in size and second to none in heterogeneity.

There are morphological notes on species of *Ipomopsis* by Darwin (1877, ch. 3), Brand (1907, p. 12), and Martin (1946). An ecological note is given by Wherry (1936). Observations on flower pollination have been made by Ferguson (1921), Wherry (1936), and Grant (unpubl.). Chromosome counts have been published by Flory (1937); additional counts obtained by Hunziker, Grant and Latimer will be published in a future contribution. Studies of artificial and natural hybridization have been commenced by Grant and Grant. Several species of *Ipomopsis* are very attractive and have been brought into cultivation to some extent as garden ornaments. Horticultural notes are given by Bonstedt (1932), Bailey and Taylor (1933), and Wherry (1936). Attempts are being made at the Rancho Santa Ana Botanic Garden to breed forms of greater attractiveness and easier culture.

The taxonomy of *Ipomopsis* is at present in a rather unsatisfactory state. Incomplete accounts exist for different species groups by Wherry (1936, 1946), Constance and Rollins (1936), and Kearney and Peebles (1943). The South American species, *I. gossypifera*, is discussed by Reiche (1910) and Borsini (1942). A cooperative

program of field and herbarium studies designed to clear up some of the problems in the *Ipomopsis aggregata* group is currently underway by G. Thomas Robbins of the University of California, Alva Grant, and myself. Work is also proceeding on other groups in the genus.

In the following paragraphs I have attempted to circumscribe the genus *Ipomopsis* and to divide it into sections. The most commonly used specific names are placed in the new combinations at the end of the paper so that they can be available for published discussion. These steps serve to set the genus up as a working unit. On the other hand, a number of good taxa such as *macrosiphon*, *texana*, *whitingi*, etc. are not being transferred at this time because of uncertainty, pending the outcome of revisional studies, as to their position and rank in the system.

SYNOPSIS

IPOMOPSIS Michx.

Ipomopsis Michx., Fl. Bor. Am., ed. 1, 1: 141, 1803; type *Ipomopsis elegans* Michx.
(=*Ipomopsis rubra* (L.) Wherry).

Ipomeria Nutt., Gen. N. Am. Pl. 1: 124, 1818; type *Cantua coronopifolia* Willd.
(=*Ipomopsis rubra* (L.) Wherry).

Batanthes Raf., Atl. Jour. 1: 145, 1832; type here selected as *Cantua aggregata* Pursh.

Callisteris Greene, Leaf. Bot. 1: 159, 1905; type here selected as *Cantua aggregata* Pursh.

Perennial, biennial or annual herbs, often with a basal rosette of leaves and with leafy stems, and one shrub. Herbage frequently villous, sometimes with stipitate glands, or sometimes glabrous. Leaves pinnatifid, the lateral segments well developed or some times reduced, the tips of the segments bearing horny mucros. Inflorescence cymose, varying from loosely racemose to tightly congested, bracteate, each individual flower ordinarily subtended by a bract. Calyx consisting of herbaceous mucronate lobes joined by broad hyaline sinuses, villous, glandular or glabrous. Corolla salverform or tubular, the veins branching in the tube and limb and usually not anastomosing, violet, red, white, or varying shades of yellow or pink. Stamens inserted in the tube or in the sinuses of the corolla, often unequal in length and point of insertion, sometimes declined, the anthers exerted or included, pollen blue, white or yellow. Capsules freely or tardily dehiscent, the locules containing 1 or 2 to several seeds each. Seeds long and slender, often bent, to spheroidal, rounded or angular, white or brown, the surface smooth or corrugated. Basic chromosome number $x=7$.

A genus of approximately 23 species. Rocky Mountains and adjacent plains, south to Texas and Mexico, west to the Pacific Coast and Southwest, east to Florida and the Carolinas, recurring with one species in the Argentine Andes and Patagonia. Related to *Gilia* and *Eriastrum*.

(i) *Ipomopsis* sect. *Phloganthea* (Gray) V. Grant, comb. nov.

Fig. 1

Collomia sect. *Phloganthea* Gray, Proc. Amer. Acad. 8: 260, 1870;

type here selected as *Phlox pinnata* Cav.

Loeselia sect. *Giliopsis* Gray, Proc. Amer. Acad. 11: 86, 1876;

type here selected as *Loeselia tenuifolia* Gray.

Loeselia subg. *Giliopsis* Gray ex Peter, Nat. Pflzfam. 4 (3a): 54, 1891.

Spreading perennials with numerous slender stems from base, lacking a conspicuous basal rosette of leaves in mature plants; or low rounded shrubs. Corolla slightly zygomorphic, violet or red-violet or white, tube long to medium-long. Stamens long exerted. Pollen blue. Southwest and Mexican highland. *Ipomopsis gloriosa*, *bavardi*, *multiflora*, *pinnata*, *polyantha*, and *tenuifolia*.



Fig. 1. *Ipomopsis tenuifolia*. (from Brand, Das Pflanzenreich).
(Habit x 1; flower x 2).

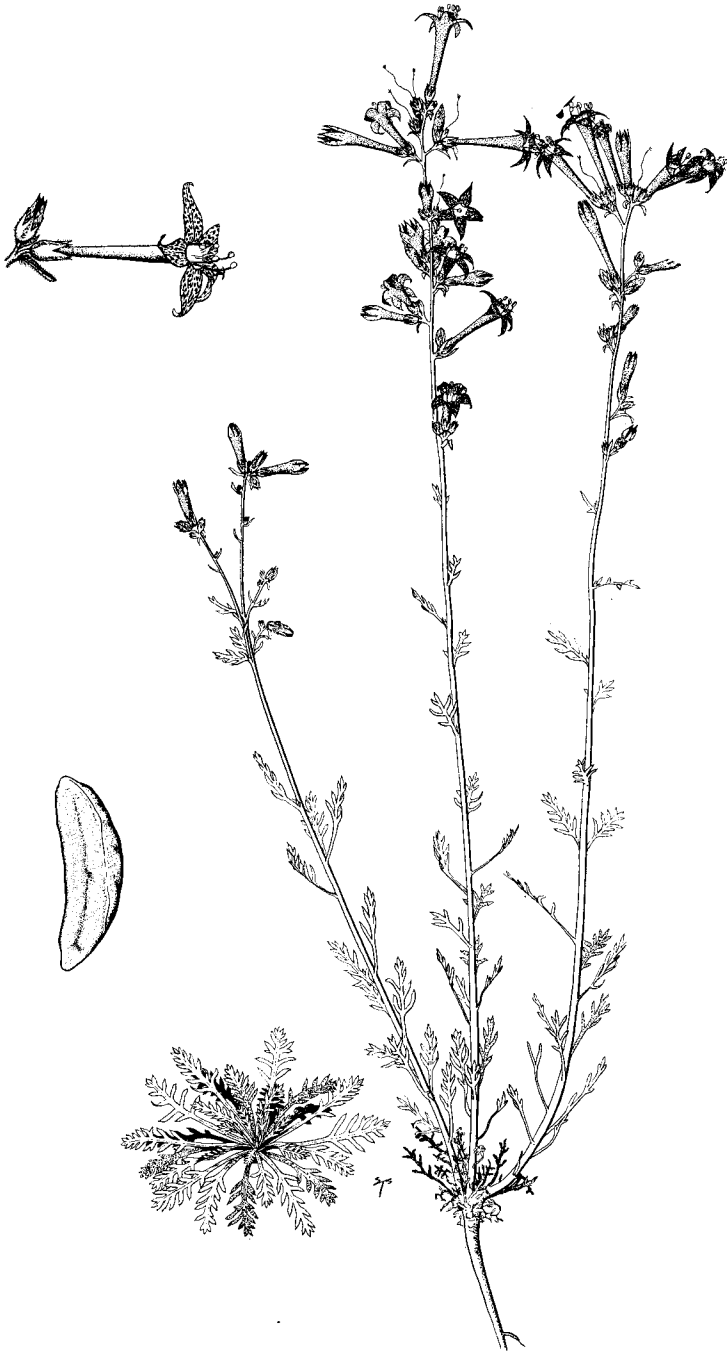


Fig. 2. *Ipomopsis aggregata*, Sierra Nevada race. (Original).
(Habit x 0.4; flower x 0.8; seed x 9).



Fig. 3. *Ipomopsis tenuituba*, Kaibab Plateau. (Original).
(Habit x 0.4; flower x 0.8).

(ii) IPOMOPSIS sect. IPOMOPSIS.

Figs. 2, 3

Ipomopsis Michx., loc. cit.*Ipomeria* Nutt., loc. cit.*Batanibes* Raf., loc. cit.*Callisteris* Greene, loc. cit.*Gilia* sect. *Ipomopsis* Benth., Bot. Reg. 19: sub t. 1622, 1833.*Gilia* subg. *Ipomopsis* Milliken, U.C. Publ. Bot. 2: 24, 1904.*Gilia* ser. *Aggregatae* Rydb., Fl. Rocky Mts., ed. 1, 691, 1917; type*Cantua aggregata* Pursh.*Gilia* ser. *Longiflorae* Rydb., op. cit. 691; type *Cantua longiflora* Torr.

Perennials, biennials and 2 annuals. Habit erect and fairly tall with one to several stout stems from base, a basal rosette present. Corolla regular, red, yellow, white or pinkish, the tube long. Stamens exerted or included. Pollen blue or yellow. Rocky Mountain region to Florida and the Pacific coast. In western North America: *Ipomopsis aggregata* and its allies, *laxiflora*, *longiflora*, *macombii*, *tenuituba thurberi*. In southeastern North America: *I. rubra*.

(iii) *Ipomopsis* sect. *Microgilia* (Benth.) V. Grant, comb. nov.

Figs. 4, 5, 6

Gilia sect. *Microgilia* Benth., DC. Prodr. 9: 315, 1845; type*Gilia minutiflora* Benth.*Collomia* sect. *Picracolla* Nutt., Jour. Acad. Nat. Sci. Philadelphia, ser. 2, 1: 159, 1848; type *Collomia linoides* Nutt. (= *Gilia minutiflora* Benth.).*Gilia* sect. *Elaphocera* Nutt., op. cit. 155; type here selected as *Gilia congesta* Hook.*Gilia* subg. *Elaphocera* Milliken, U. C. Publ. Bot. 2: 24, 1904.*Navarretia* subg. *Hugelia* sect. *Langloisiastrum* Brand, Pflzr. 250: 168, 1907;type *Gilia wrightii* Gray.*Gilia* ser. *Congestae* Rydb., Fl. Rocky Mts., ed. 1, 690, 1917; type *Gilia congesta* Hook.*Gilia* ser. *Pumilae* Rydb., op. cit. 691; type *Gilia pumila* Nutt.*Gilia* ser. *Minutiflorae* Rydb., op. cit. 692; type *Gilia minutiflora* Benth.

Annuals and perennials. Habit low with simple stems or branching from base, a basal rosette present or absent. Corolla regular, white or violet, the tube quite short. Stamens short, slightly exerted or included. Pollen blue. Rocky Mountain region to the Pacific slope and Mexico, and in Argentina and Chile. In North America: *Ipomopsis congesta*, *depressa*, *frutescens*, *gunnisonii*, *minutiflora*, *polycladon*, *pumila*, *roseata*, *sonorae*, *spicata*. In South America: *I. gossypifera*.

NEW COMBINATIONS IN IPOMOPSIS

IPOMOPSIS SECT. PHLOGANTHEA (GRAY) V. GRANT

1. *Ipomopsis gloriosa* (Brandege) A. Grant, comb. nov.*Gilia gloriosa* Brandege, Proc. Calif. Acad. Sci., new ser., 2: 184, t. 9, 1889;*Leptodactylon gloriosum* Wherry, 1945.2. *Ipomopsis havardi* (Gray) V. Grant, comb. nov.*Loeselia havardi* Gray, Proc. Amer. Acad. 19: 87, 1883;*Gilia havardi* Gray, 1886.3. *Ipomopsis multiflora* (Nutt.) V. Grant, comb. nov.*Gilia multiflora* Nutt., Jour. Acad. Nat. Sci. Philadelphia, ser. 2, 1: 154, 1848.4. *Ipomopsis pinnata* (Cav.) V. Grant, comb. nov.*Pblox pinnata* Cav., Icones 6: t. 528, 1801; *Gilia pinnata* Brand, 1907.5. *Ipomopsis polyantha* (Rydb.) V. Grant, comb. nov.*Gilia polyantha* Rydb., Bull. Torr. Bot. Club 31: 634, 1904.6. *Ipomopsis tenuifolia* (Gray) V. Grant, comb. nov.*Loeselia tenuifolia* Gray, Proc. Amer. Acad. 11: 86, 1876;*Gilia tenuifolia* Gray, 1886.



Fig. 4. *Ipomopsis spicata*. (from Brand, Das Pflanzenreich).
(Habit x 0.5; flower x 3).

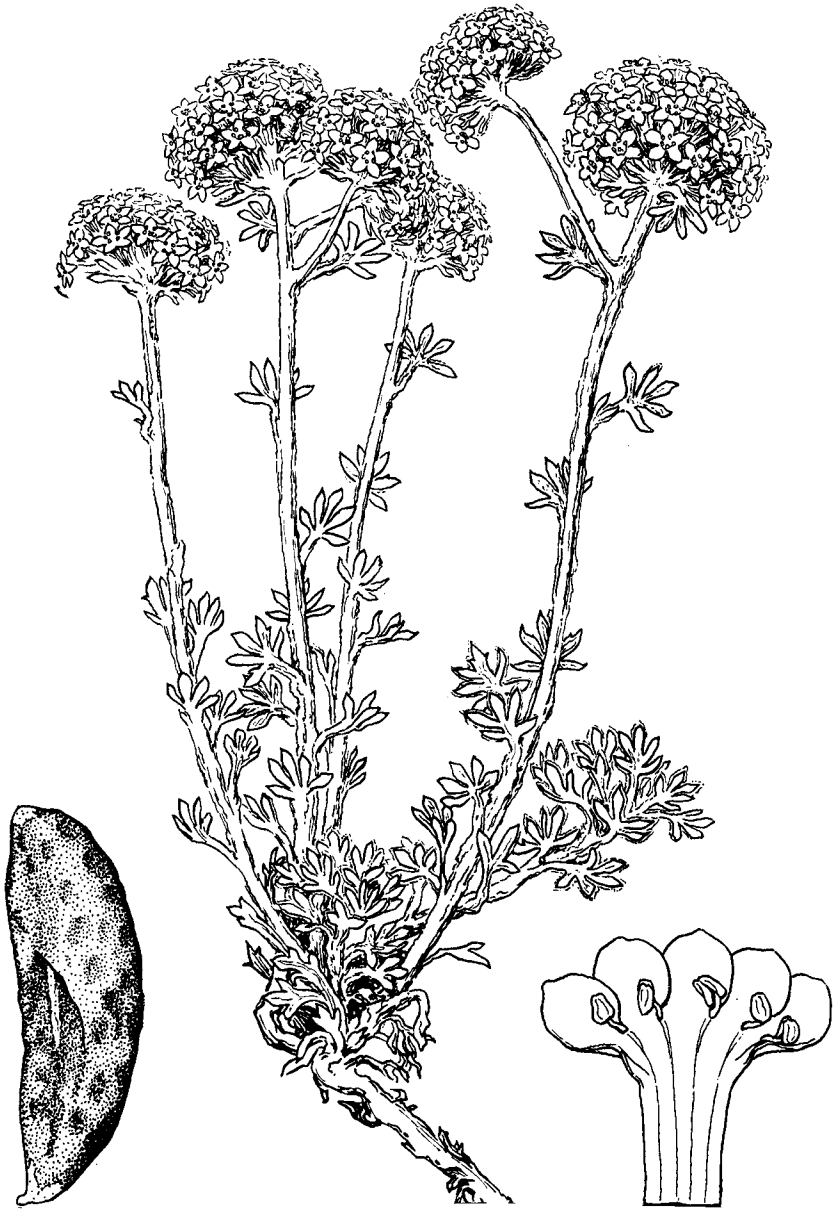


Fig. 5. *Ipomopsis congesta*. (from Abrams, Illustrated Flora; seed original).¹
(Habit x 1; seed x 20).

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Fig. 6. *Ipomopsis polycladon*. (from Abrams, Illustrated Flora). (Habit x 1).

IPOMOPSIS SECT. IPOMOPSIS

7. *Ipomopsis aggregata* (Pursh) V. Grant, comb. nov.
Cantua aggregata Pursh, Fl. Amer. Sept. 1: 147, 1814;
Ipomeria aggregata Nutt., 1818; *Gilia aggregata* Spreng., 1825.
- 7a. *Ipomopsis aggregata* ssp. *attenuata* (Gray) V. & A. Grant, comb. nov.
Gilia aggregata var. *attenuata* Gray, Syn. Fl. 2 (1): 145, 1878.
- 7b. *Ipomopsis aggregata* ssp. *candida* (Rydb.) V. & A. Grant, comb. nov.
Gilia candida Rydb., Bull. Torrey Bot. Club 28: 29, 1901.

- 7c. *Ipomopsis aggregata* ssp. *bridgesii* (Gray) V. & A. Grant, comb. nov.
Gilia aggregata var. *bridgesii* Gray, Proc. Amer. Acad. 8: 276, 1870.
- 7d. *Ipomopsis aggregata* ssp. *arizonica* (Greene) V. & A. Grant, comb. nov.
Callisteris arizonica Greene, Leaf. 1: 160, 1905; *Gilia arizonica* Rydb., 1913;
Gilia aggregata var. *arizonica* Fosb., 1942.
8. *Ipomopsis laxiflora* (Coul.) V. Grant, comb. nov.
Gilia Macombii var. *laxiflora* Coul., Contr. U.S. Nat. Herb. 1: 44, 1889;
Gilia laxiflora Osterh., 1897.
9. *Ipomopsis longiflora* (Torr.) V. Grant, comb. nov.
Cantua longiflora Torr., Ann. Lyc. New York 2: 221, 1826;
Gilia longiflora Don, 1837.
10. *Ipomopsis macombii* (Torr.) V. Grant, comb. nov.
Gilia macombii Torr. ex Gray, Proc. Amer. Acad. 20: 301, 1885.
11. *Ipomopsis tenuituba* (Rydb.) V. Grant, comb. nov.
Gilia tenuituba Rydb., Bull. Torrey Bot. Club 40: 472, 1913.
12. *Ipomopsis thurberi* (Torr.) V. Grant, comb. nov.
Gilia thurberi Torr. ex Gray, Proc. Amer. Acad. 8: 261, 1870.

IPOMOPSIS SECT. MICROGILIA (BENTH.) V. GRANT

13. *Ipomopsis congesta* (Hook.) V. Grant, comb. nov.
Gilia congesta Hook., Fl. Bor. Amer. 2: 75, 1838.
- 13a. *Ipomopsis congesta* ssp. *montana* (Nels. & Kennedy) V. Grant, comb. nov.
Gilia montana Nels. & Kennedy, Proc. Biol. Soc. Wash. 19: 37, 1906;
Gilia congesta var. *montana* Const. & Roll., 1936.
14. *Ipomopsis depressa* (Jones) V. Grant, comb. nov.
Gilia depressa Jones ex Gray, Proc. Amer. Acad. 16: 106, 1880.
15. *Ipomopsis frutescens* (Rydb.) V. Grant, comb. nov.
Gilia frutescens Rydb., Bull. Torrey Bot. Club 40: 471, 1913.
16. *Ipomopsis gossypifera* (Gill.) V. Grant, comb. nov.
Gilia gossypifera Gill. ex Benth., DC. Prodr. 9: 310, 1845.
17. *Ipomopsis gunnisonii* (Torr. & Gray) V. Grant, comb. nov.
Gilia gunnisonii Torr. & Gray, Pacific Railw. Report 2: 129 & t. 9, 1855.
18. *Ipomopsis minutiflora* (Benth.) V. Grant, comb. nov.
Gilia minutiflora Benth., DC. Prodr. 9: 315, 1845.
19. *Ipomopsis polycladon* (Torr.) V. Grant, comb. nov.
Gilia polycladon Torr., Bot. Mex. Bound. 146, 1859.
20. *Ipomopsis pumila* (Nutt.) V. Grant, comb. nov.
Gilia pumila Nutt., Jour. Acad. Nat. Sci. Philadelphia, ser. 2, 1: 156, 1848.
21. *Ipomopsis roseata* (Rydb.) V. Grant, comb. nov.
Gilia roseata Rydb., Bull. Torrey Bot. Club 31: 633, 1904.
22. *Ipomopsis sonora* (Rose), A. Grant, comb. nov.
Gilia sonora Rose, Contrib. U. S. Nat. Herb. 1: 90, 1890.
23. *Ipomopsis spicata* (Nutt.) V. Grant, comb. nov.
Gilia spicata Nutt., Jour. Acad. Nat. Sci. Philadelphia, ser. 2, 1: 156, 1848.
- 23a. *Ipomopsis spicata* ssp. *capitata* (Gray) V. Grant, comb. nov.
Gilia spicata var. *capitata* Gray, Proc. Amer. Acad. 8: 274, 1870.

SUMMARY

A number of species of Polemoniaceae are distinguished from the rest of the family by their perennial habit, leafy stems, pinnatisect leaves, individually bracted flowers, throatless salverform corollas, waxy arcuate seeds, and 7 pairs of large chromosomes. The 23 species which either exhibit these characteristics or show relationships by reduction to other species that do are distributed in current classifications among several subgenera and sections of *Gilia* and in *Loeselia* and *Leptodactylon*. Their removal from their present positions makes those genera more natural. The grouping of the 23 species together in one taxon gives expression for the first time

to their interrelationships. This taxon, *Ipomopsis*, is regarded as worthy of generic rank on the basis of a consideration of the degree of distinctness of other polemoniaceous genera. The transfer of a large series of species to the new genus *Ipomopsis* will work a temporary inconvenience on botanists in the western states; but against this inconvenience must be set the advantage to be gained by having a more natural and workable system of classification.

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