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THE GENUS *ALLOPHYLLUM* (POLEMONIACEAE)

ALVA GRANT AND VERNE GRANT

INTRODUCTION

The genus *Allophyllum*, or the "*Gilia gilioides* complex" of the manuals, comprises a small and inconspicuous, but highly variable group of annual herbs in the mountainous regions of California and the bordering states. This group affords favorable material for studies of natural and artificial hybridization. The species have overlapping ranges and introgressive hybridization has occurred between them. The plants can be handled easily in the experimental garden. There are many well defined character differences which can be used as markers of the genetic differences. Fertility barriers are weak so that large F_2 and backcross populations can be grown and analyzed.

Not the least important advantage of *Allophyllum* for studies of the evolutionary role of natural hybridization is the fact that this genus is small and well isolated from any other phyletic line in the family. Where a large number of entities exist between which gene exchange can have occurred, as in the related genus *Gilia*, the number of possible hybrid combinations which the investigator must consider becomes so great that a phylogenetic analysis of the complex may be virtually impossible. No single species group can be considered as a unit in itself. Species outside the immediate group, and even species belonging in separate sections and subgenera, are potential sources of germplasm which may have contributed genes to the populations under investigation. The possibilities of hybridization are much simpler in a comparium of small size.

Field studies on natural hybridization and experimental studies of artificial hybridization in *Allophyllum* were begun in 1949 and are still underway. A discussion of the results obtained from these studies must necessarily be conducted within an adequate taxonomic framework. Existing treatments do not conform well with the true nature of the group. Our first task, therefore, has been to devise a new and more natural taxonomic arrangement. This has involved decisions of two orders relating respectively to the minor systematics of the group and to its status in the systematic hierarchy. The solution to the first problem seems to be the recognition of five species in place of the one or two polytypic species listed in the manuals. The solution offered for the second problem is the elevation of the group out of *Gilia* to the level of an independent genus, *Allophyllum*. A systematic revision of *Allophyllum*, embodying the new proposals, is set forth in the present paper. The formal treatment is preceded by a discussion of the reasons for making the various taxonomic changes.

The problem was discussed with Prof. Herbert L. Mason who has studied the group extensively in the field and has long advocated a thorough analysis of its variations. Dr. Mason kindly read and criticized the manuscript. Many nomenclatural problems were discussed with Prof. Philip A. Munz, to whom thanks are also due.

GENERAL DESCRIPTION

The *Allophyllums* are leafy annuals with more or less glutinous and sometimes odorous herbage. The small blue-violet, red-violet or white flowers are borne near the ends of leafy stems. The stamens are usually unequally inserted in the corolla tube. The seeds are large and black and are borne singly or in pairs in the locules

of the capsules. The few (unpublished) chromosome counts so far obtained indicate that the species are diploid with $n=8$ and 9.

The species fall into two main series. *Allophyllum giliioides* and *A. violaceum* are small plants with narrow, almost linear leaf segments; lightly pubescent stems; small, regular, dark blue-violet corollas with included stamens; and a chromosome number of $n=9$ (figs. 1, 7). These plants occur in open sunny places in the mountains from southern Oregon, through California, to Arizona and Nevada.

Fig. 1. Flowers of *Allophyllum*. A—*A. divaricatum*, Sierra Nevada race from Groveland. B—*A. divaricatum*, San Gabriel race from Claremont. C—*A. glutinosum*, from Santa Ana Mts. D—*A. integrifolium*, from Kern River. E—*A. giliioides*, from Pinnacles National Monument. All localities in California; all to same scale.

A contrasting combination of characteristics is found in the second series. These are frequently large and robust plants with broad leaf segments, villous stems, and larger flowers. There are three species in this series. Ranging through the foothills and lower elevations of the Sierra Nevada, Coast Ranges, and San Gabriel Mountains is a tall form with an erect central leader, a regular corolla with a long slender reddish-violet or purple tube, and unequal stamens the longest of which may be well exerted beyond the orifice of the corolla tube. This is *A. divaricatum* ($n=8, 9$), (figs. 1, 3). The coastal mountains of southern California are inhabited by smaller plants with branches arising from the base; a short-tubed, pale blue-violet, two-lipped corolla; exerted and declined stamens and style; and a chromosome number of $n=9$. This is *A. glutinosum* (figs. 1, 6). At higher elevations in the Sierra Nevada and the San Bernardino and San Gabriel Ranges there occurs a sparingly branched plant with few leaves, few small white flowers, and included stamens and styles, which is recognized as *A. integrifolium* ($n=8, 9$), (figs. 1, 5).

THE SPECIES PROBLEM

The first author to deal with the "*giliioides* group," Bentham (1833, 1845), pro-

posed two species, *gilioides* and *glutinosum*.* Brand (1907) retained both of Bentham's species and took up two others, *traskiae* and *divaricatum*; in addition he added several new varieties of his own. Most authors, however, since the time of Gray (1870, 1878) have tended to place the whole group into just one species, *gilioides*, with one to three named varieties. In the words of Gray (1886: 408), the group is "very variable in size, form and division of leaves, and degree of viscidty, but apparently [is] all of one species." The most recent revision of the group by Mason and A. Grant (1948, 1951) maintained *gilioides* as a polytypic species composed of three subspecies, *gilioides*, *glutinosum*, and *volcanicum*.

The taxonomic studies of the present authors at first seemed to confirm the system of classification of Mason and A. Grant. The main morphological types in the group seemed to be adequately defined by the three names, *gilioides*, *glutinosum*, and *divaricatum* (= *volcanicum* in the treatment of Mason and A. Grant). Insofar as these units were found to reach their most extreme forms in separate geographical areas and apparently to intergrade in the zones of contact, it seemed appropriate to regard them as geographical races and hence to treat them as subspecies of one polytypic species. Artificial hybridization studies showed that the different morphological types could be intercrossed with ease to give fertile F_1 hybrids and wholly vigorous F_2 progeny.

A very different light was thrown on the problem by continued field studies, which showed that two or more of the different morphological types might occasionally occur sympatrically. Thus on Charlton Flat in the San Gabriel Mountains we discovered *glutinosum* growing together with *violaceum*. Both *divaricatum* and *glutinosum* occur in this mountain range, sometimes in the same canyon and rarely in a mixed population. On Mount Diablo in the San Francisco Bay area *divaricatum* and *gilioides* were found occurring several hundred feet apart. Three taxa, *divaricatum*, *violaceum* and *integrifolium*, were found growing side by side along the Kern River in the southern Sierra Nevada. Not far distant from this locality *gilioides* grows intermixed with *violaceum*. A perusal of herbarium sheets brought to light a number of mixed collections indicating sympatric occurrences of *divaricatum* and *gilioides* in the San Bernardino Mountains, *divaricatum* and *integrifolium* in the Sierra Nevada, and *integrifolium* and *violaceum* in the Sierra Nevada.

A careful distributional study of the *Allophyllums* based on herbarium specimens revealed some 36 localities where two or more dissimilar forms occur together in the same territory (fig. 2). In some of these cases the different entities grow side by side in the same colony; in others they occupy adjacent habitats a few hundred feet to a few miles apart. Morphologically different organisms which are sympatric may be different phenotypic aspects of some common basic genotype which has been exposed to different environmental influences during development, or genetically different individuals of the same variable population, or members of different reproductively isolated populations. The finding that the different entities of *Allophyllum* come true to type in progeny tests shows that they are neither formae nor variants of one polymorphic population. The remaining alternative is to regard them as distinct species.

The facts of distribution can be explained on the assumption that there are five species which occur sympatrically in every possible combination. The map in figure 2 shows the localities of the ten possible sympatric combinations of five species. This map shows a few localities where as many as three or four species occur to-

*In the interest of simplicity we will eliminate the generic name; the fact that Bentham's species were placed in the genus *Collomia* and Brand's in *Gilia*, etc., is irrelevant to the present discussion.

gether. In small areas in the San Gabriel and San Bernardino Mountains all five species of *Allophyllum* are found.

It is not the purpose of this paper to identify the isolating mechanisms which permit the different *Allophyllum*s to coexist in the same or adjacent habitats. For the taxonomic problem confronting us here it is sufficient to establish, from inferences from the distributional record, that such reproductive isolating mechanisms do exist between five entities, which we therefore treat as species.

Fig. 2. Map of the known sympatric occurrences of the species of *Allophyllum*.

GENERIC RELATIONSHIPS

Bentham (1833, 1845) placed the "*gilioides* group" in the genus *Collomia*. In this disposition he was at first followed by Gray (1870, 1879). The latter author, however, in his final treatment of the Polemoniaceae (Gray 1886) sank *Collomia* along with all the other temperate herbaceous genera except *Polemonium* and *Phlox* into the genus *Gilia*. This brought the "*gilioides* group" into the genus *Gilia* where it has remained ever since.

Gray's system of classification of the herbaceous Polemoniaceae has proved unnatural in theory and cumbersome in practice and is not now followed by any serious student of the family. For two recent critiques of Gray's concept of genera, see Wherry (1944) and Mason (1945). One by one the unnatural elements in Gray's collective genus *Gilia*, thus *Collomia*, *Linanthus*, *Navarretia*, *Eriastrum*, etc., have been reestablished as independent genera. Though the "*gilioides* group" has remained in *Gilia* during the course of all these transfers, it has usually been set apart in a special section (see below for a list of the sectional and subgeneric names). Mason & A. Grant (1948) gave the group subgeneric status and called attention to its distinctiveness.

Our studies support the original view of Bentham (op. cit.) and of Nuttall (1848) that the "*gilioides* group" is related to *Collomia*. This relationship is indicated by a large number of similarities. The cotyledons of *Allophyllum* are broad and oval with prominent raised veins and a notched apex; in *Collomia* the cotyledons are of the same shape and sometimes display a notch. The foliage of *Allophyllum* has a blue-green cast, is frequently glutinous and mephitic, and remains active well into the summer, as in *Collomia*. The leaf segments are broad and the stem hairs are long and shaggy in some members of both groups. The upper parts of the plant including the inflorescences are leafy. The corolla has the same general form and is sometimes reddish-violet. The stamens are unequally inserted and the point of insertion is inside the corolla tube. The locules of the capsules contain only one, two or three seeds which are ovoidal with a rounded blackish surface. The chromosome number of $n=8$, a relatively uncommon number in the family, is characteristic of *Collomia* and is found in *Allophyllum*. Of the species of *Allophyllum*, *A. divaricatum* appears to be the closest to *Collomia*.

Several of the foregoing characteristics define the whole *Collomia* phylad comprising (in our opinion) the genera *Polemonium*, *Collomia*, *Phlox*, *Microsteris*, and *Gymnosteris*. *Allophyllum* evidently belongs in this branch of the family tree. The pinnate dissection of the leaves and the presence in some species of $n=9$ may indicate that the *Allophyllum*s are closer in some respects to the annual *Polemonium*s than to *Collomia*. In other words, *Allophyllum* may have diverged from *Collomia* at some point close to the divergence of the latter from *Polemonium*, so that *Allophyllum* has retained resemblances to each.

The inclusion of the "*gilioides* group" in *Gilia*, based on tradition since the time of Gray, has in fact little else in its favor. The character resemblances which are sometimes cited in favor of the traditional arrangement are the basal rosette of some species of *Allophyllum*, the alternate leaves, the pinnate dissection of the leaves, the loose open inflorescence of some species, and particularly the type of calyx with herbaceous lobes connected by membranous sinuses. Inclusion of the "*gilioides* group" in *Gilia* on the basis of these characters will not stand analysis. When the sum total of leaf characters is taken into consideration, the leaves of *Allophyllum* are a good deal like those of *Collomia* and not at all like those of *Gilia*. The pinnate dissection could, as suggested above, have been inherited from a *Polemonium* ancestor. As regards the membranous sinuses of the calyx, this feature is found not

only in *Gilia* and its relatives, but also in some members of the *Collomia* phylad, particularly *Pblox*. Actually the shape and general aspect of the calyx lobes are strongly suggestive of a *Collomia* rather than of a *Gilia* type of calyx. Basal leaf tufts are sometimes developed in *Polemonium* and *Collomia*, and loose open inflorescences are found in some species of *Pblox*. No character has yet been found in *Allophyllum* which is not present elsewhere in the *Collomia* phylad.

Bentham (1845), Milliken (1904) and Brand (1907) placed *Microsteris gracilis*, and Gray (1886) placed *Collomia heterophylla* in the same section with the "*gilioides* group." There are indeed resemblances which account for this manner of treatment. But after studying the situation we are convinced that this trio does not form any natural grouping at all. The relationships of *Microsteris* (or *Pblox*) *gracilis* and *Collomia heterophylla* seem to be properly indicated by their present generic assignments. The points which they share in common with *Allophyllum gilioides* are probably the result of convergence in the direction of reduction by three members of the same phylad.

Attempts were made in 1950 and 1951 to cross two species of *Allophyllum* with *Microsteris gracilis* and *Collomia heterophylla*. No capsules and of course no hybrid seeds were obtained from the controlled pollinations. Crosses were also attempted between three species of *Allophyllum* and various species of *Gilia* § *Gilia*. Ten strains were intercrossed in 14 different combinations; approximately 90 flowers were cross-pollinated under controlled conditions. A few capsules ripened but these contained no hybrid seeds. These negative results cannot be regarded as conclusive since, in relation to the wideness of the crosses attempted, relatively few pollinations were made. The attempts to produce hybrids between *Allophyllum* and these other groups were abandoned at an early stage, however, precisely because our increasing understanding of the morphological relationships convinced us of the futility of further efforts to demonstrate close genetic affinity.

Of all the existing genera of Polemoniaceae only one, *Collomia*, can be seriously considered as an assemblage which might be expanded to include *Allophyllum*. *Allophyllum* and *Collomia* are indeed close; they are also different in respect to important characters of the calyx sinuses, leaf dissection, and inflorescence. *Collomia* as it now stands is a natural and well defined genus (see Wherry 1944). It would not be well defined if enlarged by the incorporation of *Allophyllum*. It is an open question whether the working taxonomist is any more inconvenienced by having to learn two generic names than by having to acquire two separate concepts for one heterogeneous genus.

The step of setting up *Allophyllum* as a new genus was not taken without exploring every possible alternative. When no such alternative was found, the advice of two of the foremost contemporary students of the Polemoniaceae, Herbert L. Mason and Edgar T. Wherry, was sought, both of whom counselled the course now followed. The name, *Allophyllum*, selected for this new genus is an old sectional epithet of Nuttall, which was accompanied by an accurate designation of the diagnostic characteristics and the relationships of the group; in taking up this name we wished to give recognition to Nuttall's clear perceptions of over a century ago.

SYSTEMATIC TREATMENT

Allophyllum (Nutt.) A. & V. Grant, gen. nov.

Gilia sect. *Allophyllum* Nutt., Jour. Acad. Nat. Sci. Philadelphia, Ser. 2, 1: 155, 1848.

Collomia sect. *Gilioides* Benth. in de Candolle, Prodr. 9: 308, 1845, in part as to type.

Collomia sect. *Eucollomia* ser. *Giliaeformes* Gray, Proc. Amer. Acad. 8: 260, 1870, in part as to type.

Gilia sect. *Courtoisia* Gray, Syn. Fl. N. Amer., 2d ed., 2 (1): 408, 1886, in part but not as to type.

Gilia subg. *Microsteria* Milliken, Univ. Calif. Publ. Bot. 2: 23, 1904, in part but not as to type.

Gilia sect. *Pblogastrum* Brand, Pflzr. 250: 88, 1907, in part as to type, which is here chosen *Gilia divaricata* Nutt.

Gilia subg. *Greenianthus* Mason & A. Grant, Madroño 9: 206, 1948, in part as to type.

Erect annual herbs, 1-6 dm. tall. Stems slender or stout, leafy, usually well branched cymosely or sometimes simple, lightly pubescent to villous or glutinous, often with a strong odor. Cotyledons dark green, oblong and truncate with a shallow notch at apex, pinnately veined, the veins depressed on the ventral side. Leaves pubescent like the stems or with shorter, coarse hairs, the lower leaves petiolate, simple and entire to irregularly toothed, or pinnately to bipinnately lobed, the upper leaves digitately 3-5-lobed, the segments linear-lanceolate to oblong, sessile or petiolate. Flowers borne at end of branches in loose to somewhat congested 2-8-flowered cymose glomerules, each glomerule subtended by a leaf; pedicels usually much elongated in fruit. Calyx glandular-pubescent, accrescent, 3.3-7.5 mm. long in fruiting stage, the lobes joined by the sinus membrane about to the middle. Corolla funnelform, regular to somewhat bilabiate, light to dark blue-violet, red-violet or white. Stamens unequally or equally inserted in upper half of tube, subequal to very unequal in length and included or exserted. Style maturing within the tube or beyond the orifice. Capsule almost spherical, 3-celled, containing 1-3 seeds in each locule. Seeds black at maturity, 1.3-2.8 mm. long, plump, rounded on one side, or angular on one end when 2 or 3 seeds occur in the same locule. $N=8, 9$.

Southern Oregon through the mountains of California to Baja California and east to Arizona and Nevada. 100 to 9000 feet.

Type species.—*Gilia divaricata* Nutt.

Neotypes.—The types of several taxa described by Brand were in the Berlin Herbarium, which was largely destroyed during World War II. A post-war report on the condition of this herbarium by Pilger (1953: 16 ff and 25 ff) does not mention the preservation of any type material in the family Polemoniaceae. Nor are there any photographs of these types available, so far as we can determine. Under these circumstances it is appropriate to designate neotypes, wherever possible, for the Brand varieties and species. This is a necessary step in working out the nomenclature of the group within the framework of the type method.

Gilia divaricata var. *volcanica* Brand—George Hansen 1764, Volcano, Amador County, California, Dudley Herbarium 25610, Stanford University, an isotype, is now designated as neotype.

G. gilioides var. *integrifolia* Brand:—H. M. Hall and H. P. Chandler 67, Pine Ridge, Fresno County, California, University of California Herbarium 23582, an isotype, becomes the neotype.

G. gilioides var. *Benthamiana* Brand:—Thomas Howell, June 24, 1884, Grants Pass, Oregon, University of Oregon Herbarium, an isotype, becomes the neotype.

Nomen dubium.—*Gilia gilioides* var. *Greeneana* Brand, Pflzr. 250: 93, 1907. This is based on a Greene specimen from Sonoma County, California, in the Berlin Herbarium. The type is probably no longer in existence. A search for an isotype in the Greene Herbarium at Notre Dame, the University of California Herbarium, and the Herbarium of the California Academy of Sciences was unsuccessful. The description fails to provide any certain means of identification of the name. Brand did cite three additional specimens considered to represent his variety *Greeneana*. Only one of these has been found, Palmer 394. It is *A. divaricatum*. But it was obviously

not Brand's intention to merge *divaricatum* with *gilioides* since in his treatment he maintained them as separate species. Brand's cotypes are frequently found to belong to quite different species or even sections from the type specimens, and are consequently unreliable as criteria for typification. There seems to be no way at present of placing the name *Greeneana* in the synonymy. Since this name has no priority over the names of the two taxa which occur in the type locality, *A. gilioides* and *A. divaricatum*, the simplest course is to exclude *Greeneana* from synonymy.

Herbaria consulted.—University of Oregon; Oregon State College: Willamette University; University of California at Berkeley; California Academy of Sciences; Dudley Herbarium of Stanford University; Pomona College; Rancho Santa Ana Botanic Garden; and University of Arizona. In addition reports on special type material were received from the curators of the Greene Herbarium, University of Notre Dame, and the Academy of Natural Sciences, Philadelphia. Altogether 791 specimens were inspected. The kind cooperation of the curators and staff of the various herbaria is greatly appreciated.

Fig. 3. *Allophyllum divaricatum*. A—Sierra Nevada race from Groveland. B—San Gabriel race from Claremont. Scale in inches.

KEY TO THE SPECIES

Segments of cauline leaves lanceolate to oblong, 3-15 mm. wide, the terminal segments 3-8 times longer than broad; flowers pale to medium blue-violet, white, or red-violet to purple with pink lobes, 6.0-22.0 mm. long; stamens exserted or included; herbage lightly pubescent to glandular-villous and with a skunky odor.

Corolla regular, white throughout or red-violet to purple with pink lobes; stamens quite unequal and included or sometimes two of them exserted; stigma included or sometimes exserted; usually no basal leaf tuft; lower leaves entire to pinnately lobed, only slightly narrower than the upper; locules 1-seeded, or sometimes in southern California 2-3-seeded. Northern and southern California.

- Corolla tube 6-16 mm. long, red-violet to purple with pink lobes; inflorescence usually consisting of 4-8 flowers subtended by a leaf. Foothills and lower slopes, 1000-5600 ft. 1. *A. divaricatum*
- Corolla white, the tube 5-8 mm. long; inflorescence usually consisting of only 2 flowers subtended by a leaf. Higher elevations, 4500-9000 ft. 2. *A. integrifolium*
- Corolla slightly bilabiate, pale to medium blue-violet; stamens subequal and all five usually well exerted; stigma exerted; a basal tuft of leaves well developed; lower leaves narrower than the upper, and pinnately to bipinnately lobed; locules 2-3-seeded, occasionally 1-seeded. Southern California. 3. *A. glutinosum*
- Leaf segments linear to narrowly lanceolate, not exceeding 3.0 mm. in width, the terminal segments of upper leaves 8-14 times longer than broad; flowers dark blue-violet, 5.0-9.5 mm. long; stamens included; herbage puberulent, not conspicuously glandular or villous.
- Inflorescence glomerate with 4-8 flowers subtended by a leaf; pinnately lobed leaves many; inflorescence branches arising mainly above the middle of the plant. Lower and middle elevations, 700-6000 ft. 4. *A. gilioides*
- Inflorescence loose with 2-3 flowers subtended by a leaf; pinnately lobed leaves few; inflorescence branches arising throughout plant. Middle and higher elevations, 4000-8500 ft. 5. *A. violaceum*

1. *Allophyllum divaricatum*, comb. nov.

(Figs. 3, 4)

Gilia divaricata Nuttall, Jour. Acad. Nat. Sci. Philadelphia 1: 155, 1848, (photograph of type seen).

Gilia divaricata var. *volcanica* Brand, Pflzr. 250: 94, 1907, (neotype seen).

Gilia gilioides var. *volcanica* Jepson and Hoover ex Jepson, Fl. Calif. 3 (2): 197, 1943.

Gilia gilioides subsp. *volcanica* Mason and A. Grant, Madroño 9: 207, 1948.

Plant robust, up to 60 cm. tall or taller, stems stout, usually with one main leader, alternately branched, lightly pubescent to villous and viscid, with strong skunk-like odor, lower part of plant not densely leafy; lower leaves entire to irregularly toothed or most often pinnately lobed with 1-6 pairs of lobes, segments of lower leaves 2.4-7.5 mm. wide, those of the upper leaves about the same width or a little broader, the terminal segments of the upper leaves the broadest, 3.0-8.5 times as long as wide; inflorescence congested in early stages of flowering but the pedicels elongating as the capsules form, sympodially branched with pedicels unequal, the shortest less than 5 mm. long in fruit; calyx in fruiting stage about 4.0-5.5 mm. long in northern California and about 6.0-7.0 mm. long in southern California; corolla regular, 7.5-22.0 mm. long, the tube red-violet and the lobes pink, or the tube purple and the lobes pinkish-violet, tube 2.5-4.5 times as long as the lobes; stamens unequally inserted and unequal in length, the longest just included to well exerted; stigma included or exerted; locules of capsules 1-seeded, or in southern California 2-3-seeded; $n=8, 9$.

Range.—Foothills and lower elevations in the mountains from 1000 to 5600 (rarely to 6000) feet. Coast Ranges from Monterey Co. to Humboldt Co.; through Shasta Co.; and south on the western slope of the Sierra Nevada; on Mt. Pinos, Ventura Co.; in the San Gabriel Range, and occasional on the southwestern edge of the San Bernardino Range. Flowering in April, May and June, and occasionally into July.

Type.—*Wm. Gambel*, Monterey, California. Herbarium of the Academy of Natural Sciences, Philadelphia. The specimen is a fragment of an upper branch virtually without flowers or capsules and not showing any basal parts. It was finally possible to identify it by the width of the upper cauline leaves and the looseness of the inflorescence.

Fig. 4. Distribution map of *A. divaricatum*, *A. integrifolium*, and *A. glutinosum*.

Representative specimens.—CALIFORNIA. *A. D. E. Elmer* 3256, *V. & A. Grant* 17600, Tassajara Springs, Monterey Co.; *H. K. Sharsmith* 3365, Mt. Hamilton, Santa Clara Co.; *M. L. Bowerman* 1907, 1941, Mt. Diablo, Contra Costa Co.; *W. L. Jepson* (in 1893), Howell Mt., Napa Co.; *M. S. Baker* 9622, Lakeport, Lake Co.; *C. L. Hitchcock* 6617, Fall River, Lassen Co.; *A. Eastwood* 500, Grass Valley, Nevada Co.; *A. M. Alexander & L. Kellogg* 3631, 3665, Twain Harte, Tuolumne Co.; *V. & A. Grant* 17587, Kaweah River, Tulare Co.; *H. M. Hall* 6463, *W. R. Dudley & F. H. Lamb* 4695, Mt. Pinos, Ventura Co.; *H. L. Mason* 3742, Mt. Wilson, Los Angeles Co.; *V. & A. Grant* 16008, Cow Canyon, San Gabriel Mts., Los Angeles Co.; *P. A. Munz* 11316, Devore Station, San Bernardino Co.

2. *Allophyllum integrifolium*, comb. nov.

(Figs. 4, 5)

Gilia gilioides var. *integrifolia* Brand, Pfizr. 250: 93, 1907, (neotype seen).

Plant about 15 cm. tall (10-25 cm.); stems villous, slender or stout, with one main leader, branching alternately; lower leaves few, not forming a basal tuft, usu-

ally a little narrower than upper leaves, oblong to lanceolate, entire or with shallow or deep irregular teeth, cauline leaf segments oblong, the terminal segment broadest, 4.8-15.0 mm. wide, and 3-6 times as long as broad; flowers borne in loose pairs (sometimes in fours) subtended by a leaf, pedicels slender, unequal, the shortest and longest measuring 1-4 mm. and 6-18 mm. long respectively in fruit; calyx in fruiting stage 5.0-6.4 mm. long; corolla white or pale blue, regular, 6.5-11.0 mm. long, tube 5.5-8.0 mm. long; stamens unequal, 0.4-2.0 mm. long, included in corolla tube; stigma maturing just below level of shortest stamen; locules of the capsules 1-seeded or sometimes 2-seeded in southern California; $n=8, 9$.

Fig. 5. *Allophyllum integrifolium*, from Cow Creek, Tuolumne Co., Sierra Nevada.

Range.—Open rocky or sandy places at higher elevations in the mountains from 4500 to 9000 feet. Southern Cascade Mts. of Shasta Co., through the Sierra Nevada, to the San Gabriel and San Bernardino Mts. of southern California. Flowering in June, July and August.

Type.—*H. M. Hall* and *H. P. Chandler* 67, Pine Ridge, 5300 ft., Fresno Co., California, June 15-25, 1900. Herbarium of the University of California at Berkeley 23582. See above p. 99.

Representative specimens.—CALIFORNIA: *G. L. Stebbins* & *J. A. Jenkins* 2422, Red Mt., Shasta Co.; *M. E. Jones* 10185, Mt. Lassen, Shasta Co.; *E. B. Copeland* 393, Jonesville, Butte Co.; *A. A. Heller* 6901, Donner Lake, Nevada Co.; *V. & A. Grant* 8800, Echo Summit, El Dorado Co.; *H. L. Mason* 12479, Miguel Meadow west of Hetch Hetchy Valley, Tuolumne Co.; *V. & A. Grant* 19685, Cow Creek, Tuolumne Co.; *P. A. Munz* 4610, Swartout Valley Saw Mill, San Gabriel Mts., Los Angeles Co.; *H. M. Hall* 1266, head of San Gabriel River, San Gabriel Mts., Los Angeles Co.; *V. & A. Grant* 16061, between Lake Arrowhead and Big Bear Lake, San Bernardino Mts., San Bernardino Co.

3. *Allophyllum glutinosum*, comb. nov.

(Figs. 4, 6)

Collomia glutinosa Benth., Bot. Reg. 19, sub t. 1622, 1833, (photograph of type seen).*Collomia gilioides* var. *glutinosa* Gray, Proc. Amer. Acad. 8: 260, 1870.*Gilia glutinosa* Gray, Syn. Fl. N. Amer., 2nd ed., 2 (1): 408, 1886, not *Gilia glutinosa* Phillippi.*Gilia Traskiae* Eastwood ex Milliken, Univ. Calif. Publ. Bot. 2: 26, 1904, (type seen).*Microsteris Traskiae* Davidson and Moxley, Fl. S. Calif. 287, 1923.*Gilia gilioides* subsp. *glutinosa* Mason and A. Grant, Madroño 9: 207, 1948.

One to several moderately stout stems arising from near base, 10-60 cm. tall or taller, alternately branched, villous and viscid, with strong skunk-like odor; lower leaves numerous and crowded, forming a basal tuft, pinnately lobed with 3-10 pairs of lobes which are often irregularly toothed or lobed, segments of basal leaves 1-2 mm. wide, those of the upper leaves broader, 3-11 mm. wide, the terminal segments of the upper leaves the broadest, 3-7 times as long as wide; inflorescence loose, somewhat dichotomously branched, 2-8-flowered, the pedicels almost equal in length, 0.5-2.0 cm. long in fruit; calyx in fruiting stage 4.7-7.5 mm. long, or in plants with 1-seeded locules 3.6-4.9 mm. long; corolla pale or sometimes medium blue-violet, 6.2-11.0 mm. long, the lobes 2.5-5.0 mm. long, spreading widely in a slightly bilabiate manner from the expanded orifice, tube 4.0-7.5 mm. long; style and stamens lying together along lower lip of corolla and curving upward at their tips; stamens equally to subequally inserted and usually all 5 well exerted, the

Fig. 6. *Allophyllum glutinosum*. A—San Diego race from Santa Ana Mts. B—Santa Monica race from Topanga Canyon.

longest 3.5-8.5 mm. long, the shortest two-thirds to subequal the longest; stigma exerted, usually conspicuously so; locules of the capsules 2-3-seeded, or sometimes 1-seeded; $n=9$.

Range.—Shaded brushy slopes and ravines, from 100 to 4000 and occasionally to 5300 feet. Coastal mountains from Monterey Co. to Baja California, and on Santa Catalina Island. Flowering in April, May and June, occasionally into July and August.

Type.—Douglas, in 1833, California. Royal Botanic Gardens, Kew.

Representative specimens.—CALIFORNIA: I. J. Condit (in 1908), Trout Creek, San Luis Obispo Co.; D. D. Keck 1964, San Marcos Pass, Santa Barbara Co.; I. W. Clokey & B. Templeton 4468, Santa Monica Mts., Los Angeles Co.; M. B. Dunkle 1934, Santa Catalina Island, Los Angeles Co.; V. & A. Grant 8639, Santa Ana Mts., Orange Co.; C. B. Wolf 5399, Santiago Peak, Santa Ana Mts., Riverside Co.; H. L. Mason 3131, V. & A. Grant 16009, Temecula, Riverside Co.; E. Jaeger (in 1938), Laguna Mts., San Diego Co.

BAJA CALIFORNIA: I. L. Wiggins & J. L. Gillespie 4077, Ojos Negros.

4. *Allophyllum gilioides*, comb. nov.

(Figs. 7, 8)

Collomia gilioides Benth., Bot. Reg. 19 sub t. 1622, 1833, (isotype and photograph of type seen).

Gilia gilioides Greene, Erythra 1: 93, 1893.

Gilia gilioides var. *Benthamiana* Brand, Pflzr. 250: 93, 1907, (neotype seen).

Microsteris gilioides Davidson and Moxley, Fl. S. Calif. 287, 1923.

Microsteris gilioides var. *Benthamiana* Davidson and Moxley, loc. cit.

Gilia gilioides var. *ianthina* Jepson and Hoover ex Jepson, Fl. Calif., 3 (2): 197, 1943, (type seen).

One to several main stems 10-40 cm. tall arising usually from a leafy base, and bearing numerous, pinnately-lobed leaves up to the branches of the inflorescence; herbage puberulent throughout and somewhat glandular in the inflorescence; lower leaves having 2-5 pairs of linear lobes, rachis and lobes 2-3 (-4) mm. broad, lobes (2-) 5-15 mm. long; upper leaves shorter, pinnately to almost digitately lobed with 2 pairs of lobes, 2-4 mm. broad; inflorescence glomerate, each flowering branch subtended by a leaf, terminated by 4 (sometimes 2-3) short-pedicellate flowers, and bearing another (2-) 4-flowered glomerule laterally on a short peduncle; calyx in fruiting stage about 5 mm. long (4.5-5.5 mm); corolla dark blue-violet, 6.5-9.5 mm. long (rarely smaller); stamens subequal in length, subequally inserted in upper half of corolla tube, included, or 1 or 2 stamens slightly exerted from orifice of tube; stigma included; locules of the capsules 1-seeded; $n=9$.

Range.—Moderately dry soil of open slopes and flats from 700 to 6000 feet. Cascade Mts. of southern Oregon; throughout the California Coast Ranges; southern Sierra Nevada in Kern Co.; San Gabriel, San Bernardino, and Laguna Mts. of southern California; Guadalupe Island; Panamint Mts.; to the east in the mountains of central and south-central Arizona (Bradshaw, Mazatzal, Pinal, Santa Catalina, Maricopa, Baboquivari Ranges). Flowering in April, May and June.

Type.—Douglas, in 1833, California. Royal Botanic Gardens, Kew.

Representative specimens.—OREGON: E. I. Applegate 3552, Barclay Springs, Klamath Lake, Klamath Co.

CALIFORNIA: H. L. Mason 5245, Lakeport, Lake Co.; V. & A. Grant 17591, Mt. Diablo, Contra Costa Co.; H. K. Sharsmith 3002, Smith Creek, Mt. Hamilton, Santa Clara Co.; V. & A. Grant 8712, Pinnacles Natl. Monument, San Benito Co.; V. & A. Grant 8450, west of Coalinga, Fresno Co.; I. J. Condit (in 1910), Navajo Creek, San Luis Obispo Co.; H. L. Mason 8362, above Kernville on Kern River, Kern Co.; V. Grant 18441, Greenhorn Mts., Kern Co.; P. A. Munz 9663, Laguna Mts., San Diego Co.; H. M. Hall & H. P. Chandler 6967, Panamint Mts., Inyo Co.

BAJA CALIFORNIA: E. L. Greene (in 1885), Guadalupe Island.

ARIZONA: R. H. Peebles & E. G. Smith 11560, Reno Pass, Mazatzal Mts., Maricopa Co.; E. Palmer 393, Hassayampa Valley, Maricopa Co.; A. & R. Nelson 1872, between Miami and Superior, Gila to Pinal Co.; A. & R. Nelson 1437, Tanque Verde Mts., near Tucson, Pima Co.

Fig. 7. *Allophyllum violaceum* (A, B) and *A. gilioides* (C, D). A—from Cow Creek, Tuolumne Co., Sierra Nevada. B—from Ebbetts Pass, Sierra Nevada. C—from Greenhorn Mts. in the southern Sierra Nevada. D—from Laguna Mts., San Diego Co.

5. *Allophyllum violaceum*, comb. nov.

(Figs. 7, 8)

Gilia violacea Heller, Muhlenbergia 1: 56, 1904, (type seen).

Plants usually small, about 15 cm. tall (7-42 cm.), with 1 to several slender to filiform stems arising from near base, these alternately to somewhat dichotomously branched to form a diffuse inflorescence; herbage puberulent throughout, inflorescence glandular but not conspicuously so; basal and lower stem leaves few, usually not forming a basal tuft, 1.0-5.0 cm. long, 0.5-3.0 mm. broad, linear to narrowly lanceolate, and entire or pinnately lobed with usually not more than 1-2 pairs of short lobes, 1.5-8.0 mm. long; leaves of inflorescence branches shorter, digitately lobed with 1-2 pairs of lobes, the segments very little broader than those of the lower leaves; inflorescence loose, with flowers typically in pairs on a floral branch, one borne terminally and the other laterally on a short pedicel; calyx in fruiting stage about 4 mm. long (3.3-5.2 mm.); corolla regular, dark blue-violet, 5.0-8.0 mm. long; stamens subequally inserted in corolla tube, subequal in length, included or 1 or 2 slightly exserted from orifice of corolla tube; stigma included; locules of the capsules 1-seeded; $n=9$.

Range.—Sandy or gravelly places in the mountains from 4000 to 8500 feet. Through the Sierra Nevada to the San Gabriel, San Bernardino, San Jacinto and Cuyamaca Mts. of southern California; known from the California Coast Ranges in Ventura and Santa Barbara cos. in the south and Humboldt Co. in the north; to the east in the White Mts., the Panamint and Grapevine Mts. of the Death Valley area, Magruder and Stonewall Mts. of Esmeralda and Nye Cos., Nevada, and the Wassuk Range, Mineral Co., Nevada. Flowering in May, June and July, occasionally in April and August.

Type.—*A. A. Heller* 6873, lower end of Donner Lake, Nevada Co., California, July 8, 1903. Herbarium of the University of California at Berkeley 58472.

Representative specimens.—CALIFORNIA: *L. S. Rose* 41299, Lake Tahoe, Placer Co.; *H. L. Mason* 12487, south of Lake Tahoe, El Dorado Co.; *V. Grant* 17316, Ebbetts Pass, Alpine Co.; *V. & A. Grant* 18469, Rock Creek, Mono Co.; *V. & A. Grant* 19686, Cow Creek, Tuolumne Co.; *R. S. Ferris & L. Lorraine* 10872, Hockett Ranger Station, Sequoia Natl. Park, Tulare Co.; *V. & A. Grant* 16048, 18495, Mt. Pinos, Ventura Co.; *V. & A. Grant* 16034, Charlton Flats, San Gabriel Mts., Los Angeles Co.; *I. M. Johnston* 2901, *P. A. Munz* 5686, San Bernardino Mts., San Bernardino Co.; *V. & A. Grant* 18451, Cuyamaca Mts., San Diego

Fig. 8. Distribution map of *A. violaceum* and *A. gilioides*.

Co.; *P. A. Munz* 14826, Panamint Mts., Inyo Co.; *M. F. Gilman* 3223, Grapevine Mts., Inyo Co.

NEVADA: *A. M. Alexander & L. Kellogg* 2424, Mt. Magruder, Esmeralda Co.; *M. E. Jones* (in 1897), Carson City, Ormsby Co.

GEOGRAPHICAL VARIATION

There is considerable geographical variation in the species of *Allophyllum*. A convergence of the characters of different species is often found in areas where they occur together. The degree and the direction of the variation have been the principal factors which have heretofore prevented the recognition of the separate species.

A. divaricatum.—The most extreme development in this species is found in the Sierra Nevada from Mariposa to El Dorado County. In this area the two longest stamens and the stigma are exserted well beyond the corolla; the corolla tube sometimes reaches its maximum length of 14-16 mm. and is pinkish-violet; the lower leaves tend to be only slightly dissected, or with a few irregular teeth, or are even simple and entire; a basal tuft of leaves is lacking in mature plants.

In the Coast Ranges in Lake and Mendocino counties the flowers are the same as to color but less extreme in dimensions. The corolla tube is 9 to 10 mm. long; the stamens are also shorter, the longest one being only slightly exserted; and the style is included. A basal rosette is well developed and the lower leaves are pinnately lobed.

A very widespread form of *A. divaricatum* in the Coast Ranges and the southern Sierra Nevada is characterized by shorter flowers with a purple corolla tube and pinkish-violet lobes; included or slightly exserted stamens; included style; pinnately lobed lower leaves; and a well developed basal rosette. The typical Coast Range race approaches in the aforementioned characteristics *A. gilioides*.

The populations of *A. divaricatum* in the San Gabriel and San Bernardino Mountains commonly have rather densely leafy lower stems; basal leaves sometimes approaching a bipinnate condition; exserted stamens and style; dichotomously branched pedicels sometimes exceeding 0.5 cm. in length; and capsules containing two or three seeds (instead of just one) in each locule. Whereas the Coast Range and Sierra Nevada races have $n=8$, the San Gabriel race has $n=9$. These morphological and karyological variations are towards *A. glutinosum* in the San Gabriel-San Bernardino area.

A. integrifolium.—The most commonly encountered form is a dwarfish and relatively unbranched plant of higher elevations in the mountains. More luxuriant plants with a good development of branches are rather infrequently found in shaded canyons at middle elevations. The typical race has $n=8$, whereas the chromosome number $n=9$ is found in the well-branched mid-altitude race.

A. glutinosum.—The extreme form of this species occurs in moist shaded canyons in the mountains of San Diego County and northern Baja California and occasionally in the coastal ranges to the north. These are plants with a basal tuft of pinnate or bipinnate leaves; lower leaves with as many as ten pairs of lobes; upper leaves much broader than the lower ones; flowers borne in pairs with usually two pairs on a peduncle arising in the axil of a leaf; pedicels slender and equal in length, often up to 2 cm. long in the fruiting stage; corolla pale blue-violet with a short (4-6 mm.) tube and relatively long lobes which vary from one-half to almost as long as the tube; all stamens and the stigma long and well exserted. The flowers are oriented in a bilabiate manner.

A distinctive race is found in exposed and arid habitats at higher elevations (up

to 5700 feet) and particularly on mountain tops from Baja California to Santa Barbara County. The plants are usually much branched with slender branches; the leaves are small and only slightly dissected; the flowers are similar in shape and proportions to those of the extreme form described above but may be smaller and medium (instead of pale) blue-violet. The mountain top race differs from all other forms of the species in having small capsules with one-seeded cells.

On the lower slopes of the San Bernardino and San Gabriel Ranges occur populations with a less leafy base; lower leaves which are broader and less dissected or sometimes almost entire; unequal pedicels which are in general shorter than in extreme *A. glutinosum*; a longer corolla tube and shorter lobes; corolla color medium rather than pale blue-violet; stamens and style less conspicuously exerted than in extreme *A. glutinosum*. The bilabiate condition of the flowers is evident but not so well developed. The San Gabriel race approaches in many of its characteristics the combination found in *A. divaricatum*.

In the Santa Monica Mountains there occurs a race which possesses floral characters somewhat like the San Gabriel race combined with a leafy base and much dissected leaves as in the San Diego forms.

A. gilioides.—Most populations are relatively uniform except for differences in the stature and leafiness of the plants correlated with habitat conditions. The plants of the Mazatzal, Santa Catalina and Baboquivari Ranges of Arizona, while vigorous and not especially distinctive in other respects, possess unusually small flowers, 4.8 mm. long. A race in the Panamint Mountains of the Death Valley region is distinguished by an unusually small calyx; a slender corolla tube; stamens inserted very high in the tube; and one stamen well exerted.

A. violaceum.—In the central Sierra Nevada this species is a diminutive plant often no taller than 15 cm., with delicate stems, leaves 1 mm. or less in width, and tiny flowers about 5 mm. long. The lower leaves may be entire or with a few very short lobes. In other areas the plants may vary in the direction of larger size, broader leaves with longer lobes, and/or larger flowers up to 8 mm. long.

It is not necessary, perhaps, to give formal nomenclatural status to the major variants described in the foregoing account. This procedure would only further complicate the systematic treatment, whereas the races can be adequately identified in the vernacular as the "San Diego," "mountain-top," or "San Gabriel" race of *A. glutinosum*, etc. It is, however, desirable to make more detailed studies of the variability designed to explain its origin. As already noted, the species of *Allophyllum* frequently converge morphologically in areas where they overlap geographically. This suggests that the non-random convergent variations have arisen through introgressive hybridization between the various species. Investigations of the role of introgression in the enhancement of the variability of the *Allophyllums* are in progress.

SUMMARY

Allophyllum is a genus of five species of annual herbs of mountainous regions of California and bordering states. The group, which has been included in *Gilia* by Asa Gray and subsequent authors, is actually related by the sum total of its characters to the *Collomia* branch of the polemoniaceous family tree. The species possess distinctive morphological characters, definite geographical ranges, and occur sympatrically.

The species fall into two series. (I) The *A. divaricatum* group consists of three species with broad leaves, frequently long stem hairs, and usually relatively large flowers. (1) *A. divaricatum*: robust plants lacking a basal tuft of leaves and

possessing slender long reddish-violet corollas and unequal stamens, in the foothills of the California Coast Ranges and Sierra Nevada. Four geographical races are recognized and designated as the Sierra Nevada, the Lake County, the typical Coast Range, and the San Gabriel races. (2) *A. integrifolium*: high montane plants chiefly of the Sierra Nevada with entire or nearly entire basal leaves and small white corollas. A widespread race and an infrequently encountered mid-altitude race are distinguished. (3) *A. glutinosum*: tufted annuals with pinnate leaves, pale blue-violet bilabiate corollas, and well exerted stamens, which occur in the foothills of coastal southern California. The main geographical races are the San Diego, San Gabriel, Santa Monica, and mountain top races. (II) The *A. gilioides* group includes two species with narrow leaves, puberulent herbage, and small dark blue-violet corollas. (4) *A. gilioides*: tufted plants with glomerate inflorescences in the Coast Ranges from Oregon to southern California and east to central Arizona. A Mazatzal and a Panamint race can be distinguished from the widespread form of the species. (5) *A. violaceum*: small non-tufted plants with loose inflorescences, ranging through the Sierra Nevada to southern California and east to Nevada. A central Sierran race can be distinguished from the more widespread, somewhat larger form of the species.

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