STUDIES IN STREPTANTHUS. A NEW STREPTANTHUS COMPLEX IN CALIFORNIA

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In recent years intensive exploration of the many isolated serpentine areas of Sonoma and adjacent counties in California has revealed several hitherto undescribed taxa of the genus *Streptanthus*. Among these is a group of four closely related taxa which occupy a phylogenetically intermediate position in that they possess the foliage and stem characters of the *Streptanthus tortuosus* complex of subgenus *Pleiocardia* together with the bractless inflorescence, zygomorphic, flask-shaped calyx, and two pairs of connate filaments of the *S. Breweri* complex of subgenus *Euclisia*. Two species, one with three subspecies, are represented in this new group of four taxa; all are biennials and serpentine endemics of limited range, and they are here treated as belonging to the subgenus *Euclisia*.

Subgenus *Euclisia*, as constituted up to the present time, is a heterogeneous assemblage of many polymorphic species, the only common characters being zygomorphic flowers and one or two pairs of stamens with connate or partially connate filaments. Neither of these characters, however, is unique with *Euclisia*. The flowers of the subgenus *Pleiocardia* are to a certain degree zygomorphic, and connate filaments are common to the subgenera *Caulanthus* and *Paracaulanthus* of *Streptanthus* as well as to some species of the closely related genus

Thelypodium (W. L. Jepson, 1936).

Almost all of the taxa of subgenus *Euclisia* have been grown by the author from seed, and the morphological variations in the various organs of each plant have been recorded. No characters better reveal the phylogenetic relationships within this subgenus than those of the juvenile rosette leaves. The shape, color, and texture of the juvenile leaves of closelyrelated taxa of the genus Streptanthus are characteristic of those taxa, and the juvenile leaves of each closely related group have a characteristic aspect. A knowledge of these lower leaves is often desirable for the proper classification of a taxon. They are usually shed by the plant before full anthesis and hence are seldom collected and seen on herbarium specimens. Some botanical descriptions are therefore inadequate because of a lack of knowledge of these lower leaves. As an illustration, E. L. Greene (1888, p. 217) described S. barbiger as having "linear entire leaves," having seen only the upper leaves. This incomplete description has remained in the literature for many years. It is believed that the type specimen is non-existent (Morrison, p. 51), but the plant has recently been re-collected at the type locality and found to have palmately-lobed juvenile,

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TABLE 1. COMPARISON OF JUVENILE FOLIAGE CHARACTERS IN STREP-TANTHUS, SECTION EUCLISIA AND CLOSELY RELATED SECTIONS.

Subgenera	Plejocardia	Complex	group		Juvenile andlower leafform.	Pubescence	Cabbage-like texture	Glaucum	Spotted or mottled
	Meio	S.tortuosus			D	0	X	X	0
	Euclisia	S.Morrisonii	Z.	Morrisonii	3	0	X	X	0
				elatus		0	X	X	X
				hirtiflorus		0	X	X	X
				brachiatus		0	X	X	X
		S.Breweri	2		PP	0	X	X	×
		S.niger	3			03	0	0	ΧŞ
		S.glandulosus	4		MANAGE	X	0	0	XŞ
		S.insignis	5		燈	X	0	0	0
		S.polygaloides	6		FF	0	0	0	0
	Plei	S.insignis S.polygaloides S.diversifolius			Profes	0	0	0	0
	00-00								

In the above table a zero (0) indicates the character at the head of the column as being absent; an \times indicates the character as being present; an interrogation point (?) indicates that the character is sometimes present $(\times?)$, or sometimes absent (0?).

and coarsely-serrate lower cauline leaves, only the upper leaves being "linear and entire."

Based upon the shape, color, and texture of the juvenile leaves of each taxon and supported by morphological evidence from the other organs, six groups of taxa may be formed in the subgenus *Euclisia*, as listed in Table 1. Corresponding characters of their nearest affiliates in the subgenus *Pleiocardia* are included in Table 1 at each end of the sequence of groups.

In groups 1 and 2 there may be noticed in the juvenile leaves a certain degree of maculation or mottling which is common to three of the four members of Group 1 and to all the members of Group 2. These leaves in groups 1 and 2, as well as in the *S. tortuosus* complex, are cabbage-like in texture, glab-

rous, and glaucous. In Group 3 maculation is either absent or reduced to a few spots; the leaves remain glabrous, or almost so, there is no glaucescence, and the texture is no longer cabbage-like. The form of the leaf also changes to approach that of groups 4 and 5. In these two groups a new character, pubescence, is introduced. In Group 6, the S. polygaloides complex, none of the juvenile leaf characters of the other five groups is present. In these characters the S. polygaloides complex strikingly resembles the S. diversifolius complex of the subgenus Pleiocardia, to which it may be closely related. Except for the connate filaments and zygomorphic corollas, the phylogenetic relationship of the S. polygaloides complex with the other groups of *Euclisia* must be very remote. Species complexes such as these under consideration, it should be noted here, are common within the genus Streptanthus, most of its species being polymorphic to such a degree that it becomes difficult to determine whether closely related forms should be regarded as one species or as belonging to distinct species. To give one example, at least eight or ten distinct forms of

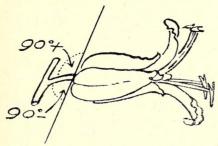


Fig. 1. Diagram of flower, Streptanthus Morrisonii complex.

S. barbiger of the S. Breweri complex, subgenus Euclisia, are known to exist; yet its specific status is in doubt. It can be stated, however, that S. barbiger is probably a member of the S. Breweri complex which is here used to include such closely related taxa as S. hesperidis Jepson, S. batrachopus Morrison, and additional entities not yet described.

The flowers of groups 1 and 2 are quite similar in form. They are zygomorphic in the sense that they are somewhat bilabiate. The stamens are in three sets: upper, lower and lateral. Those of the upper set have connate filaments, are longest, and protrude from beneath the upper sepal; those of the lower set usually have connate filaments, are next longest, and protrude from above the lower sepal; those of the lateral set are free, arcuate, usually included and are the shortest, each being contained within a lateral sepal. The sepals, likewise, are in three sets: the upper is always narrowest, lightly keeled, and not saccate at the base; the two lateral sepals are alike in form, being boat-shaped, heavily keeled, saccate at the base and broader than the others; the lower sepal is lightly keeled, boat-shaped and saccate at the base. All sepals are somewhat connivent towards their apices, and, because of their spreading or recurved tips, form a flask-shaped calyx. In the flower, viewed laterally (fig. 1), a line tangent to all the sepal bases forms an acute angle with the pedicel below the receptacle and an obtuse angle above the receptacle, instead of a

right angle as in most actinomorphic flowers. There is no enlarged torus as is characteristic of the *S. tortuosus* complex.

The taxonomic position of the four new taxa in relation to the preceding six groups of subgenus *Euclisia* and their nearest affiliates in subgenus *Pleiocardia* is represented in the following keys to the genus *Streptanthus*.

KEY TO THE SUBGENERA OF STREPTANTHUS

Stigma 2-lobed; seeds wingless or narrowly winged; cotyledons obliquely incumbent.

Cauline leaves petioled; filaments in one set of equal length, or, if in two sets, then the sets of a different length; distinct

Caulanthus
Cauline leaves sessile, amplexicaul; filaments in three sets, each
of a different length, distinct, or with one or two pairs connate

Paracaulanthus

Stigma usually entire or indistinctly 2-lobed; seeds mostly winged, sometimes wingless; cotyledons accumbent.

Filaments in three sets, each set of a different length, distinct; plants glabrous and glaucous; flowers slightly zygomorphic *Pleiocardia*.

KEY TO THE GROUPS OF STREPTANTHUS, SUBGENUS EUCLISIA

Plants glabrous and glaucous; seeds usually wingless or with a suggestion of wing at the tip.

Juvenile leaves cabbage-like in texture, broad, palmately lobed, dentate, or serrate, upper surface usually mottled.

Biennials Group 1, S. Morrisonii complex.
Annuals Group 2, S. Breweri complex.

Juvenile leaves not cabbage-like in texture, deeply incised or pinnate, not mottled Group 6, S. polygaloides complex. Plants pubescent at the base; seeds usually winged all around.

Juvenile leaves glabrous or with a few hairs; some maculation present Group 3, S. niger.

Juvenile leaves pubescent, never glabrous; maculation usually

Juvenile leaves pubescent, never glabrous; maculation usually absent.

Inflorescence with a terminal highly colored cluster of infertile

Inflorescence with a terminal highly-colored cluster of infertile flowers; upper and lower sets of filaments connate

Inflorescence without a terminal highly-colored cluster of infertile flowers; upper set of filaments connate, lower set usually free Group 4, S. glandulosus complex.

KEY TO THE SUBSPECIES OF GROUP 1, STREPTANTHUS MORRISONII COMPLEX Calyx greenish-yellow to golden-yellow, occasionally purplish; upper connate filaments without longitudinal colored lines.

connate filaments without longitudinal colored lines.

Upper and lower surfaces of juvenile and lower leaves usually uniformly green; upper connate filaments uniformly orange or orange-yellow; plants endemic to serpentines of Big and East Austin creeks. Sonoma County S. Morrisonii subsp. Morrisonii

 Calyx purple or rose, never yellow, upper connate filaments with two purple longitudinal lines.

Streptanthus Morrisonii sp. nov. Herbae biennes glabrae glaucae foliis rosulatis juvenilibus latis palmatilobatis dentatis serratisve textura eas brassicae simulantibus paginis superioribus plerumque marmoratis seminis plerumque sine alis vel

apice laevissime tantum alatis.

Strict or diffuse, somewhat woody biennials, forming in the first year rosettes of leaves that are cabbage-like in texture, glabrous, glaucous, uniformly gray-green both above and beneath, or the lower surface somewhat purple-tinged, or the upper surface heavily mottled with purplish or brownish blotches and the lower surface purple, petiolate, broadly-ovate to spatulate-obovate or fan-shaped with margin entire basally and coarsely dentate apically, up to 4.5 cm. in width and 7.5 cm. in length, in the second year the stem extended and producing auriculate-spatulate to auriculate-ovate, sessile, clasping, entire or few-toothed leaves, these passing into auriculate-lanceolate acute, sessile leaves and awl-shaped bracts; flowers zygomorphic, scattered along the flowering stems or concentrated towards the tips of the branches; calyx flask-shaped, densely pubescent, with a few scattered hairs, or entirely glabrous, golden-yellow, greenish-yellow or deep purple, at least 0.8 cm. long; sepals ovate-lanceolate, strongly-keeled, acute, tips scarious and recurved; petals white, cream-colored or slightly salmon-tinted, with yellow, brown or purple forked veins, the upper pair turned upward and recurved, the lower pair turned downward and recurved; stamens in three sets, the upper set connate, uniformly colored yellow or orange or with two purple, longitudinal lines when the corolla is purple, protruding, turned upwards and strongly recurved, the lower set partially connate, protruding, turned downwards and strongly recurved, the lateral set included, free; siliques erect, divergent or reflexed, straight or slightly curved, flattened parallel with the partition, 2.0-10.0 cm. long, up to 0.2 cm. wide, usually torulose; seeds brown or greenish-brown, with a wing at the tip, cotyledons accumbent; style short; stigma entire.

Under S. Morrisonii three subspecies are recognized and

described as follows:

STREPTANTHUS MORRISONII subsp. Morrisonii Herba erecta biennis usque ad 10 dm. alta foliis basalibus juvenibusque petiolatis glabris glaucis eis brassicae similibus omnino griseoviridibus late ovatis vel spathulato-obovatis ad apicem versus dentatis foliis superioribus sessilibus amplectentibus integris vel sparse dentatis auriculato-spathulatis vel ovatis etiam

subulatis calycibus flavovirentibus glabris vel leviter pubescentibus petalis eburneis vel lateritiis venis brunneis vel flavis praeterea ornatis filamentis staminorum duorum superiorum eisque eorum duorum inferiorum inter se in paribus connatis eis paris lateralis liberis siliquis torulosis erectis vel diver-

gentibus seminibus sine alis.

Flowering stems tall (up to 10 dm.) and strict; juvenile and adult leaves gray-green on both surfaces, or a little purplish beneath, without maculation; upper stem leaves auriculate-spatulate to auriculate-ovate, sessile, clasping, entire or fewtoothed; flowers discretely produced towards the tips of ascending or divergent branches; calyx greenish-yellow becoming golden-yellow with age, glabrous or with a few scattered hairs, up to 0.8 cm. long; petals creamy-white to light-salmon with brownish or orange-colored veins, most prominent on the lower petals, 1.0 cm. long; upper filaments recurved, broadly connate, uniformly orange-colored; siliques erect or divergent, 2.0-7.0 cm. long, 0.15 cm. wide, straight, or slightly curved, torulose.

Type. Serpentine outcrop, headwaters of Big Austin Creek at Layton Chromite Mine, Sonoma County, California, September 26, 1946, Freed Hoffman 1020 (Herbarium of the University of California no. 936537). Subsequent collections have been made at the type locality and also at Red Slide on Bargeman Creek, Hoffman 1029; Devil Creek, Hoffman 2995; Gilliam Creek, Hoffman 1053, all of these creeks being tributaries of East Austin Creek and located in the same serpentine area.

This species has been named for Dr. John Morrison of New York State College of Forestry, Syracuse, New York, in recog-

nition of his studies in the genus Streptanthus.

Following is a partial list of the associated flora: Cheilanthes siliquosa Maxon, Cupressus Sargentii Jepson, Pseudotsuga taxifolia (Lamb.) Britt., Allium falcifolium H. & A., Fritillaria lanceolata Pursh, Calochortus pulchellus Dougl., Cypripedium californicum Gray, Solanoa purpurascens (Gray) Greene, Dendromecon rigida Benth., Cordylanthus Pringlei Gray, Parnassia palustris L. var. californica Gray, Phacelia egena Gray,

EXPLANATION OF FIGURE 2.

Fig. 2. Streptanthus Morrisonii subsp. Morrisonii: a, seed \times 5; b, seedling with cotyledons \times 4; c, seedling with first stem leaves \times 1; d, mature growth of first year \times $\frac{1}{2}$; e, typical leaves of first year mature growth \times $\frac{1}{2}$; f, habit, fruiting stage \times 1/6; g, flowering branch \times $\frac{1}{2}$; h, types of stem leaves of second year mature growth \times $\frac{1}{2}$; i, lateral view of flower \times 2; i, upper and lower petals \times 2; i, upper, lateral and lower sepals \times 2; i, androecium and gynoecium: 1, side view, 2, front view, lower stamens front, 3, front view with lower stamens removed to show connate upper stamens, all \times 1½; i, stigma i 2; i 2, fruiting branch showing torulose siliques i 3.



Fig. 2. Streptanthus Morrisonii subsp. Morrisonii.

Eriodictyon californicum (H. & A.) Greene, Rhododendron occidentale Gray, Eriogonum Kelloggii Gray, Dentaria integrifolia Nutt., Erysimum asperum (Nutt.) DC., Streptanthus barbiger Greene (subspecies), Streptanthus glandulosus Hook. (two subspecies).

Streptanthus Morrisonii subsp. hirtiflorus subsp. nov. A subspecie *Morrisonii* altitudine tantum ad 8 dm. foliorum paginis superioribus maculoso-versicoloribus paginis inferioribus purpureotinctis calycibus hirsutissimis petalis albis pur-

pureovenosis siliquis plerumque reflexis discedit.

Strict or much branched and diffuse, up to 8.0 dm. tall; upper surface of juvenile leaves heavily mottled with purple-brown, lower surface uniformly purple; upper stem leaves similar to those of the foregoing subspecies; inflorescence secund; flowers abundant, scattered along the flowering branches; calyx somewhat inflated, red-purple, up to 1.0 cm. long, abundantly clothed in long hairs (0.2 cm.) which gives the plant a grayish appearance; petals dull-white with purplish veins, 1.0 cm. long; upper filaments broadly connate, orange-colored with two longitudinal, parallel, purple stripes, exserted and curved back over the petals in full anthesis; siliques abundantly produced, up to 10.0 cm. long, 0.2 cm. wide, erect, divergent or reflexed on the same plant.

Serpentine bluffs and talus slopes with western exposure. This rare serpentine endemic was found by the author to occupy an area of not over one hundred square yards on west-facing serpentine bluffs and slopes at the type locality. It has

not been collected elsewhere.

Type. Headwaters of East Austin Creek, a short distance above Dorrs' Cabin, Sonoma County, California, June 16, 1948, Freed Hoffman 2344 (Herbarium of the University of California no. 936538).

Associated flora like that of subspecies Morrisonii with the

addition of Fremontia californica Torr.

Streptanthus Morrisonii subsp. elatus subsp. nov. A subspecie *Morrisonii* aspectu stricto altitudine ad 12 dm. foliis longipetiolatis obovatis vel flabellatis paginis superioribus dense tessellatis paginis inferioribus purpureotinctis siliquis torulosissimis discedit.

Strict, remotely branched up to 12 dm. tall; upper surface of juvenile leaves mottled with purplish-brown, lower surface

EXPLANATION OF FIGURE 3.

Fig. 3. Streptanthus Morrisonii subsp. hirtiflorus: a, seed, \times 5; b, seedling with cotyledons, \times 1; c, juvenile growth of first season, \times ½; d, unbranched habit of second year, \times ½; e, branched habit of second year, \times ½; f, fruiting branch, f ½; f0, lateral view of flower, f 3; f1, side view of stamens and pistil, f3; f3; f4, lateral stamen, f5; f7, upper connate stamens, f7, f8, lower partially connate stamens, f8, f9; f9, petals, f9; f9, stigma, f9.

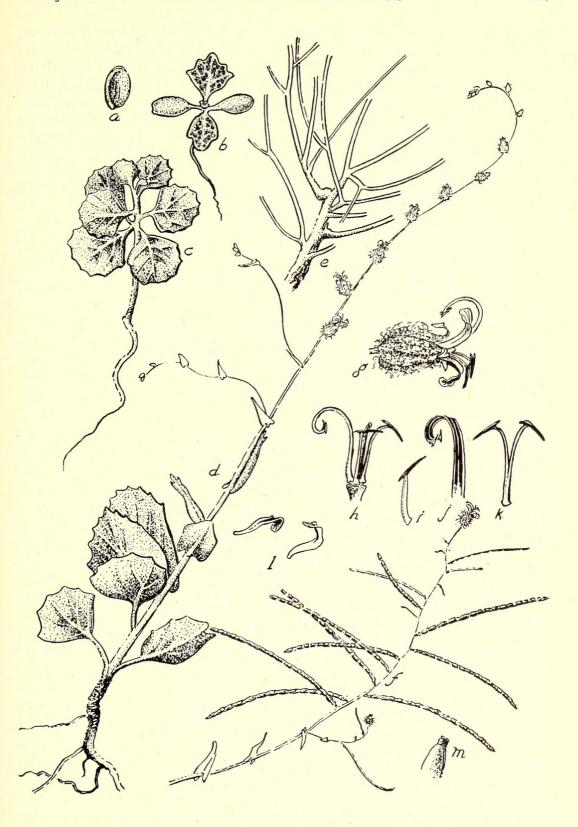


Fig. 3. Streptanthus Morrisonii subsp. hirtiflorus.

uniformly purple, long-petioled, obovate or fan-shaped, prominently veined, with margins entire basally and coarsely dentate apically; upper stem-leaves oblong-spatulate, cymbiform, clasping; flowers produced towards the tips of ascending branches; calyx greenish turning golden-yellow with age, glabrous or sparsely pubescent, up to 0.7 cm. in length; petals white turning yellowish with age, recurved at the tips, lightly veined with purple, up to 0.9 cm. long; upper filaments broadly connate, exserted, uniformly greenish-yellow, strongly recurved; siliques erect or spreading, up to 7.5 cm. in length by 0.15 cm. in width, flattened, straight, very torulose.

Type. Serpentine outcrop on low saddle ¼ mile west of White's Point, Table Mountain Road, ca. 5 miles east of Mountain Mill House, Napa-Lake County line, May 3, 1947, A. R. Kruckeberg 1438 (Herbarium of the University of California no. 939444).

Associated flora: Pinus Sabiniana Dougl., Cupressus Sargentii Jepson, Calochortus pulchellus Dougl., Fritillaria recurva Benth., Quercus durata Jepson, Ceanothus Jepsonii Greene, Eriodictyon californicum (H. & A.) Greene, Arctostaphylos viscida Parry, Silene californica Dur., Dendromecon rigida Benth., Senecio Greenei Gray.

Streptanthus brachiatus sp. nov. Herba stricta vel patens biennis usque ad 4.5 dm. alta foliis basalibus juvenibusque flabelliformibus glabris glaucis eis brassicae similibus valde venatis longipetiolatis supra tessellatis infra purpureotinctis eis superioribus orbicularibus vel orbiculari-spathulatis etiam subulatis sessilibus auriculatisque undulatis integris vel grosse serratis calycibus roseopurpureis reticulatis glabris petalis albis venis purpureis ornatis filamentis staminorum duorum superiorum eisque eorum duorum inferiorum inter se in paribus connatis eis paris lateralis liberis siliquis torulosis erectis seminibus apice alatis vel sine alis.

Strict, often somewhat woody biennial, up to 4.5 dm. tall; forming in its first year rosettes of leaves that are cabbage-like in texture, glabrous, glaucous, prominently veined, graygreen, mottled with purple-brown above, uniformly purple beneath, petioled (equaling the blade), fan-shaped, margin entire basally, coarsely dentate apically, in the second year the original stem extending and producing more or less brachiate branches bearing short-petiolate and sessile, undulate, auriculate, orbicular to orbiculate and oblong-spatulate, prominentlyveined leaves up to 2.5 cm. in width and 5.5 cm. in length with entire or coarsely serrate margins or with the margins entire basally and serrate apically, passing into narrowly-lanceolate, usually toothed bracts; flowers 0.8 cm. long, zygomorphic, ascending on pedicels 0.1-0.15 cm. long, disposed in discrete racemes, bracteate or not; calyx rose-purple with yellowish base, 0.5-0.6 cm. long, surface glabrous and reticulate with

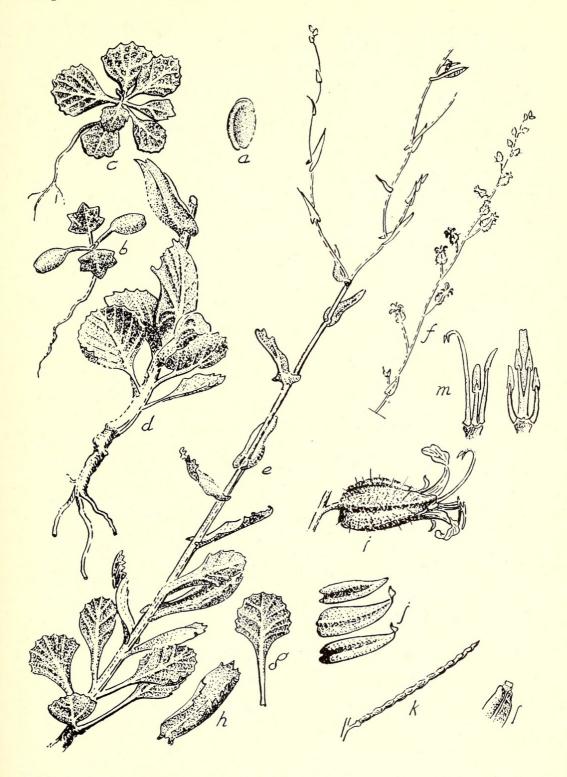


Fig. 4. Streptanthus Morrisonii subsp. elatus: a, seed, \times 5; b, seedling with cotyledons, \times 1; c, juvenile rosette of first year, \times ½; d, basal leaves, second year, \times ½; e, habit, \times ½; f, inflorescence, \times ½; g, basal leaf, \times ½; h, stem leaf, \times ½; h, lateral view of flower, \times 3; h, sepals, h0; h1, silique, h2; h3, stigma, h3; h4, stamens lateral and front views, h5.

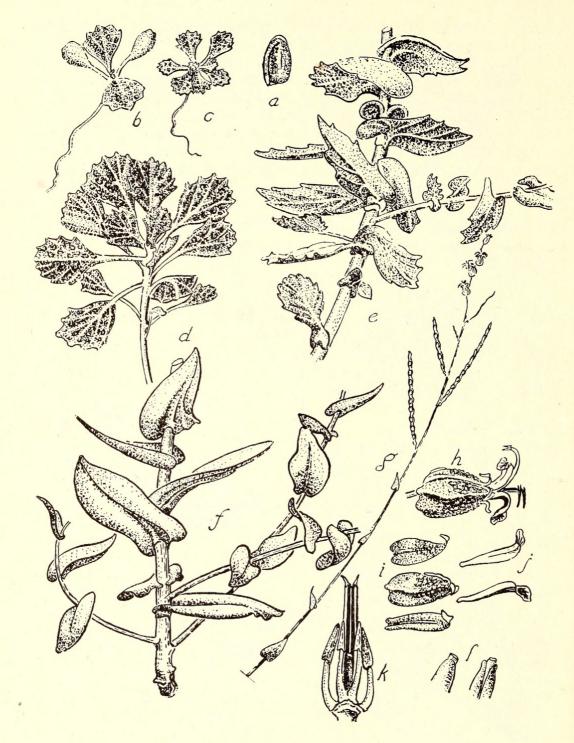


Fig. 5. Streptanthus brachiatus: a, seed, \times 5; b, seedling, \times 2; c, juvenile rosette, \times $\frac{1}{2}$; d, growth of first season, \times $\frac{1}{2}$; e, one type of adult leaves and branching, \times $\frac{1}{2}$; f, another type of leaves and branching, \times $\frac{1}{2}$; g, flowering branch with flowers and fruit, \times $\frac{1}{2}$; h, lateral view of flower, \times $2\frac{1}{2}$; i, sepals, \times 2; i, petals, \times 2; k, androecium and gynoecium, \times 3; i, stigma, \times 3.

fine lines; sepals broadly lanceolate with recurved, scarious tips, prominently keeled, the keel of the lateral sepals a deeper purple; petals white, 0.8 cm. long, recurved, the upper with faint purplish, forked veins, the lower with a deep-purple, palmate-branching blotch; stamens in three sets, the upper set 0.8 cm. long, exserted, recurved, filaments orange-colored with two, longitudinal, purple lines, connate to the reduced anthers, the lower set 0.5 cm. long, exserted, recurved, connate for about one-fifth of their length, greenish, with large anthers 0.2 cm. long, the lateral set free, 0.4 cm. long, usually included, with arcuate filaments and large anthers 0.2 cm. long; siliques erect, flattened, torulose, purplish, up to 6.5 cm. long, 0.15 cm. wide; seeds greenish-brown, narrowly-elliptic, 0.1 cm. wide, 0.25 cm. long, winged at the tip or not, cotyledons accumbent; style short; stigma round, entire.

Type. Exposed serpentine ridge near Contact Mine, east of Pine Flat, Sonoma County, California, on the Sonoma-Lake county line at an elevation of 3000 feet, June 5, 1949, Kruckeberg and Hoffman 2905 (Herbarium of the University of Cali-

fornia no. 936539).

Associated flora: Pinus attenuata Lemmon, Bromus rubens L., Poa scabrella (Thurb.) Benth., Allium falcifolium H. & A., Iris macrosiphon Torr., Quercus durata Jepson, Eriogonum vimineum Wats., Streptanthus glandulosus Hook., Adenostoma fasiculatum H. &. A., Photinia arbutifolia Lindl., Pickeringia montana Nutt., Ceanothus integerrimus H. & A., Ceanothus Jepsonii Greene, Rhamnus californica Esch., Umbellularia californica Nutt., Arctostaphylos viscida Parry, Solanoa purpurascens (Gray) Greene, Eriodictyon californicum (H. & A.) Greene, Senecio Greenei Gray, Rhus diversiloba T. & G., Sitanion jubatum J. G. Sm.

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Guerneville, California

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