

A REVISION OF *SALVIA* SECTION *HETEROSPFACE* (LAMIACEAE) IN WESTERN NORTH AMERICA

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ABSTRACT

A revision of the western North American members of *Salvia* L. section *Heterosphace* Benth. is presented. Three species are here recognized: *S. roemeriana* Scheele, *S. henryi* A. Gray, and *S. summa* A. Nels. *Salvia davidsonii* Greenm. is treated as a synonym under *S. henryi*. We present a discussion of subgeneric relationships and morphological variation of the group, as well as keys to the species, distribution maps, illustrations, and a complete account of typification and synonymy for each species.

RESUMEN

Se revisan taxonómicamente los representantes norteamericanos occidentales de *Salvia* L. sección *Heterosphace* Benth. Aquí se reconocen tres especies: *S. roemeriana* Scheele, *S. henryi* Gray y *S. summa* A. Nels. Se trata *Salvia davidsonii* Greenm. como un sinónimo de *S. henryi*. Presentamos una discusión de las relaciones subgenéricas y variación morfológica del grupo, claves para las especies, mapas de la distribución, ilustraciones y un informe completo de la tipificación y sinonimia de cada especie.

INTRODUCTION

The genus *Salvia* L. (Lamiaceae) is the largest of the mint genera, consisting of over 900 species worldwide and nearly 500 species in the New World (Alziar 1988). The present taxonomic treatment revises the western North American members of section *Heterosphace* Benth., a group of closely allied species of *Salvia* native to southwestern United States and northern Mexico placed by Briquet (1897) in subgenus *Leonia* (La Llave & Lex.) Benth. Prior to this treatment, four species were recognized in this group: *Salvia roemeriana* Scheele, *S. summa* A. Nels., *S. henryi* A. Gray and *S. davidsonii* Greenm. All are restricted generally to limestone substrates and to north- or east-facing cliffs or slopes. These species produce chasmogamous, tubular flowers that are pink, red, or purple-colored and are presumably adapted for hummingbird pollination in the spring and fall, and produce cleistogamous flowers that are self-pollinated throughout the growing season.

There has been considerable variance surrounding proposed species relationships within this group of *Salvia* (Epling 1944, 1960; Spellenberg 1993). Much of the taxonomic confusion has related to character polymorphisms within the species and to unclear specific boundaries of *S. davidsonii*. Three

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species are recognized in the present treatment: *Salvia summa*, *S. roemeriana* and *S. henryi*. *Salvia davidsonii* is synonymized with *S. henryi*.

Infrageneric relationships within *Salvia*

Despite its widespread distribution and the attention the genus has received horticulturally, there is no modern comprehensive taxonomic treatment of species or of infrageneric relationships within *Salvia*. The most recent classification of supraspecific taxa of *Salvia* (Hruby 1962) lists eight subgenera and 17 sections. Many of the subgenera and sections proposed in Hruby (1962) and proposed in the only two comprehensive treatments of the genus (Bentham 1848; Briquet 1897) are generally viewed as artificial (Hedge 1974). Over 400 new species of *Salvia* have been described since the last generic treatment in 1897 by Briquet.

The species studied in this treatment have been classified in Bentham's section *Heterosphace* by most previous workers (Briquet 1897; Fernald 1900; Neisess 1984). Section *Heterosphace* is notable in that it is the only one of the five sections of New World *Salvia* with both New and Old World members. The section is represented in the Old World by nine species native to South Africa, and one in central and eastern Africa (Hedge 1974). *Heterosphace* is represented in the New World by the southwestern USA species reported here and by *Salvia lyrata* L. of the southeastern United States. Other sections of *Salvia* native to the New World are: sects. *Audibertia* Benth. (15 species) and *Echinosphace* Benth. (4 species), both restricted to the California Floristic Province and adjacent deserts; sect. *Salviastrum* Scheele (3 species), restricted to Texas and northeast Mexico; and sect. *Calosphace* Benth. (ca. 470 species) which occurs primarily in Central and South America.

In all species of *Salvia*, only two stamens are functional; the other two stamens typical of the majority of Labiates are reduced to staminodes. In sect. *Heterosphace*, the upper two stamens are reduced to staminodes, and the lower two are fertile with the two thecae of each anther separated by an elongated connective. Whereas the majority of New World *Salvia* have sterile posterior anther thecae, sect. *Salviastrum* and sect. *Heterosphace* are unique in the New World because their posterior thecae consistently produce viable pollen. Section *Salviastrum* is distinguished from sect. *Heterosphace* by a dense annulus in the calyx and by simple leaves. Although the presence of an annulus was not noted in the initial description of sect. *Heterosphace* (Bentham 1832–1836), *S. henryi* and *S. summa* have a thin annulus, which may indicate a close relationship between sects. *Heterosphace* and *Salviastrum*. Section *Salviastrum* has been described as “...nearest *Heterosphace*, from which it differs in habit and in the calyx closed by hairs” (Torrey 1859). Further investigations into the relationship between these two groups are necessary based on their sharing of an an-

nulus and the fertile posterior anther thecae. The relationship of species in these two sections to the Texas endemic *Salvia penstemonoides* Kunth & Bouche, which shares characters of both sections, has not been resolved.

MORPHOLOGY AND CHARACTER ANALYSES

Morphological investigations were conducted on 537 herbarium specimens from 13 herbaria (ARIZ, ASU, GH, MEXU, MO, NMC, NY, OKL, RM, RSA, SRSC, TEX, UTEP; Holmgren et. al. 1990) and on live plants collected from 29 native populations (listed with specimens examined). Each population collection was based on material from 5–10 individuals. Analyses of morphological variation were conducted on individuals or collections representing a total of 59 localities: 13 localities for *Salvia summa*, 22 localities for *S. roemeriana*, and 24 localities for *S. henryi*. Localities were selected to represent the geographic range and extent of morphological variation of each species. The specimens examined are indicated in the list of representative specimens examined for each species.

Morphological data were scored for thirty-seven characters that had been used previously to classify and identify species in the group. Results were tabulated and morphological characters were evaluated for their utility to discriminate among species in the group. Representative characters employed by past authors to distinguish among species include: height of plant, petiole length, leaf length, leaflet number, leaf shape, calyx length, calyx lip length, calyx pubescence, calyx tube length, corolla color, corolla length, corolla lip length, corolla shape, corolla throat width, exertion of stamens, and symmetry of style branches (Epling 1960; Peterson ined.; Correll & Johnston 1970). The characters we found most useful in differentiating among species in this treatment are leaflet size, calyx length, calyx tube length, corolla length and color, and corolla lip length (Table 1).

Habit

Each species is a mildly aromatic perennial herb from a woody caudex; the stems generally die back to the rootstalk or to basal leaves in the winter. Height of the plant ranges from 1–9 dm; number of stems ranges from one to many. Observations among natural populations and plants cultivated in greenhouse conditions suggest that habit is variable and affected by environmental factors such as exposure to sun and availability of water. It is not unusual to find two plants of the same population demonstrating distinctly different growth habits, one with simple leaves and flowers in the axils of leaves, and the other with compound leaves and a distinct inflorescence. Such differences usually are associated with occurrence at the edge of a stream or on a cliff face above it. Individuals displaying such characteristics that are transplanted and grown in a greenhouse under equivalent environmental conditions assume similar growth forms.

TABLE 1. Variation among diagnostic morphological characters in three species of *Salvia* sect. *Heterosphace*.

	<i>S. roemeriana</i> (N=22) mean (range)	<i>S. henryi</i> (N=24) mean (range)	<i>S. summa</i> (N=13) mean (range)
Calyx Length (mm)	11.8(8–15)	10.2(7–13)	8.5(8–11)
Calyx Tube Length (mm)	6.8(5–9)	4.2(3–6)	3.1(2–5)
Corolla Length (mm)	33(24–47)	34(28–39)	39(26–48)
Corolla Lower Lip Length (mm)	7.1(6–9)	4.4(2–6)	8.3(7–12)
Ratio of Lateral Leaflet Length/ Terminal Leaflet Length	0.23(0.05–0.31)	0.61(0.44–1.16)	0.54(0.43–0.75)
Corolla Color	Red/Scarlet	Red/Scarlet	Pink/Purple

Leaf shape, division and texture

The plasticity of leaf characters also has been examined in experiments conducted under uniform greenhouse conditions. Individuals of *S. summa* with compound leaves of 5–7 leaflets in natural populations, consistently produce simple leaves when grown in the greenhouse with a daily watering regimen. *Salvia roemeriana* exhibits less plasticity than the other species, and consistently produces either simple leaves or leaves with 2–4 small lateral leaflets. Regardless of growth and environmental conditions, the terminal leaflet of *S. roemeriana* maintains a reniform to cordate shape; if lateral leaflets form, they are consistently less than 1/3 the length of the terminal leaflet (Table 1). The leaves of *S. henryi* and *S. summa* are rarely simple, and the lateral leaflets are greater than 1/3 the length of the deltoid terminal leaflet.

Salvia roemeriana is distinctive among the species examined due to the close resemblance of the basal and cauline leaves (Fig. 3). *Salvia henryi* and *S. summa* generally demonstrate dimorphic leaves; the basal leaves are compound, and the cauline leaves often simple and graded into the bracts of the inflorescence. In all three species, pubescence type varies between cauline and basal leaves. This variation is particularly evident in *S. summa* where the compound basal leaves generally have a thick vestiture of grayish trichomes and the simple cauline leaves are more sparsely pubescent. Whereas the basal and cauline leaf margins of *S. roemeriana* are generally crenate, those of *S. henryi* and *S. summa* are irregularly-toothed.

Pubescence

Pubescence is always present on vegetative and reproductive structures in these species, although indumentum is variable and includes pilose, setose, hirsute, densely rusty pubescent, white tomentose, and sparsely pubescent. The only pubescence character we find to be reliable in distinguishing species is that of the calyx; consistently hirsute in *S. henryi* and *S. summa* contrasted to a

puberulous vestiture in *S. roemeriana*. Resinous dotting is always represented on stems, leaves and calyces, although it varies considerably between populations. Vegetative pubescence varies similarly and is not used to differentiate species in this treatment.

Inflorescence

The inflorescence of *S. roemeriana* is well-defined and raceme-like, with bracts to nearly 1.0 cm long and with 2–6 flowers/verticillaster. *Salvia henryi* and *S. summa* occasionally exhibit a well-defined inflorescence, but more often there is a gradation from solitary flowers in the axils of cauline leaves to a raceme-like inflorescence with 4–6 flowered verticillasters and bracts of 0.5 cm in length. Flowers borne in the axils of cauline leaves always are cleistogamous, whereas fully chasmogamous flowers are only borne in the verticillasters. In all species, the persistence and size of bracts is variable.

Cleistogamy and Polymorphism in Corolla Size and Shape

Two of the most taxonomically significant characters in sect. *Heterosphere* are corolla polymorphism and cleistogamy. Cleistogamy has been documented in the species studied here, as well as in the closely related *S. lyrata* of the southeastern USA (Uttal 1963) and in African species of the genus (Hedge 1974). Inflorescences of each of the species observed throughout a growing season under greenhouse conditions produce fertile flowers ranging from fully closed cleistogamous flowers less than 0.5 cm long, to barely open flowers of 1.0 cm in length, to fully developed flowers of 3.5 cm or more. With the initial flush of growth in the early spring, fully developed chasmogamous flowers are produced. As the season progresses, progressively smaller flowers are produced from the same indeterminate inflorescence. This was observed among *S. henryi*, *S. roemeriana*, and *S. summa*, and consisted of chasmogamous flowers grading to smaller flowers continued until exclusively cleistogamous flowers were produced in late spring and summer. In the fall, the sequence is often reversed; cleistogamous flowers grade into small chasmogamous flowers until eventually fully developed chasmogamous flowers are produced. In wild populations of *S. henryi*, *S. roemeriana* and *S. summa*, the only time of year when plants were not observed with cleistogamous flowers was in spring. All flowers, regardless of size, have fertile pollen and can produce four viable nutlets, although preliminary observations found a lower number of nutlets produced in fully chasmogamous flowers than in cleistogamous flowers. Despite variation in size and shape of the corolla, calyx and nutlet characters remain relatively constant.

Calyx

The calyx provides reliable characters by which to distinguish species (Fig. 1, A,D,G). The upper lip of the calyx is two or three-lobed and the lower is two-lobed. The calyces of all species are persistent, and the previous year's calyces are often found on the dried inflorescences adjacent to flowering inflorescences.

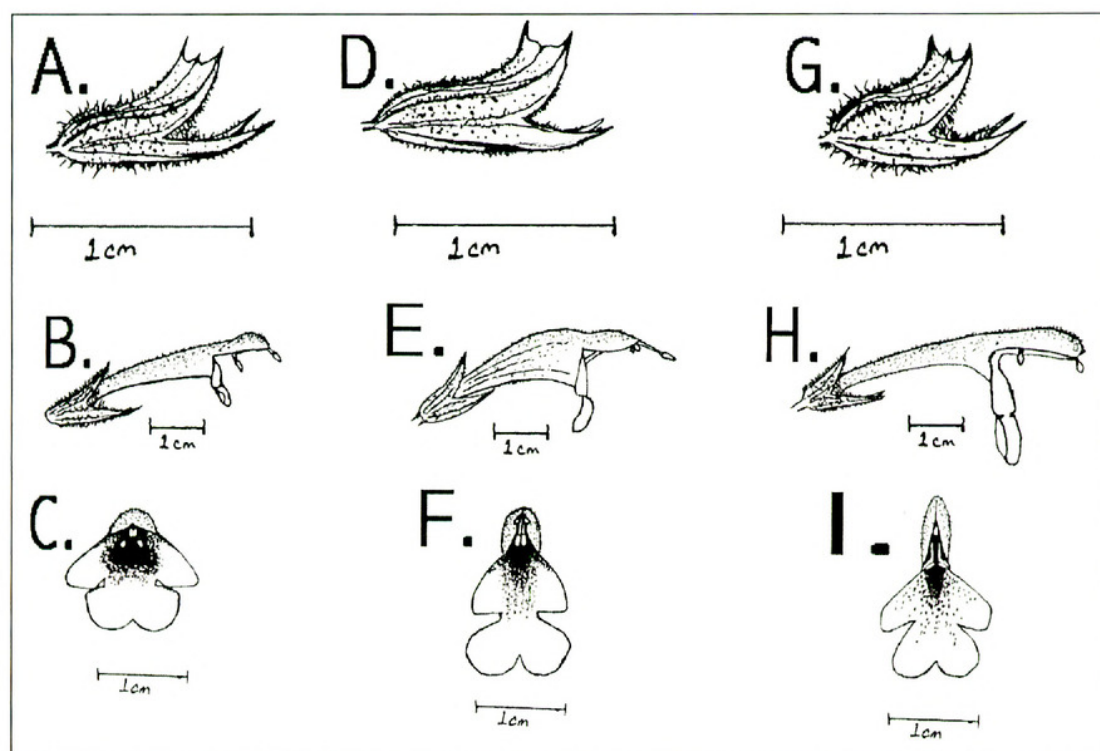


FIG. 1. Morphological features of western North American species of *Salvia* section *Heterosphace*. Floral morphology of *Salvia henryi* (A–C), *Salvia roemeriana* (D–F), and *Salvia summa* (G–I): A, D, G. Oblique view of calyx. B, E, H. Lateral view of corolla. C, F, I. Frontal view of corolla.

Salvia summa always has a shorter calyx tube than *S. roemeriana*, but calyx length and calyx tube length overlap between *S. summa* and *S. henryi* (Table 1). *Salvia roemeriana* and *S. henryi* are not significantly different ($p > 0.05$) in calyx length, but these species exhibit consistent differences in calyx pubescence and structure.

The calyces of both *Salvia summa* and *S. henryi* are hirsute pubescent, with ciliate nerves and a bearded sinus resulting from a thin annulus present in the calyx throats. The calyx of *Salvia roemeriana* is uniformly puberulous on the exterior of the calyx and naked within.

Salvia roemeriana has a repressed (0–0.2 mm) middle upper lobe of the calyx, compared to the larger middle upper calyx lobe in *S. summa* (average = 1.2 mm) and *S. henryi* (average = 1.0 mm). In addition, the apices of each calyx lobe of *S. henryi* and *S. summa* are generally rigid and spine-tipped, whereas the apices of *S. roemeriana* are less rigid.

Corolla

The corollas of these species are tubular and bilabiate; the upper lip has two lobes which are often folded together at the apex, and the middle lobe is the largest of the three lower lobes. Cleistogamy and polymorphism in corolla size and shape complicates the use of corolla characters in identification and clas-

sification. Because of size variation among corolla characters, only fully developed, chasmogamous flowers provide reliable morphological characters by which to classify and identify species.

The corolla characters most useful in distinguishing *S. summa* from the other species are differences in corolla length and color. Fully chasmogamous flowers of *S. roemeriana* and *S. henryi* average 3.4 cm long and are scarlet or red, whereas those of *S. summa* average 4.2 cm and are purple or pink (Table 1, Fig. 1 B,E,H). Additionally, the corolla throat of *S. roemeriana* and *S. summa* is taller than wide, compared to *S. henryi* which is wider than tall (Fig. 1, C,F,I). Whereas *S. henryi* has a straight corolla, the corolla of *S. roemeriana* and *S. summa* is arcuate. Finally, although the length of the upper lip of the corolla does not significantly differ among the three species, the lower lip of *S. roemeriana* (avg. 7.1 mm) and *S. summa* (avg. 8.3 mm) is equal to or longer than their respective upper lips, and the lower lip of *S. henryi* (avg. 4.4 mm) is shorter than its upper (Table 1, Fig. 1). With fresh material, when the two lobes of the corolla are pressed together, only in *S. henryi* will the upper lobe exceed the lower.

Androecium

One of the diagnostic characters of *Salvia* section *Calosphace* is the fusion of the sterile posterior anther thecae into a rudder which blocks the throat of the corolla. In sect. *Calosphace* this rudder acts as a lever, which is pushed by the pollinator as it attempts to access the nectary at the base of the corolla (Serna & Ramamoorthy 1993). This action deposits the pollen on the head or back of the pollinator; the fulcrum of the lever is the junction of the filament and the elongate connective. A similar floral mechanism is shared by members of sect. *Heterosphace* except that the posterior thecae are fertile and not fused. In chasmogamous flowers, the posterior thecae block the throat of the corolla in *S. henryi* and *S. summa*, but do not block the throat of *S. roemeriana*, thereby affecting the lever mechanism of pollen deposition in the latter. The difference in thecal placement and mechanism is only visible in fresh material and is not observable on herbarium specimens. In fully chasmogamous flowers of *S. roemeriana*, the two staminodes develop to 5 mm in length; anthers were never observed to develop on the staminodes.

Gynoecium

Style characters, such as exsertion from galea and symmetry of stylar branches, have been used in previous treatments (Peterson, in ed.) to differentiate species, but our observations indicated these characters were not informative taxonomically. Whereas the upper style branch had previously been reported to be absent or less than 0.5 mm in *S. henryi* (Peterson, in ed.), our observations found considerably more variation (0 to 4.1 mm) in the upper branch of the style both in fresh and dried material. Symmetry of stylar branches was not found to vary

significantly among the species included in this treatment. Variation in the length of the style was observed in *S. roemeriana* and *S. henryi*. For example, style lengths in fully developed, chasmogamous flowers on the same inflorescence of a plant representative of *S. henryi* ranged from 2.5 cm and included within the galea, to 4.1 cm and exerted 1.2 cm from the galea. Because heterostyly has been documented in sect. *Audibertia* (Neisess 1984), the role the variation in style length plays in *S. henryi* and *S. roemeriana* needs further investigation.

As with all species of *Salvia*, the bi-loculed, bi-carpellate ovaries of sect. *Heterosphace* divide to produce a maximum of four nutlets. A comparative study of nutlet characters for species in sect. *Heterosphace* and other sections of *Salvia* (J. Walker, unpublished data) showed uniformity in nutlet size and pericarp anatomy among *S. roemeriana*, *S. henryi*, and *S. summa*. Additional studies by Hedge (1970), Ryding (1995), and Wojciechowska (1958) indicate that pericarp anatomy is potentially useful for resolving supraspecific relationships in *Salvia* and for testing proposed taxonomic relationships among New World and Old World species of the genus. The uniformity in nutlet characters in the three species in question further support the closely related nature of these species.

CHROMOSOME NUMBERS

Mitotic counts made by the senior author yielded sporophyte chromosome numbers of $2n = 28$ among populations of *S. roemeriana*, *S. henryi*, and *S. summa*. The specimens used in chromosome counts are indicated in the list of representative specimens for each species. Published diploid counts of $2n = 28$ are represented in only three other species of *Salvia* (Hedge 1974), all of which are native to northern Africa and none of which is placed in sect. *Heterosphace*: *S. aegyptiaca* L. (also $2n = 12, 26$ reported), *S. chudaei* Battand. & Trab., and *S. taraxicifolia* Hook. (also $2n = 26$ reported; Goldblatt 1981). Of the ten African species currently placed in sect. *Heterosphace*, chromosome counts are known from only two, *S. nilotica* Juss. ex Jacq. ($2n = 30$) and *S. aurita* L.f. ($2n = 18$) (Hedge 1974). Radford et al. (1964) reported $2n = 18$ for *S. lyrata* L., the only other New World representative of sect. *Heterosphace*, although this count was not verified through a literature reference. Further investigations of chromosome number variation are needed to elucidate base numbers and the extent of polyploidy and aneuploidy in sect. *Heterosphace* and in the genus *Salvia*. However, Hedge (1974) reported base numbers $x = 7, 8, 9, 10$, and 11 for African species of *Salvia* and concluded that chromosome numbers shed "...little light upon species affinities or evolutionary developments in the genus."

GEOGRAPHIC DISTRIBUTION

Salvia roemeriana is the most widely distributed of the species investigated here; it ranges from south-central Texas to central Mexico (Fig. 2). In Mexico, the species is found throughout the state of Coahuila and is restricted to the

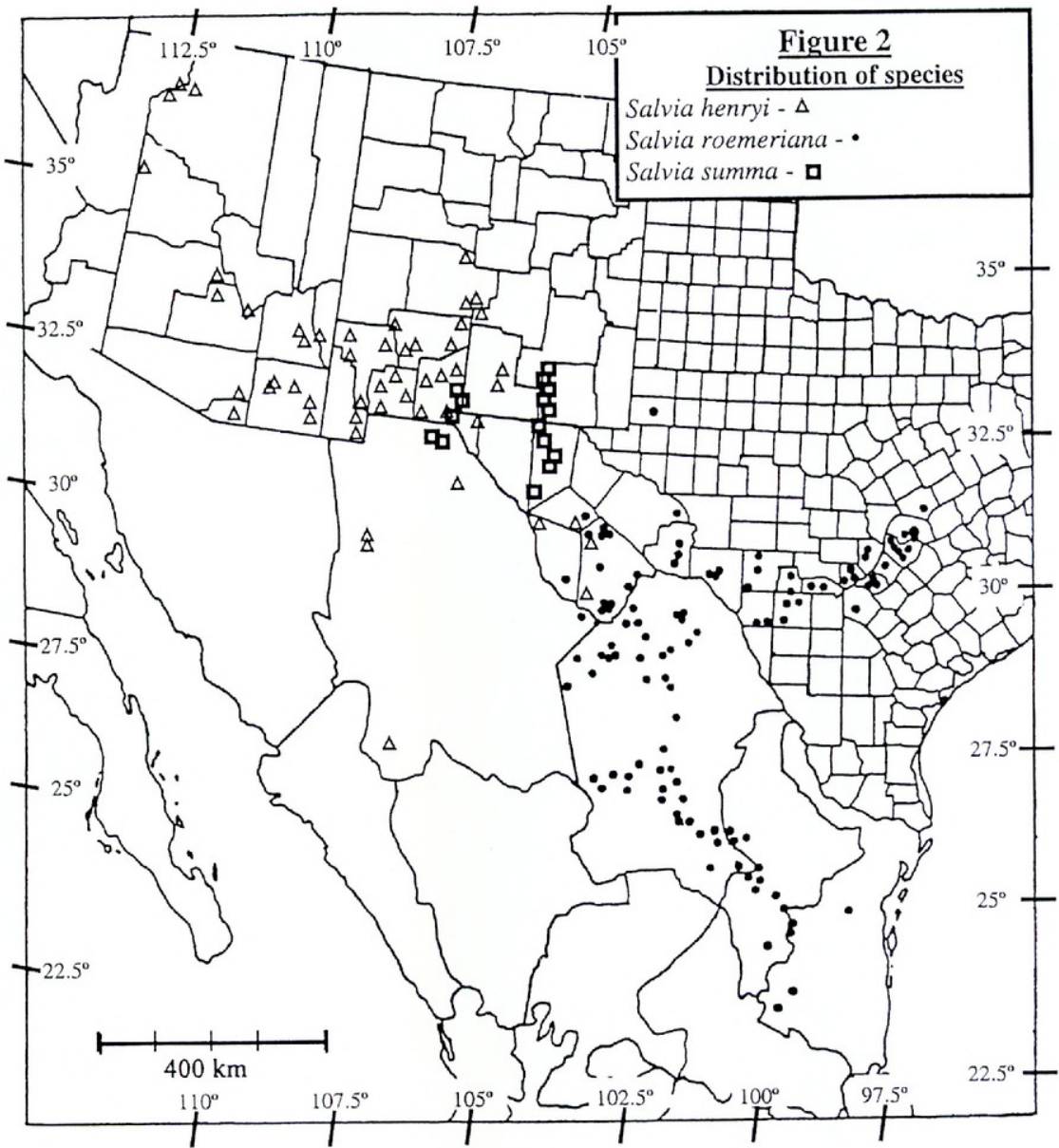


FIG. 2. Distribution of *Salvia henryi*, *Salvia roemeriana*, and *Salvia summa*.

Sierra Madre Oriental to southern regions of the state of Tamaulipas. The range of *S. henryi* is centered in south-central New Mexico and southeastern Arizona, with disjunct populations in the central and southern parts of the state of Chihuahua and as far west and north as the Grand Canyon region in Arizona. *Salvia summa* is restricted to limestone outcrops in mountain ranges of southeastern and south-central New Mexico.

Salvia summa, *S. henryi* and *S. roemeriana* are morphologically and geographically distinct and overlap in range with one another in only two regions (Fig. 2). In both of these areas of sympatry, hybridization, which is well documented in *Salvia* (Emboden 1971), may be present. The Oscura Mountains of

south central New Mexico is a zone of sympatry between *S. summa* and *S. henryi*. Several collections from this area (Spellenberg & Anderson 10865, Anderson & Morrow 5085) exhibit intermediacy in vegetative and calyx characters between these species, which suggests interspecific hybridization. A similar example of sympatry and possible hybridization is the Big Bend region of Texas and Mexico, continuing northwest along the Rio Grande. This is the only region where the distributions of *S. henryi* and *S. roemeriana* overlap, and a number of collections demonstrate morphological intermediacy (Hinckley 1669, Worthington 4425). Plants from this area possess the calyx pubescence and spine-tipped calyx lobes of *S. henryi*, but have a suppressed middle upper lobe of the calyx and a red-tinged calyx, both of which are similar to *S. roemeriana*. Experimental studies are needed to test these hypotheses of hybridization.

TAXONOMY

Key to the Species

1. Corolla red; fully chasmogamous corolla less than 3.8 cm long
 2. Lower lip of corolla shorter than upper; corolla straight; calyx sinus bearded; lateral leaflets greater than 1/3 the length of the terminal. _____ **1. *Salvia henryi***
 2. Lower lip of corolla equal to or longer than upper; corolla arcuate; calyx sinus naked; lateral leaflets less than 1/3 the length of the terminal. _____ **2. *Salvia roemeriana***
1. Corolla pink to purple; fully chasmogamous corolla 3.8 cm to 4.8 cm long. _____ **3. *Salvia summa***

1. *Salvia henryi* A. Gray (**Figs. 1 A,B,C**), Proc. Amer. Acad. Arts 8:368. 1872. TYPE: U.S.A. NEW MEXICO: on the Mimbres, May 1851, *Thurber 245* (LECTOTYPE, here designated: GH!; ISOLECTOTYPE: NY!). U.S.A. NEW MEXICO: Mimbres, *Henry s.n.* (SYNTYPE: GH! #1552). U.S.A. 1849. *Wright s.n.* (SYNTYPE: GH! #1551). U.S.A. NEW MEXICO: River Mimbres, *Bigelow s.n.* (SYNTYPE: NY! #7479).

Thurber 245 is selected as lectotype due to the complete nature of the collection, the presence of fully chasmogamous flowers, and its distribution at two major herbaria.

Salvia davidsonii Greenm., Proc. Amer. Acad. Arts 41:246. 1905. TYPE: U.S.A. ARIZONA: Chiricahua Mountains, Sep 1881, *Lemmon 3077* (LECTOTYPE, here designated: GH!). U.S.A. ARIZONA: Southern Arizona, *Lemmon 492*, (SYNTYPE: GH!) U.S.A. ARIZONA: Metcalf, Oct 1900, *Davidson 615* (SYNTYPE: GH!, RSA!).

Lemmon 3077 is selected as lectotype due to its being the most complete specimen, although still containing only cleistogamous flowers.

Salvia blumeri Greene *nom. nud.* U.S.A. ARIZONA: Chiricahua Mts., Paradise, Cedar Gulch, 24 Sep 1907, *Blumer s.n.* (GH!, MO!).

Perennial to 6 dm from woody caudex. Stems erect to trailing, generally unbranched, one to several. Stem puberulous to pilose or hirsute, sparsely resinous dotted. Basal leaves generally pinnately compound, 3–5(–7) foliate, terminal leaflet deltoid, lateral leaflets greater than 1/3 the length of the terminal. Cauline leaves often simple, deltoid or less frequently cordate/reniform and reduced upwards and grading into bracts. Margins of all leaves irregularly toothed and lobed. Leaf size and shape quite variable depending on environment and time of year.

Inflorescence raceme-like to 25 cm, verticillasters 5–10, each bearing 1–6 flowers. Lower-most bracts most often indistinguishable from uppermost leaves, the flowers thus appearing axillary in some instances. Bracts rarely deciduous. Calyx 8–11(–13) mm long, the tube 3–6 mm, hirsute outside, particularly on veins, puberulous inside with thin annulus, sinuses bearded. Lobes of calyx firmly mucronate, middle upper lobe 1 mm (occasionally suppressed). Calyx green throughout. Corolla red, puberulous, generally not arched, 3.0–3.8 cm, often reduced and cleistogamous. Upper lip of corolla galeate, 6–8 mm, lower middle lobe 2–6 mm, the lower lip of the corolla shorter than the upper. Corolla throat 5–6 mm in height, wider than tall. Upper anther thecae exerted as much as 6 mm from the galea, the lower anther thecae bent downward into throat of corolla. Style bifid, exerted from galea, top branch 1–2 mm, lower branch 2–6 mm. $2n = 28$.

Producing fully developed, chasmogamous flowers April–May. Cleistogamous flowers produced May–October.

Distribution and habitat.—Preferring limestone talus or cliffsides, in canyons or north-facing slopes; 800 m–2000 m. Texas along Rio Grande and canyons in Brewster, Presidio, Jeff Davis, Hudspeth and El Paso counties; New Mexico in Otero County west to Arizona and north to northern Socorro County; Arizona in eastern Pima County, north to Maricopa County and in disjunct populations northwest to Grand Canyon. Mexico along Rio Grande (Rio Bravo) and west to Santa Eulalia Mountains in Chihuahua, with a disjunct population in southern Chihuahua.

Comments.—The three individuals which serve as syntypes for *S. davidsonii* were plants collected late in the flowering season (September and October) and had cleistogamous flowers with corollas 1 cm long or less. Subsequent collections made earlier in the growing season by other botanists at the type localities exhibited fully chasmogamous flowers with corollas to 3 cm long (see discussion under corolla characters). The foliar and inflorescence characters outlined in Greenman's description were all commonly found in populations of *S. henryi*. Greenhouse-grown plants propagated by seed from New Mexico populations of *S. henryi* and from a type locality of *S. davidsonii* (Chiricahua Mts., north of Paradise, AZ) were similar morphologically and appeared to be conspecific. For the above reasons, *S. davidsonii* is treated as a synonym with *S. henryi*, the latter having priority by 33 years.

Disjunct populations of *S. henryi* in Arizona occur along Fish Creek in Maricopa County, Peoples Spring in the Arrastra Mountains in Yavapai County, and various locations along the Grand Canyon of the Colorado River. Each of these disjunct populations have plants with slight morphological differences. Most of the differences observed, such as simple leaves, larger growth habit, and pink or purple flowers, may be the result of environmental conditions; these characters are apparently phenotypically plastic and not suitable to delimit

infraspecific taxa. Collections from populations growing along an environmental gradient, from mesic and shaded to xeric and exposed, showed variation in leaf shape from simple to compound, and in corolla color from red to pink to purple. Additional investigation is required to determine the basis for the observed morphological variation.

Common name.—Henry's Sage.

Representative Specimens: * = Specimens used in analyses of morphological characters. † = Specimens used in chromosome counts. **UNITED STATES. ARIZONA. Cochise Co.:** Chiricahua Mts, 2mi N of Paradise, 2 May 1935, *Maguire 11134* (NY)*; Little Dragoon Mts, NE of Benson, E of San Pedro River, 5 May 1993, *Van Devender 93-632* (ARIZ)*. **Coconino Co.:** Havasupai Cyn, 23 May 1941, *Whiting 1047* (ARIZ)*; Colorado River, Matkatamiba Cyn, 26 Oct 1990, *Scott 882* (NYBG)*; Matkatamiba Cyn, mi 148 of Colorado River, 18 May 1973, *Phillips s.n.* (ARIZ)*. **Gila Co.:** Pinal Mts, S of Globe, Jun 1995, *Walker 1971* (OKL)†. **Graham Co.:** Upper Gila River drainage, 20 Apr 1978, *McGill 2376* (ASU, NYBG, TEX)*; Bonita Creek between Midnight Cyn and San Carlos Indian Reservation, 21 Apr 1978, *McGill 2388* (ASU, RSA)*. **Greenlee Co.:** 15mi N of Clifton, 7 Jun 1935, *Maguire 11854* (NY)*; 14 mi N of Clifton, 1 Apr 1960, *Crosswhite 803* (ASU)*. **Maricopa Co.:** Fish Creek, 1 Apr 1926, *Peebles 5233* (ARIZ)*. **Mohave Co.:** along Colorado River, 1/4mi below Matkatamiba Cyn, 4 May 1970, *Holmgren 15536* (ARIZ, GH, NY); Frasier's Well, off hwy 93, between Wickenburg and Kingman, 2 Nov 1968, *Niles 906* (ARIZ)*. **Pima Co.:** Empire Mts, 31 May 1987, *Montgomery s.n.* (ARIZ)*. **Pinal Co.:** Superstition Mts, Fremont Pass, 24 Mar 1972, *McGill 433* (ASU)*. **Santa Cruz Co.:** Santa Rita Mts, 25 May 1884, *Pringle s.n.* (GH, NY); west end of Canelo Hills, above Monkey Springs, 11 Jun 1978, *Kaiser 1193* (ARIZ). **Yavapai Co.:** Southern Arastra Mts, People's Cyn, South People's Spring, 4 Jun 1979, *Fischer 6628* (ARIZ, ASU)*. **NEW MEXICO. Dona Ana Co.:** 43 air km NNE of Las Cruces on W side of San Andres Mts, 15 May 1993, *Spellenberg 11799* (BRIT, MT, NMC); East Portrillo Mts, 25 Apr 1992, *Worthington 20581* (UTEP)*; 11 air mi NW of Las Cruces, N end of Robledo Mtn, 27 Apr 1983, *Spellenberg 7007* (NMC)*. **Grant Co.:** 10mi NE of Red Rock, 21 May 1935, *Maguire 11552* (ARIZ); Little Hatchet Mts, Howell's Ridge, 14 May 1992, *Worthington 20802* (UTEP). **Hidalgo Co.:** Big Hatchet Mts, 2 air mi NNE from top Big Hatchet Peak, 19 May 1992, *Worthington 20891* (UTEP). **Lincoln Co.:** 12 mi E of Carizozo, 22 May 1987, *Barneby 18236* (NY)*; WSMR, Oscura Mts, Cottonwood Spring, 3 Jun 1993, *Anderson 6205* (TEX)*. **Luna Co.:** Florida Mts, Mahoney Park, 18 Apr 1982, *Worthington 8117* (ASU)*. **Otero Co.:** Sacramento Mts, Dog Cyn, 3 Jun 1979, *Van Devender s.n.* (UTEP, ARIZ)*; Sacramento Mts, 0.3mi W of Fresno Cyn Tunnel, 11 May 1980, *Worthington 5898* (ARIZ, UTEP)*. **Sierra Co.:** Fra. Cristobal Range, cliffs of S side of Chalk Gap, 16 Jun 1981, *Van Devender 16191* (UTEP); Bear Den Cyn, WSMR, 28 Aug 1991, *Anderson 5085* (NMC). **Socorro Co.:** White Sands Missile Range, N end of Oscura Mts, 19 Aug 1991, *Spellenberg 10865* (NMC, UNM, NY, MO, RSA, ID, UC, TEX)*. **TEXAS. Brewster Co.:** 4mi NE of Lajitas, 18 Apr 1973, *Jump s.n.* (ARIZ). **El Paso Co.:** Franklin Mts, 6 May 1983, *Worthington 10287* (UTEP)*; Franklin Mts, 8 Apr 1978, *Worthington 2508* (UTEP)*; Hueco Pass, Hueco Mts, 27 Apr 1976, *Butterwick 2619* (TEX)*. **Hudspeth Co.:** Central Hueco Mts, along hwy 180 near Hueco Inn, 26 Apr 1975, *Everitt 75255* (ARIZ). **Jeff Davis Co.:** N of Alpine in Fern Cyn, 20 Apr 1938, *Warnock T399* (TEX). **Presidio Co.:** at base of south bluff in Bracks Cyn, 11 Jun 1941, *Hinckley 1669* (GH, NY, SRSC)*.

MEXICO. Chihuahua: Santa Eulalia Mts, Apr 1886, *Pringle 704* (MEXU, TEX)*; Canon del Rayo at northern end of the Sierra del Diablo, 25 Jul 1941, *Stewart 907* (TEX); 23 air mi ENE of Villa Ahumada in northwestern cyn of Sierra de la Alcaparra NE of Rancho El Palmar, 12 Sep 1973, *Henrickson 12853b* (TEX); SE of Lajitas, TX, 5 May 1979, *Worthington 4425* (UTEP)*.

2. *Salvia roemeriana* Scheele (Figs. 1 D,E,F, Fig. 3), *Linnaea* 22:586. 1849. TYPE: U.S.A. TEXAS: fertile soil in shady woods on the upper Guadalupe, *Lindheimer 145* (LECTOTYPE, here designated: GH!; ISOLECTOTYPE: MO!).

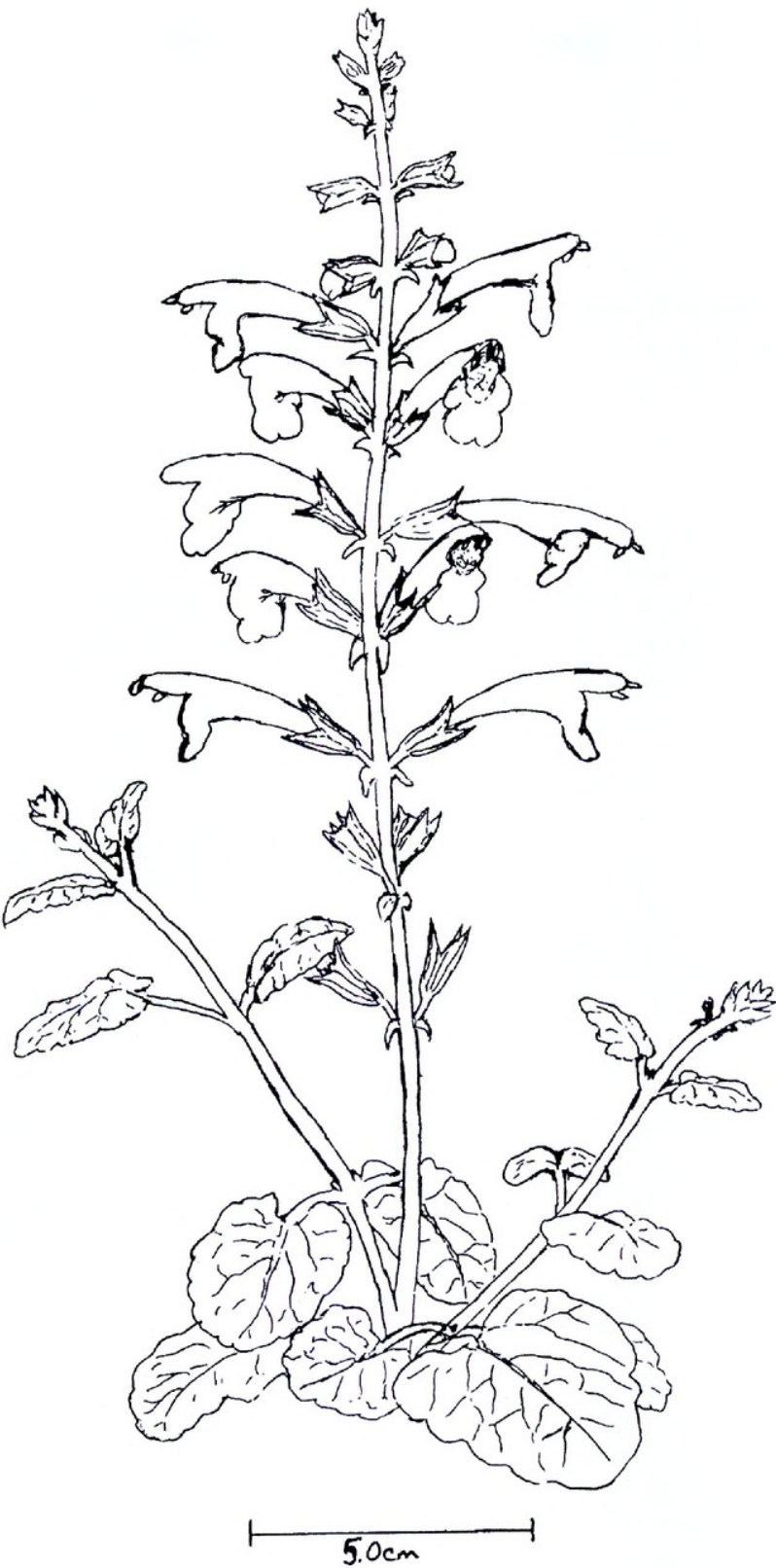


FIG. 3. Habit of *S. roemeriana* (adapted from Decaisne 1854).

Scheele described this species from a Roemer collection (In silva prope Neubraunfels leg. Roemer. Aprili). However, no Roemer collection of *S. roemeriana* is present in any of the herbaria surveyed within this project. Neither are any at the Munich herbarium (M) where many of Scheele's specimens are deposited. Roemer was in the vicinity of New Braunfels, Texas both in April of 1846 and 1847. During the April of 1846, Roemer's journal states he collected with Lindheimer in the New Braunfels area (Mueller, 1935). As is recounted by McKelvey (1955) "Lindheimer and Roemer made many botanical excursions together during 1846...At the end of the season they appear to have exchanged a set of the collections made by each during the year and Roemer, on his return to Germany, placed Lindheimer's with his own botanical specimens in the hands of Adolph Scheele who...published the descriptions in Linnaea from 1848 to 1852. Not only did he publish the 'new species' of Roemer's collecting, but also those found among Lindheimer's duplicates, though he knew that Englemann and A. Gray had already undertaken to describe these collections in their *Plantae Lindheimerianae*, and so industriously did he continue his work that he soon completely outdistanced his American competitors and left little for them to describe." Owing to the lack of any Roemer collections of *S. roemeriana*, the authors of this paper assume that the type specimen was not a Roemer collection as suggested by Scheele, but the Lindheimer collection here designated as lectotype.

Salvia porphyrantha Decne, Rev. Hort. ser. 4, 3:301. 1854. TYPE: This species was described from specimens grown from seed at the Paris Museum. The source of the seed is unknown. *Salvia porphyrata* Hook, Bot. Mag. t.4939. 1856. (orth. var.)

Perennial to 9 dm from woody caudex. Stems erect to trailing, generally unbranched, one to several. Stem puberulent to white tomentose or densely rusty pubescent, most often pilose-setose, sparsely or rarely densely resinous dotted. Basal and cauline leaves similar, petiolate, simple or 3-5 foliate with lateral leaflets not greater than 1/3 the length of the terminal leaflet. Lateral leaflets sessile (rarely petiolate), orbicular and irregularly toothed, occasionally reduced to tooth-like appendages. Terminal leaflet 1-5 cm, cordate to reniform, crenate or less often irregularly toothed, often denticulate. Leaves often somewhat rugose, pubescence variable and generally reflecting that of the stem. Inflorescence an raceme-like, 5-15(-30) cm, verticillasters 4-10(-17), each bearing 1-6 flowers. Bracts generally distinct from cauline leaves and reduced upwards, early deciduous or persistent. Calyx puberulous and sparsely resinous dotted outside, naked inside, (8-)10-12(-15) mm long, the tube 3-6 mm long. Middle upper lobe of the calyx generally suppressed (occasionally expressed and 0.1-0.3 mm) lower lip 2-lobed, softly mucronate. Calyx green blending to red at the apex of the lobes. Calyx sinuses naked. Corolla red, puberulous, arcuate, 2.8-3.6(-4.7) cm, often reduced and cleistogamous. Upper lip of corolla weakly galeate, 6-8 mm, lower middle lobe 6-9 mm, the lower lip equal to or longer than the upper. Corolla throat 5-7 mm in height, taller than wide. Two staminodes to 5 mm in fully chasmogamous flowers. Upper anther thecae included or exerted as much as 6 mm from the galea, the lower anther thecae bent outward or rarely

somewhat downward. Style bifid, exerted from galea, top branch 1 mm, lower branch 2–3 mm. $2n = 28$.

Producing fully developed, chasmogamous flowers March–May. Cleistogamous flowers produced May–October.

Distribution and habitat.—Preferring limestone cliffs and talus and juniper or oak/pine woodlands; 500 m – 2000 m. Texas along Edwards Plateau and north to Bell County, west to Presidio County. Mexico along Rio Grande (Rio Bravo) from Big Bend National Park and south along Sierra Madre Oriental to southern Tamaulipas.

Comments.—Several local variants characterize *S. roemeriana*. For example, a densely rusty pubescent form of *S. roemeriana* is found in the vicinity of Melchor Muzquiz in Coahuila and a densely white pubescent form is found along the coastal plain northeast of Ciudad Victoria in Tamaulipas. Individuals of *S. roemeriana* found in the Sierra Madre Oriental south of Monterrey are considerably larger than their northern counterparts and reach a meter in height, with flowers of 4.7 cm long. Because there exists a continuous gradation of size and pubescence types among each of these local variants and the more northern members of the species, discrete morphological and geographic groupings are not apparent and subspecific rank is not warranted.

Salvia roemeriana is distinguished from *S. henryi* by a larger lower corolla lip compared to the upper lip, a corolla throat that is taller than wide, the lack of an annulus or bearded sinus in the calyx, the lack of a middle upper calyx lobe, and lateral leaflets less than 1/3 the length of the terminal leaflet.

Common name.—Cedar Sage.

Representative Specimens: * = Specimens used in analyses of morphological characters. † = Specimens used in chromosome counts. **UNITED STATES. TEXAS. Andrews Co.:** 15 mi W of Andrews, 10 May 1958, *Scudday 222* (SRSC). **Bandera Co.:** just NE of Can Creek, 18 Jun 1975, *Smith 684a* (TEX)*. **Bell Co.:** Tennessee Valley area, 17 Apr 1954, *York 54156* (TEX)*. **Bexar Co.:** 18 mi SW of San Antonio, Helotes Creek, 15 May 1932, *Metz 256* (NYBG, RSA). **Blanco Co.:** at "The Narrows" of the Blanco River, 19 Apr 1969, *Correll 37019* (TEX)*. **Brewster Co.:** 28 mi E of Marathon, 23 Apr 1949, *Warnock 8522* (SRSC)*. **Comal Co.:** W edge of New Braunfels, 17 Apr 1966, *Correll 32508* (TEX)*; **Coryell-Bell Co.:** line: 8.8 mi NE of Killeen, 23 May 1979, *Sherwood 554* (OKL). **Edwards Co.:** 1/2 mi S of the dam on the west bank of Hackberry Creek, 21 Jul 1974, *Smith 253* (TEX). **Hays Co.:** College Camp, 8 April 1963, *Pete Abrigo s.n.* (TEX). **Jeff Davis Co.:** NE Davis Mts, Nations Ranch, eastern edge of Timber Mtn, 3 Jun 1987, *Larke 777* (SRSC). **Kendall Co.:** below Edge Falls, 3 May 1947, *Tharp 17T151* (TEX)*. **Kinney Co.:** Anacacho Mts., Anacacho Ranch, 19 Apr 1966, *Correll 32539* (TEX). **Pecos Co.:** Near Sheffield, Owens Ranch, 18 Apr 1953, *Soudy 48* (SRSC). **Presidio Co.:** Bofecillos Mts., Bofecillos Cyn., at Aqua Adentro and Cuevas Amarillas, 25 Mar 1994, *Worthington 23073* (UTEP)*. **Real Co.:** 5 mi N of Leakey, along Frio River, 24 Jun 1946, *Correll 12865* (NY, TEX). **Terrell Co.:** 30 mi. NE of Sanderson on Sheffield road, 10 Jul 1950, *Surratt 277* (SRSC); 3 mi W of Austin, 20 Oct 1996, *Walker 1962* (OKL)†. **Travis Co.:** 5 mi W of Austin, 7 April 1949, *Rogers 6736* (TEX)*. **Uvalde Co.:** along Rio Frio, 22 Jun 1963, *Correll 28018* (TEX). **Val Verde Co.:** on Fawcett Ledge 20–30 mi up Devil's River, 3 Apr 1953, *Warnock 11178* (SRSC, TEX)*. **Williamson Co.:** 3 mi W of Georgetown, along north fork of Gabriel River, 28 Sep 1958, *Correll 20479* (TEX).

MEXICO. Chihuahua: 23 air mi ENE of Villa Ahumada in northwestern cyn of Sierra de la Alcaparra NE of Rancho El Palmar, 12 Sep 1973, *Henrickson 12853b* (TEX); 3mi W of Santa Elena picnic Area of Big Bend NP, Fern Cyn, side cyn of Santa Elena Cyn, 2 Nov 1973, *Wendt 82* (TEX). **Coahuila:** Muzquiz, 1935, *Marsh 152* (TEX)*; Mcpo. Zaragoza, 1km W of Rancho Lagunita, 10 Apr 1976, *Riskind 1904* (TEX)*; Sierra de la Madera NW of Cuatro Cienegas, in Canada Charretera, 14 May 1992, *Mayfield 1348* (TEX); W of Buenavista, Saltillo, Canon de San Lorenzo, 9 Apr 1976, *Marroquin 3557* (MEXU)*; Mcpo. Villa Acuna, 80km SE of Big Bend NP, on SW margin of Serranias del Burro (part of the Sierra del Carmen), Rancho El Rincon, 22 Jun 1991, *Ruiz 31* (SRSC)*; 28 air mi WSW of Cuatro Cienegas, Canon Los Pozos, 5mi W of Rancho Cerro de la Madera towards Canon Desiderio, 2 May 1977, *Henrickson 15989a* (TEX)*; Mcpo. Ramos Arizpe, Sierra S. J. de los Nuncios, 2 Apr 1993, *Hinton 22769* (TEX)*. **Nuevo León:** S of Monterrey on road W of Horsetail Falls, Huesteca Cyn, 13 Nov 1989, *Starr s.n.* (TEX)*; Mcpo. Galeana, 10 km NE of Pocitos, 26 Aug 1984, *Hinton 18768* (TEX)*; Mcpo. Santiago, San Isidro, 16 Jun 1994, *Hinton 24366* (MEXU, TEX)*; SE of Casablanca-Villa de Garcia, Canada Cortinas, 20 Apr 1983, *Villarreal 2046* (MEXU)*. **Tamaulipas:** Mcpo. Hidalgo, Los Mimbres, 5 Jun 1994, *Hinton 24189* (MEXU, TEX)*; Mcpo. San Carlos, Sierra de San Carlos, Cerro del Diento, 17 km S of San Carlos, 22 May 1988, *Hernandez 2271* (TEX)*; Ejido Ricardo Garcia o La Presita, km 66 carretera Victoria-Tula, 26 Apr 1985, *Mahinda 314* (MEXU).

3. *Salvia summa* A. Nels. (Figs. 1 G, H, I), Amer. J. Bot. 18:432. 1931. TYPE: U.S.A. NEW MEXICO: Carlsbad Caverns, rock crevices near springs, May 1930, *G. Convis 59* (HOLOTYPE: RM! 135094; ISOTYPE: RM! 138003).

Perennial to 40 cm from woody caudex. Stems erect to trailing, generally unbranched, one to several. Stem pubescent, often densely pilose at base, resinous dotted. Basal leaves thickened, generally pinnately compound with 5–7 leaflets, terminal leaflet deltoid, 10–25 mm, lateral leaflets variable in shape, greater than 1/3 the length of the terminal. Cauline leaves grading from compound near base into simple and deltoid (rarely reniform). Leaves somewhat rugose, generally pubescent with thick vestiture of appressed hairs, particularly below, margins irregularly toothed and lobed. Inflorescence raceme-like to 20 cm, verticillasters 4–8, each bearing 1–4 flowers. Lower-most bracts often indistinguishable from uppermost leaves, the flowers thus appearing axillary in some instances. Bracts rarely deciduous. Calyx 7–8 mm long, the tube 2–4 mm, hirsute outside, particularly on veins, puberulous inside with annulus; sinuses bearded. Calyx lobes firmly mucronate, the middle upper lobe 1mm (rarely suppressed). Calyx dark green throughout. Corolla purple, often with blue dots in throat, puberulous, arcuate, 3.0–4.8 cm long, often reduced and cleistogamous. Upper lip of corolla galeate, 7–9 mm, lower middle lobe 7–10 mm. Corolla throat 5–7 mm in height. Upper anther thecae exserted from galea as much as 2mm, lower anther thecae bent downward into the throat of the corolla. Style bifid, exserted from the galea, top branch 1mm, lower branch 1–3 mm. $2n = 28$.

Producing fully developed, chasmogamous flowers April–May. Cleistogamous flowers produced May–October.

Distribution and habitat.—Preferring north-facing limestone cliffs, also in canyons along water courses; 1500 m–2000 m. Known only from six mountain ranges. Texas in Culberson and El Paso Counties, New Mexico in western Eddy,

Otero, southern Chaves, and eastern Dona Ana counties. Mexico in Sierra Juarez mountains southwest of Ciudad Juarez, Chihuahua.

Comments.—*Salvia summa* has the most restricted distribution of the species studied. Described from Carlsbad Caverns in New Mexico, it was thought to be endemic to the Guadalupe Mountains until recently when new locations were described from mountain ranges farther west (Worthington 1982). Within the Guadalupe Mountains, *S. summa* is the only representative of sect. *Heterosphere*, whereas in the Oscura, San Andres and Franklin mountains, *S. summa* coexists and possibly hybridizes with *S. henryi* (see discussion under Geographic distribution and interspecific sympatry). The most distinctive feature of *S. summa* is the long, purple corolla, which is unmistakable compared to other members of the group. Its habit is more diminutive than other members of the group and its leaves are thicker. The calyx also is distinctive because of its small size and thicker annulus.

Common name.—Summa Sage.

Representative Specimens: * = Specimens used in analyses of morphological characters. † = Specimens used in chromosome counts. **UNITED STATES. NEW MEXICO. Chaves Co.:** 30mi E of Elk, 18 Apr 1949, *Goodman 5005* (OKL); 9mi W of Hope, 30 May 1997, *Walker 2160* (OKL)*. **Dona Ana Co.:** 30mi NE of Las Cruces on E side of San Andres Mts, NE side of Black Mtn, 28 Apr 1990, *Spellenberg 10170* (NMC)*; Organ Mts, Rattlesnake ridge, 31 May 1980, *Worthington 6050* (NMC, UTEP)*. **Eddy Co.:** Carlsbad Caverns, May 1930, *Convis 59* (RM); North Rocky Arroyo, 20mi W of Carlsbad, 27 May 1997 *Walker 2147* (OKL)*. **TEXAS. Culberson Co.:** Guadalupe Mts, McKittrick Cyn, 21 May 1984, *Freeman s.n.* (UTEP)*; Guadalupe Mts, McKittrick Cyn 30 Apr 1961, *Warnock 18244* (SRSU)*; Guadalupe Mts, Bear Cyn, 26 May 1979, *Warnock 21601* (SRSC)*; Guadalupe Mts, above Pine Springs campground, 27 Oct 1996, *Walker 1964* (OKL)†; Guadalupe Mts, W side of mts, Goat Spring, 29 May 1997, *Walker 2157* (OKL)*; Delaware Mts, 9 Sep 1994, *Worthington 23532* (UTEP)*; Guadalupe Mts, Pine Spring, 1 May 1971, *Weston 86* (SRSC)*; 9mi N of Van Horn, 24 Apr 1961, *Correll 23808* (MO, NY, RSA, TEX)*. **El Paso Co.:** Franklin Mts, 30 May 1981, *Worthington 7135* (UTEP)*.

MEXICO. Chihuahua: Mco. Juarez, in the Sierra Juarez in middle of range, 3 air km SW of Cd. Juarez center, 7 May 1993, *Spellenberg 11795* (BRIT, MEXU, MT, NMC)*.

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