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THE BIOSYSTEMATICS OF SCROPHULARIA IN WESTERN NORTH AMERICA[1]

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INTRODUCTION

Scrophularia, comprising the plants commonly known as figworts, is a large, wide-ranging genus of the northern hemisphere. It includes about 150 species, which are mainly in the Palaearctic Region; and although species have been described by many taxonomists, few studies have been broad in scope. This is due to several factors. First, the relatively small flowers are difficult to study when pressed and dried. Without living material it is difficult to describe the characters of corolla, color, inflorescence, pubescence or leaf margins. Furthermore, the numerous small chromosomes present problems for cytological investigation.

The object of the present study has been to develop a taxonomy that indicates as nearly as possible the evolutionary relationships of the taxa of this genus in western North America. The species are to be found in a wide diversity of habitats ranging from areas of mild climate along the Pacific Coast to high montane regions in the Sierra Nevada and Rocky Mountains. In western North America, species of *Scrophularia* are distributed from southern British Columbia to northern Mexico and even occur on Guadalupe Island, west of Baja California.

The present investigation included greenhouse cultivation, experimental crosses of cultured materials, cytological investigation, pollination studies, and the usual herbarium and field techniques. In general, the most valuable information has been obtained from field work and uniform garden culture. All western taxa, as well as many European species, have been grown in the greenhouse either at Claremont, California, or Logan, Utah, during the years 1954–60. Acquaintance with local and regional populations, their habitats, variability, and ranges has been obtained by numerous field trips to all western states during 1954–60.

During the course of this study, it has been found that all taxa of *Scrophularia* occurring in the United States are high polyploids. This fact may be valuable in a future world-wide study of the genus.

The standard abbrevations of Lanjouw and Stafleu (1959) are used in this paper for the institutions in which the specimens I have seen are deposited.

ACKNOWLEDGEMENTS

My deepest gratitude is expressed to Dr. Philip A. Munz who suggested this investigation; without his patience and stimulation it would never have reached fruition. The interest and assistance of Dr. Verne Grant in the cytological and pollination sections is greatly appreciated. Grateful acknowledgement is also made to Dr. L. Benson, Dr. G. B. Ownbey,

[1]Part of a doctoral dissertation prepared at the Rancho Santa Ana Botanic Garden and the Claremont University College, Claremont, California.

Dr. J. Thieret, Dr. S. Tillett and Mr. C. F. Smith for seed collections. I am indebted to Dr. George E. Bohart, Agricultural Research Service, Logan, Utah, for identifying the species of insects.

Following is a list of herbaria consulted during this study. I wish to express my appreciation to the curators concerned for the loan of material: Herbarium of the California Academy of Sciences; Herbarium of the Chicago Natural History Museum; Dudley Herbarium, Stanford University; Gray Herbarium, Harvard University; Herbarium of the Academy of Natural Sciences, Philadelphia; Herbarium of Pomona College; Rocky Mountain Herbarium, University of Wyoming; Herbarium of the New York Botanical Garden; Herbarium of the Rancho Santa Ana Botanic Garden; Herbarium of the University of Arizona; Herbarium of the University of California, Berkeley; Herbarium of the University of California, Los Angeles; Herbarium of the United States National Museum; Intermountain Herbarium of the Utah State University; Herbarium of University of Washington.

Thanks are also due to the following Botanic Gardens for sending seeds: Botanic Garden, Berlin; Hortus botanicus Hauniensis, Copenhagen; Botanic Garden of the University of Lisbon.

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HISTORICAL ACCOUNT

Apparently the first definite use of the name "*Scrophularia*" for the plants we now know by that name was that of Caspar Bauhin, who in 1623 in his *Pinax* so designated six species that were later given binomial names by Linnaeus (1753). Later the genus was characterized by Joseph Pitton de Tournefort in his *Institutiones Rei Herbariae* (1700, pp. 167–168). Linnaeus took *Scrophularia* in the same sense as these earlier authors, providing binomial names for 12 species in his *Species Plantarum* (1753, pp. 619–621) and formally describing the genus in the Fifth Edition of the *Genera Plantarum* (1754, p. 271). One of the 12 species described by Linnaeus was *S. marilandica,* from what is now the eastern United States.

The first comprehensive synopsis of the genus was published by Stiefelhagen (1910) and accounted for 89 species. This treatment has limited value to the study of the western American species because it included all American plants of this genus under two species: *S. macrantha* Greene and *S. nodosa* L. This treatment suggests that Stiefelhagen knew little of the genus in North America. Furthermore, his two proposed sections, based primarily upon whether the major veins of the leaf blade clearly or weakly anastomose, are of dubious phylogenetic validity.

In the western United States the taxonomic history of the genus is complex. Eighteen species and six additional varieties have been proposed. Most of the shuffling and reshuffling of names has been resolved by Pennell who worked on the group from 1923 to 1947. In 1928, he described *S. oregana,* a new species from Oregon. Pennell in 1935 treated the genus for eastern temperate North America, recognizing two species, *S. lanceolata* Pursh and *S. marilandica* L., and considering five binomials and one variety synonyms of *S. lanceolata.* Pennell considered that *S. lanceolata* had survived glaciation in western North America, and that since the glacial retreat, it has spread eastward over glaciated country to assume its present transcontinental range. The nomenclature of an Arizonan taxon claimed his attention in 1940, *S. davidsonii* being proposed as a new name for *S. glabrata* Davidson (1902), not Aiton (1789).

In 1947, Pennell studied the taxonomy of the far western species, which had previously for the most part been identified with *S. californica* Cham. & Schlecht. *Scrophularia californica* was restricted to coastal populations, and was considered to include *S. oregana.* The

specific dictinctness of *S. villosa* Pennell (1923) was re-emphasized. *Scrophularia atrata* was described as new, and *S. multiflora* was proposed as a new name at the specific level for the taxon that had previously been designated *S. californica* var. *floribunda* Greene or *S. californica* var. *laciniata* Jepson.

Tidestrom and Kittell (1941) in their flora of Arizona and New Mexico listed five species, all of which were different binomials from those used in California. One year later, Kearney and Peebles published their flora of Arizona, including only two species, *S. californica* and *S. parviflora* Wooton & Standley (including *S. davidsonii*). In Kearney and Peebles' later flora of Arizona (1951) *S. coccinea* Gray is said to occur in New Mexico and possibly eastern Arizona.

Scrophularia coccinea was described by Gray ("Report on the United States and Mexican Boundary Survey", Vol. II, 1858), but because of the earlier use of this name by Linnaeus in 1753, it is here renamed *S. neomexicana.* This rare and local species is strikingly distinct with its large, red flowers 13–21 mm long, as compared with those of other western species which are only 5–14 mm long.

Creasy (1949, 1953) was the first investigator to apply experimental taxonomic methods to the genus. He grew *S. lanceolata* and *S. marilandica* in the greenhouse to study differences in time of flowering and to make crosses between them. Anatomical studies of their roots and stems were also made. Creasy concluded that these morphologically similar taxa were distinct biologically.

Munz (1958) proposed *S. californica* var. *desertorum* to embrace a taxon with bicolored flowers found from the Sierra Nevada of California into western Nevada.

Finally, Edwin (1959) recognized four species for Nevada: *S. californica, S. multiflora, S. lanceolata* and *S. nodosa.* The last mentioned species is European and had previously been reported from North America only on the Atlantic Coast; in my opinion, it is not found in western North America.

There has been no previous work on the cytology or genetics of *Scrophularia* in western North America.

In the present revision, nine species and two additional subspecies are recognized for the area under consideration.

MORPHOLOGY

Habit.—All western North American species are tall, leafy stemmed, herbaceous perennials. One of them, *S. villosa,* of the Channel Islands off the coast of southern California tends to become somewhat woody. One European species considered briefly in this study is an annual.

Root.—Perennial species included in this study have a woody tap-root which in older plants bears branches with one to several crowns.

Aerial stems.—All species have a four-angled stem except the Palaearctic *S. lateriflora* which has a round stem. The leaves are decussate in arrangement.

Leaves.—The leaves have simple, elliptic to lanceolate blades. Variable leaf form and margin have caused taxonomic confusion in such species as *S. californica* and *S. lanceolata.* In this paper, leaves of the middle third of the plant have been used as representative.

Inflorescence.—In all species the inflorescence is a compound cymose panicle similar to that of *Penstemon.* Failure to recognize that the inflorescences continue to expand for several weeks caused the binomial *S. multiflora* to be proposed for more mature plants of *S. californica.* The environment also has an influence on the inflorescence size, as confirmed under greenhouse conditions. All flowers are pedicillate and often subtended by a bract at the base of the pedicel, which in the western species are lanceolate, attenuate, and shorter than the pedicels they subtend. *Scrophularia atrata* is distinct in that its pedicels diverge at right angles, whereas in other species they subtend an angle of about 45° (fig. 1).

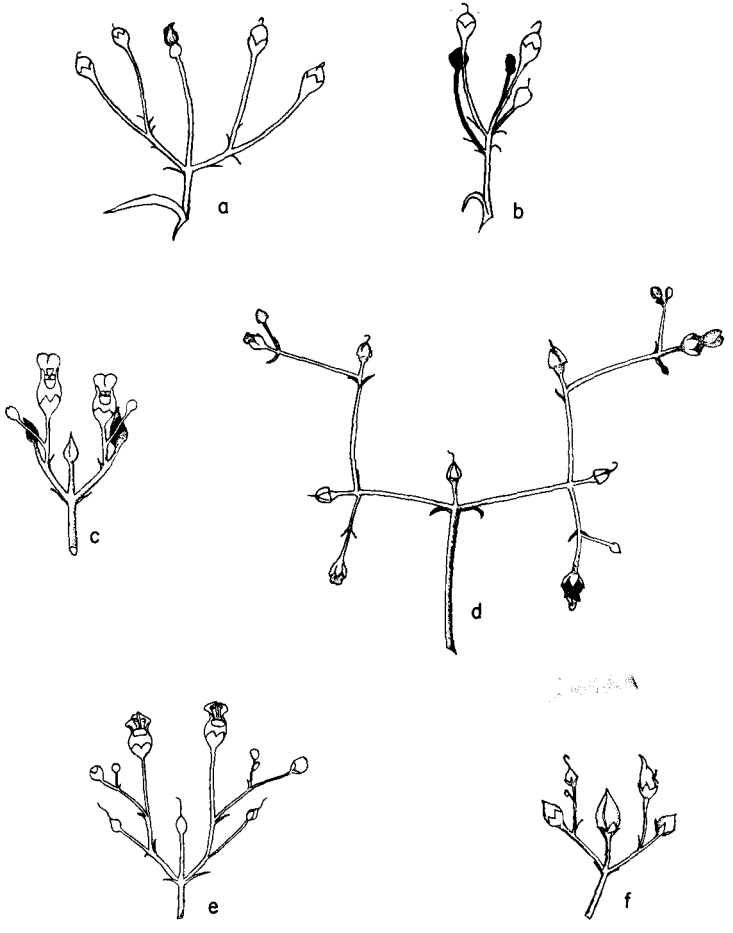

Fig. 1. Inflorescence branches of *Scrophularia.*—a–b. *S. lanceolata,* bottom and side views.—c. *S. montana.*—d. *S. atrata.*—e. *S. parviflora.*—f. *S. oregana.* All × ½.

Calyx.—The calyx is remarkably constant in the species of this study, and offers few distinguishing features in the Nearctic species. The distinct sepals are green and persist in fruit.

Corolla.—The shape of the sympetalous corolla, particularly at the throat, often varies from species to species. Its characters may be clear only in living plants. The tube is globular to ellipsoid or urceolate, and the two lobes of the upper lip project forward or flare slightly backward. The lower lip has two vertical lobes and one central lobe which is slightly to strongly deflexed. In some instances the length of the corolla is significant, varying from 7–21 mm (fig. 2, 3). Corolla color varies greatly in different species and should be included on collection labels.

Stamens.—The four fertile stamens are frequently referred to as didynamous, but measurements of them in many taxa show little difference in their length at anthesis. Since the flowers are sternotribe, the stamens are in a position near the deflexed central corolla lobe,

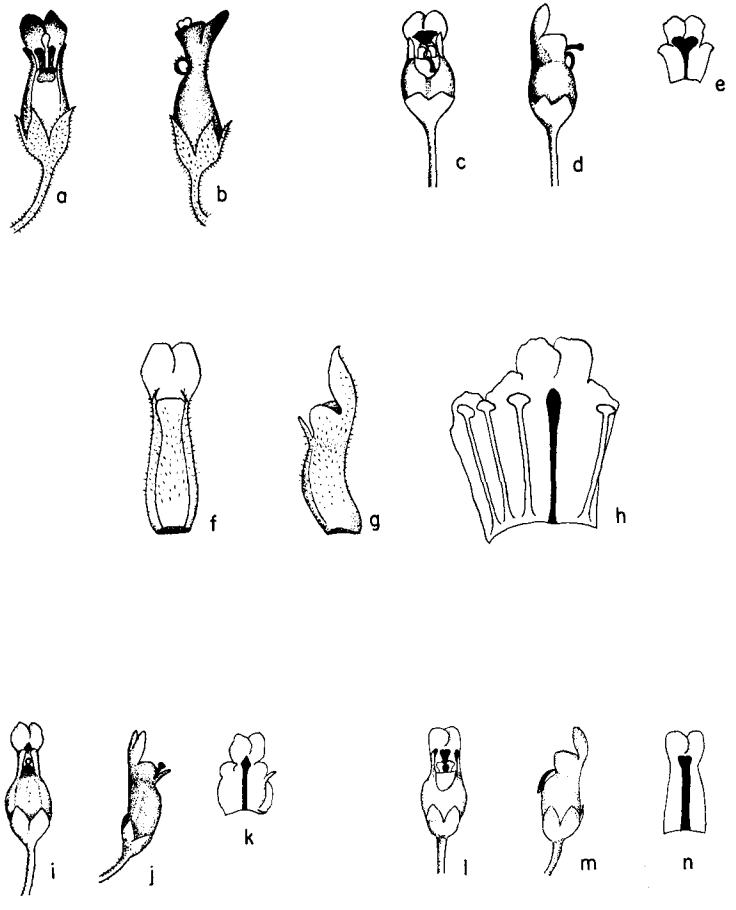

Fig. 2. *Scrophularia* flowers.—a–b. *S. villosa,* face and side views.—c–e. *S. lanceolata.*—c–d. Face and side views.—e. Sterile filament.—f–h. *S. neomexicana.*—f–g. Face and side views.—h. Opened corolla.—i–k. *S. atrata.*—i–j. Face and side views.—k. Sterile filament.—l–n. *S. montana.*—l–m. Face and side views.—n. Sterile filaments. All × 1¼.

In most cases the filaments unfold one at a time, starting with the lower pair. This unfolding requires from 24 to 36 hours. Each filament is glandular-puberulent, and the anther is divergent-reniform.

The sterile, uppermost filament is useful for distinguishing species, being scalelike, lancelike or absent (fig. 2 e, h, k, n; 3 c, h, k, n). Its lower two-thirds are often fused to the upper lip of the corolla. The abaxial surface of the scalelike portion is usually glandular-puberulent.

Pistil.—The ovary is superior, bilocular and bicarpellate. The numerous ovlues are borne on axile placentae. The single style is slender and usually crowned with a capitate stigma covered with obconical cells. At the base of the ovary is a hypogynous fleshy disc which secretes nectar from its dorsal half to the bases of the filaments of the fertile stamens.

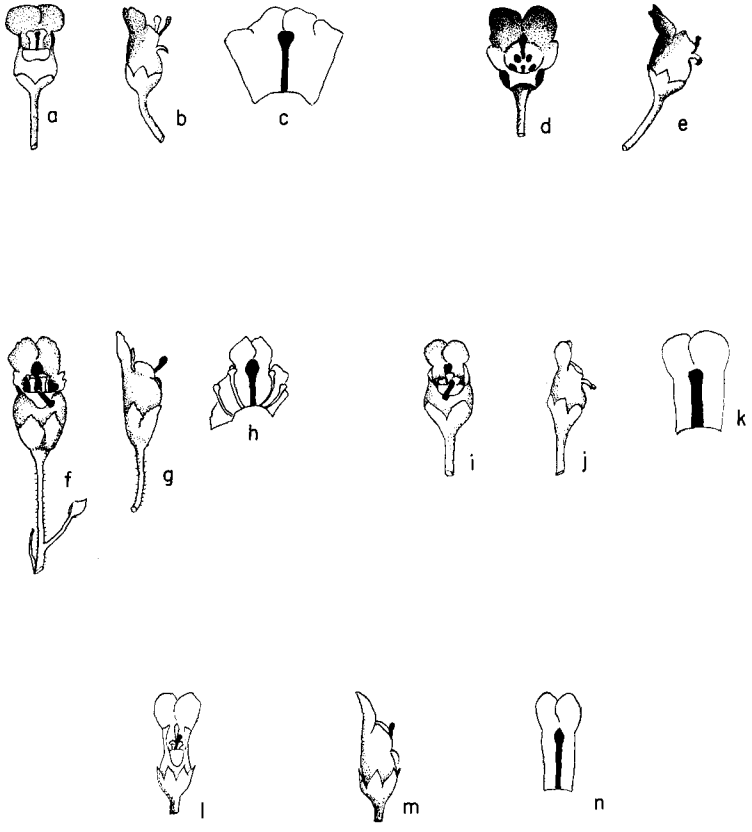

Fig. 3. *Scrophularia* flowers.—a–c. *S. parviflora.*—a–b. Face and side views.—c. Sterile filament.—d–e. *S. desertorum,* face and side views.—f–h. *S. californica* subsp. *californica.*—f–g. Face and side views.— h. Opened corolla.—i–k. *S. californica* subsp. *floribunda.*—i–j. Face and side views.—k. Sterile filament.—l–n. *S. oregana.*—l–m. Face and side views.—n. Sterile filament. All × 1¼.

At maturity the ovoid capsule dehisces along the septum. The numerous seeds are ellipsoidal, ridged and transversely sulcate. Size of seed is variable.

Indument.—The trichomes on the stems and leaves are of at least two distinct types (fig. 4). Short, stout, bicellular gland-tipped hairs and long, soft, multicellular gland-tipped hairs occur widely throughout the genus. Each type has minor modifications. In *S. neomexicana* the short, stout type is found even on the outer surface of the tubular corolla. Frequently the shorter hairs are each tipped by a purple gland which secretes a colorless liquid. The cells comprising the long hairs are normally cylindrical in form, and the entire trichome is a long, tapering cone (fig. 4 a). In *S. villosa* the long, slender hair is mixed with subsessile glandular trichomes forming a viscid pubescence.

FLORAL ECOLOGY

The flowers of *Scrophularia,* as noted by Trelease in 1881 (for *S. nodosa*), are strongly protogynous. In the greenhouse at Logan, Utah, in 1960 the author made observations on

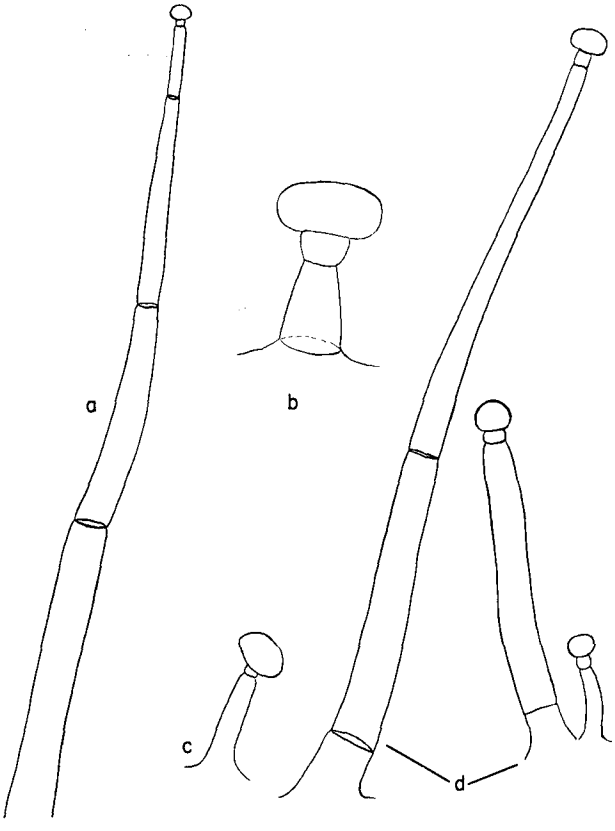

Fig. 4. Trichomes.—a. Hair of *S. chrysantha,* a European species.—b–c. Short glandular hairs of *S. parviflora* and *S. desertorum.*—d. Viscid pubescence of *S. villosa.* All × 175.

the hourly events of anthesis of five species (table 1). In all of them, the stigma was receptive at least 18 hours before the anthers began to shed pollen. Trelease concluded that in *S. nodosa,* if the insect visitors failed to transfer pollen, self-fertilization was assured. Judging from my own observations, this may be true of *S. montana, S. neomexicana* and *S. parviflora;* the first two mentioned set some selfed fruit in the greenhouse in the winter of 1959–60. However, the styles of *S. marilandica, S. desertorum* and *S. californica* become deflexed as soon as the first stamen rises from the base of the corolla; hence, self-fertilization is unlikely.

Tests on all western and a few European species showed complete self-compatability, and the protogynous condition will not prevent selfing from other flowers on the same plant. However, in view of the observations made on pollinators and their behavior, outcrossing must be common.

An exception was *S. peregrina,* an annual European species. In the greenhouse this species readily set full capsules by self-pollination. The flowers are protogynous, colored and sim-

ilar to those of their cross-pollinating relatives, being structurally modified in only two minor ways. The stigma is not capitate, but spreads into two diverging lobes just before the anthers open (fig. 5). Furthermore, the length of the style places the stigma at the same level as the open anthers, assuring that some pollen will come in contact with the receptive surface. This species supports the view of Stebbins (1959) concerning the derivation of self-pollinating taxa from cross-pollinating ancestors.

TABLE 1. *Comparison of five species of Scrophularia on events of anthesis.*

SPECIES	NUMBER OF HOURS STIGMA IS RECEPTIVE BEFORE ANTHERS OPEN	NUMBER OF HOURS REQUIRED FOR STAMEN TO EXTEND TO FULL LENGTH	NUMBER OF HOURS ALL 4 STAMENS HAVE POLLEN AVAILABLE
S. neomexicana	About 18 hours, stigma visible in throat.	About 24 hours, stigma visible above anthers, neither stigma nor anthers exserted beyond throat.	About 48 hours.
S. parviflora	About 20 hours, stigma well-exserted beyond throat.	About 20 hours, style and stigma still straight.	30 hours, later no change in stamens or style.
S. montana	About 24 hours.	About 26 hours, nectar copious, filling corolla up to base of stigma and anthers.	About 46 hours.
S. marilandica	About 21 hours.	About 20 hours, style reflexed over anterior lobe by time 3 anthers are open.	About 4 hours, then corolla falls off, style shriveled.
S. californica	About 24 hours.	About 24 hours, style reflexed over anterior lobe.	About 31 hours, corolla shriveled but still attached, stamens still have pollen.

Pollination in *Scrophularia* has been studied by many investigators, and as a result, the genus has been accepted as a classic example of a group of plants whose flowers are wasp pollinated. Among the workers who studied pollination in *Scrophularia* in Europe were: Sprengel (1793), Wilson (1878), Müller (1883), Knuth (1909), and Schremmer (1959). Of these authors, Müller and Knuth both noted visits by bees in addition to those of wasps, and Knuth and Schremmer also discussed visits to the flowers by syrphid flies. In the United States, Trelease (1881) noted visits of wasps of the genus *Eumenes* to the flowers of *Scrophularia nodosa* and considered that the flowers were well adapted to wasp pollination. In 1891, Robertson, working in Illinois, observed 14 species of bees, 11 species of wasps (Vespidae and Eumenidae), eight species of wasps of other families and also syrphid flies visiting "*S. nodosa* var. *marilandica*." He further stated that the proportion of visits by wasps was unusually high for a flower that was also visited by bees.

In the course of this study, a few records of insect visitors to various species of *Scrophularia* were obtained. Some, like a species of *Coccinella* found in a flower of *S. californica* in Orange County, California, were doubtless fortuitous. Other visitors, like the ants of the genus *Formica* visiting the flowers of *S. lanceolata* at two localities in Grant County, Oregon, were probably attracted to the secretion of nectar. On the other hand, *Bombus bifarius* Cress. and a species of *Lasioglossum* (bees), together with a wasp of the genus *Vespula,* which were observed visiting the flowers of *S. lanceolata* in Grant County, Oregon, are probably all capable of effecting cross-pollination. Similarly, in Cache County, Utah, the following bees—*Bombus bifarius, B. centralis* Cress., *B. occidentalis* Greene, *Andrena saccata* Vier., and *Lasioglossum* sp.—were visiting the flowers of *S. lanceolata.* Another bee of the genus *Lasioglossum* was taken from the flowers of *S. californica* in San Mateo

County, California; and the abundant syrphid fly, *Eupeodes volucris* O.S., was taken from the flowers of *S. oregana* in Tillamook County, Oregon.

The only other observations made were on plants grown in the greenhouse, and can, therefore, only be taken an indications of conditions in the field. At Claremont, *Eupeodes volucris* was taken at the flowers of *S. peregrina* and *S. villosa*, and another syrphid, *Allograpta* sp., at the flowers of *S. desertorum*. In Logan, queens and workers of the white-faced hornet, *Vespula maculata* (L.), were active at several species, and *Polistes fuscatus* (Fabr.) was once taken at the flowers of an F_1 hybrid. Two syrphids, *Eupeodes volucris*

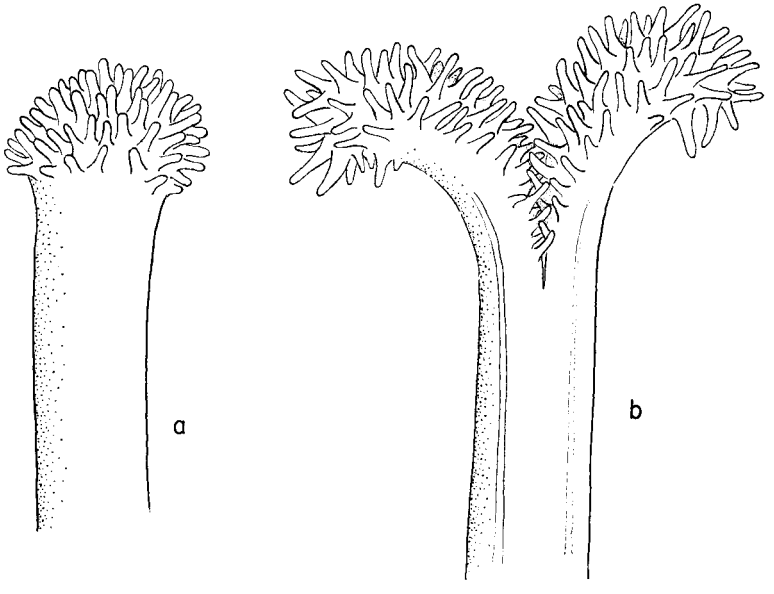

Fig. 5. Stigmatic surfaces.—a. *S. californica* subsp. *californica*.—b. *S. peregrina*. Both × 45.

and *Scaeva pyrastri* (L.), both extremely widespread species which visit a great variety of plants, were also observed: the former on *S. atrata*, the latter on *S. canina*. The individual of *Scaeva*, which was seeking nectar, was coated with pollen on its pilose thorax and capable of carrying it from flower to flower.

Thus, although the observations of insect visitors were not extensive, it is clear that all, with the possible exception of the bees of the genus *Lasioglossum*, are species of insects which visit flowers of many kinds and are doubtless incapable of distinguishing between species of *Scrophularia*. The proportion of wasps was not as impressive as it has been found to be in Europe and the eastern United States, but quite possibly if these observations were extended, this proportion would be relatively increased.

The most distinctive Nearctic species of *Scrophularia* in floral characters, *S. neomexicana*, may differ from the mode in its relationships with pollinators. Its bright rose-red corollas, 13–21 mm in length, were found to be colored entirely by red anthocyanins[2] and thus

[2]Extraction of pigment with boiling 80% ethyl alcohol; paper chromatography using petroleum ether and acetone as solvents; the anthocyanin was insoluble with these solvents.

similar in pigmentation as well as in form to other flowers of the southwestern United States known to be pollinated by hummingbirds, such as *Penstemon centranthifolius* Benth. (Straw, 1956) and *Pedicularis densiflora* Benth. ex Hook. (Sprague, 1962), also of the Scrophulariaceae. Furthermore, a plant of *Scrophularia neomexicana* in full bloom was completely ignored by *Apis mellifera* L.[3] and *Hylaeus cressoni* (Ckll.) even when placed for two and one-half days in a greenhouse containing thriving colonies of these bees. Therefore, it seems most likely that *S. neomexicana* may be pollinated by hummingbirds. In this connection, the observation by Robertson (1891) of the hummingbird *Archilochus colubris* (L.) on "*Scrophularia nodosa* var. *marilandica*" on four separate occasions in Illinois is of interest.

In summary, it does not appear that pollinating systems play an important role in isolating western North American species of *Scrophularia,* although it is likely that *S. neomexicana,* with its tubular, bright rose-red flowers, may be pollinated by hummingbirds and thus reproductively isolated from its insect-pollinated relatives.

CYTOLOGY

Methods.—Floral buds were collected preferably at mid-day, but some buds were usable when collected as early as 10:00 a.m. and as late as 2:30 p.m. They were fixed at least 48 hours in 1:3 acetic alcohol and stored in 70% alcohol under refrigeration. The pollen mother cells were strained in aceto-carmine, mounted in Hoyer's medium (Beeks, 1955), and examined with a Leitz microscope fitted with phase contrast equipment. Drawings of meiotic chromosomes were made with a camera lucida at a magnification of × 3400.

In addition to species of North America, some European species were examined cytologically. The results are summarized in table 2.

Discussion.—No previous chromosome counts have been reported for *Scrophularia* in North America, and only a few for European species. In table 2 counts are given for the first time for 16 species, including ten North American and six European species. Chromosome counts were made at metaphase I and anaphase I in pollen mother cells. In all cases the pairing relationships appeared regular and no lagging chromosomes were observed.

Even though only 20 of the 150 species in the genus have been counted, it appears that the European species show an aneuploid series of n=12, n=13, n=18, n=20, and higher polyploid numbers. Western North American species, in general, have numbers that range from n=c. 43–48, but *S. montana* has n=c. 35–38.

Since all species have normal pairing relationships, the polyploidy present seems to be interspecific; hence, alloploidy.

Guard cell length was not found to be correlated with the level of polyploidy in several species examined.

HYBRIDIZATION

Methods.—Seeds collected in the summer and fall during the years 1954 through 1959 were germinated in the greenhouses at Logan, Utah, and Claremont, California. Germination in most cases was more than 60 percent. If the seeds were planted in September, most species were flowering in April or May. A few species were also transplanted to the greenhouse.

Size 000 gelatin capsules were used to protect the stigma from chance contamination with foreign pollen and also served to catch the mature seed (fig. 7). They were prepared as follows: The short outside portion was pierced with a needle in the curved end, and then the hole was expanded to 1.5 mm in diameter. Following this, a longitudinal cut was made connecting the terminal hole to the edge of the open end. When a cross-pollination was

[3]Robertson (1891) observed *Apis mellifera* in great numbers visiting *S. nodosa* var. *marilandica.*

TABLE 2. *Chromosome numbers in Palaearctic and Nearctic species of Scrophularia*[1]

TAXON	n	SOURCE
Palaearctic species		
S. aquatica L.	40	
S. canina L.	13	
S. ehulifolia Hoffmgg. & Link	c.28–29*	Seed from Botanic Garden of University of Lisbon, *Shaw 1124*
S. grandiflora DC.	29*	Seed from Botanic Garden of University of Lisbon, *Shaw 1122*
S. lateriflora Trautv. (fig. 6a)	20*	Seed from Hortus botanicus Hauniensis, Copenhagen, *Shaw 1125*
S. lucida L. (fig. 6b)	13*	Seed from Hortus botanicus Hauniensis, Copenhagen, *Shaw 1126*
S. nodosa L.	18	
S. nodosa L.	18*	Seed from Hortus botanicus Hauniensis, Copenhagen, *Shaw 1121*
S. peregrina L. (fig. 6c)	18*	Seed from Botanic Garden, Berlin, *Shaw 1105*
S. umbrosa Dum.	26	
S. variegata Bieb. (fig. 6d)	12*	Seed from Hortus botanicus Hauniensis, Copenhagen, *Shaw 1120*
S. vernalis L.	20	
Nearctic species		
S. atrata Pennell	c.46–48*	Seed from Miguelito Canyon, Santa Barbara County, California, *Munz 19451*
S. californica Cham. & Schlecht. subsp. *californica*	47*	Seed from Olema Marshes, Marin County, California, *Munz 19894*
subsp. *floribunda* Greene	c.45–46*	Kern Canyon, Kern County, California, *Shaw 816*
subsp. *floribunda* Greene	c.47–48*	Evey Canyon, 5 miles north of Claremont, Los Angeles County, California, *Shaw 779*
S. desertorum (Munz) Shaw	48*	Seed from Marble Canyon, Inyo County, California, *Munz 20165*
S. lanceolata Pursh.	c.46–48*	Waterfall Canyon, Grand Teton National Park, Teton County, Wyoming, *Shaw 998*
S. lanceolata Pursh.	48*	Beachcreek, Grant Co., Oregon, *Shaw 1069*
S. marilandica L.	c.43*	Seed from Trail Creek, LaPorte County, Indiana, *Shaw 1150*
S. montana Wooten (fig. 6e)	c.35–38*	Wright's Cabin Forest Camp, west side of Emory Pass, Grant County, New Mexico, *Shaw 1062*
S. neomexicana Shaw (fig. 6f)	46*	Kneeling Nun Mountain, near Santa Rita, Grant County, New Mexico, *Shaw 1147*
S. oregana Pennell	45*	Beverley Beach State Park, Lincoln County, Oregon, *Shaw 1076*
S. parviflora Wooten & Standley	46*	Mt. Lemmon Road, Santa Catalina Mountains, Pima County, Arizona, *Shaw 1148*
S. villosa Pennell	c.47–48*	Avalon Canyon, Santa Catalina Island, Los Angeles County, California, progeny of *Wolf 10895*

[1]All voucher sheets are on file in the Herbarium of the Rancho Santa Ana Botanic Garden, Claremont, California, except *Shaw 998* and *Shaw 1150* which are filed in the Intermountain Herbarium of Utah State University, Logan, Utah.

*New counts made by author; all others are from Darlington and Wylie (1955).

made, a flower was selected at the time its corolla lobes were about to open. In all species of *Scrophularia* studied, the stigma was receptive at this time, but the stamens were still bent double with closed anthers. A pair of forceps was used to remove the sympetalous corolla with attached stamens. A corolla bearing pollen-laden anthers of the desired male parent was brought in contact with the receptive stigma. The short end of the gelatin capsule was subsequently slipped around the ovary with the punched end over the pedicel. The lower half of the gelatin capsule containing a small identifying tag was then slipped inside the other half and held in place with scotch tape. Within five to six days any swelling of the

Fig. 6 Camera lucida drawings of meiotic chromosome compliments.—a. *Scrophularia lateriflora,* first telophase.—b. *S. lucida,* first anaphase.—c. *S. peregrina,* first anaphase.—d. *S. variegata,* first anaphase.—e. *S. montana,* first anaphase.—f. *S. neomexicana,* diakinesis.

ovary, which indicated success of the cross, was easily observed. After 30 days, the gelatin capsules were removed, and the seeds produced were counted.

When cross-pollinations were attempted in the field, it was necsesary to cover the gelatin capsules with two coats of shellac in order to make them waterproof. Such treated capsules survived the spring and summers of 1955 and 1957 in the Wellsville Range, Cache County, Utah.

Most taxa were tested for self-fertility by enclosing an unopened flower in a gelatin capsule or by emasculating a flower and using pollen from a flower of the same plant.

Results.—The strains grown and used in this section are indicated in table 3. The fol-

lowing taxa—*S. atrata, S. californica* subsp. *californica, S. californica* subsp. *floribunda, S. desertorum, S. marilandica, S. neomexicana, S. oregana, S. parviflora* and *S. peregrina*—set abundant good seed when self-pollinated. Other species were not tested or yielded inconclusive results. In several species, no seed was set when the anthers were removed and the

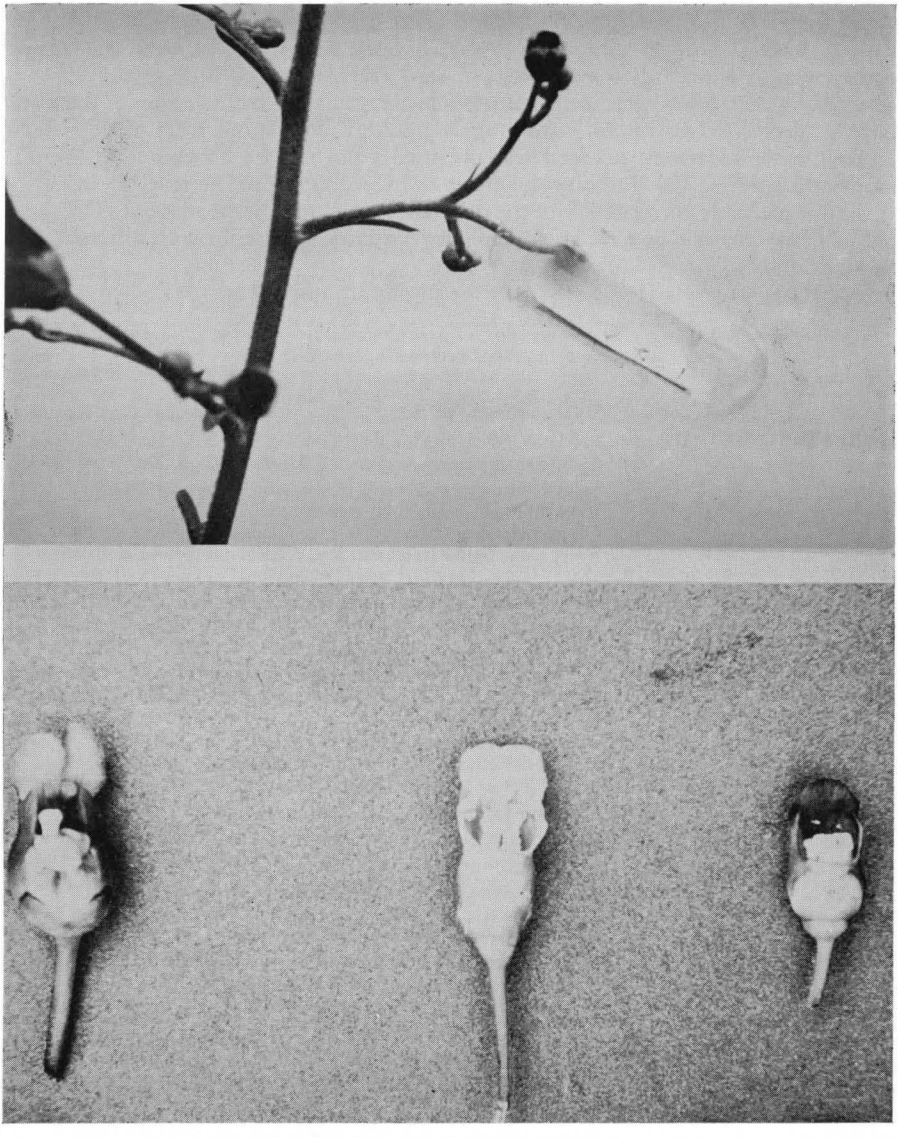

Fig. 7. *Upper*–Gelatin capsule enclosing pedicel and pistil of a flower following artificial pollination.—*Lower*.– Flowers of parents and artificial hybrid. From left to right: *S. lanceolata; S. lanceolata* × *S. californica* subsp. *californica; S. californica* subsp. *californica* (Humbolt Co.). × 2.

stigma protected from all pollen, indicating that apomixis, except possibly pseudogamy (Stebbins, 1950), is absent in these species and probably in the genus as a whole. Apomixis is unknown in the family Scrophulariaceae.

a. *Intraspecific hybridization.*—The two strains of *S. desertorum* grown were hybridized. With the Yuba County strain as female parent, a single pollination yielded 147 seeds; two pollinations made in the reciprocal direction yielded 100 seeds.

Crosses were also made within *S. californica,* both within and between the subspecies, and these generally set full complements of seed (table 4).

In summary, there was no evidence of reproductive isolation within either of these species.

b. *Interspecific hybridization.*—Although numerous pollinations were made in many of the possible combinations, no seed was obtained from crosses between Old World and New World species. This indicates a barrier to hybridization at the level of initial crossibility and is probably correlated with the differences in chromosome number. The same was noted in a few crosses that were attempted between Eurasian species with different chromosome numbers.

Scrophularia montana (n=35–38), for the most part, did not set seed when crossed with

TABLE 3. *Origin of populations of Scrophularia selected for intraspecific and interspecific crossing studies.*

TAXON	SOURCE
North American Species	
S. atrata	Surf, Santa Barbara County, California, *C. F. Smith in 1954.*
S. californica subsp. *californica*	Samoa, Humboldt County, California, *Munz 19878.* Lake County, California, *Benson in 1954.* Olema Marshes, Marin County, California, *Munz 19894.* Big Creek, Santa Cruz County, California, *Munz in 1958.*
S. californica subsp. *floribunda*	Kern Canyon, Kern County, California, *Shaw 816.* Evey Canyon, Los Angeles County, California, *Shaw 779.* Silverado Canyon, Orange County, California, *Shaw 818.* Pala, San Diego County, California, *Shaw 1086.*
S. desertorum	Marble Canyon, Inyo County, California, *Munz & Roos 20165.* Middle Fork of Yuba River, Nevada County, California, *Balls & Everett 20245.*
S. lanceolata	Beech Creek, Grant County, Oregon, *Shaw 1069.* Wellsville Range, Cache County, Utah, *Shaw 1151.* Grand Teton National Park, Teton County, Wyoming, *Shaw 998.*
S. marilandica	La Porte County, Indiana, *J. Thieret in 1958.*
S. montana	Emory Pass, Sierra County, New Mexico, *Shaw 1062.*
S. neomexicana	Kneeling Nun Mountain, Grant County, New Mexico, *Shaw 1147.*
S. oregana	South of Reedsport, Douglas County, Oregon, *Shaw 1077.* Beverly Beach State Park, Lincoln County, Oregon, *Shaw 1076.* Port of Wallapa, Pacific County, Washington, *Shaw 1073.*
S. parviflora	Mt. Lemmon, Pima County, Arizona, *Shaw 1148.*
S. villosa	Santa Catalina Island, Los Angeles County, California, *Munz in 1941.*
European Species	
S. aquatica L.	Botanical Garden, University of Lisbon, *Shaw 1123.*
S. canina L.	Botanical Garden, University of Lisbon, *Shaw 1139.*
S. lateriflora Trautv.	Hortus botanicus Hauniensis, Copenhagen, *Shaw 1125.*
S. lucida L.	Hortus botanicus Hauniensis, Copenhagen, *Shaw 1126.*
S. peregrina L.	Hortus botanicus Hauniensis, Copenhagen, *Shaw 1105.*
S. variegata Bieb.	Hortus botanicus Hauniensis, Copenhagen, *Shaw 1120.*

other western species (n=43–48), but did so once when crossed with *S. neomexicana* (table 5). The seeds from the former group, however, were tested and failed to germinate, which may indicate the presence of another kind of barrier to crossibility.

TABLE 4. *Intraspecific hybridizations in Scrophularia californica.*

SPECIES COMBINATION[1]	FLOWERS POLLINATED	NUMBER OF GOOD SEED SET	NUMBER OF F_1 HYBRIDS OBTAINED
*"californica"** Humboldt × *"californica"* Marin	9	637	85
"californica" Lake × *"californica"* Humboldt	1	80	SNT**
"californica" Lake × *"californica"* Marin	1	24	SNT
"californica" Marin × *"californica"* Humboldt	3	198	SNT
"californica" Marin × *"californica"* Lake	1	0	0
"californica" Humboldt × *"floribunda"** Kern	1	0	0
"californica" Humboldt × *"floribunda"* Pala	1	42	SNT
"californica" Santa Cruz × *"floribunda"* Kern	1	0	0

[1] "Female" parent given first.
* *"californica"* = *S. californica* subsp. *californica; "floribunda"* = *S. californica* subsp. *floribunda.*
** Seeds not tested.

The information in tables 5 and 6 indicates that all western species, with the exception of *S. montana* and *S. desertorum,* cross fairly easily and form plump, fully filled capsules. Nineteen hybrid combinations of the successful crosses were grown in the greenhouse. All of them yielded vigorous plants with characteristics intermediate between those of the parents (fig. 7 through 10).

Cytological examination of hybrids was limited to three combinations. Figure 11 and table 7 point to the fact that these three hybrids were similar to their parents in cytological behavior. No bridges were seen in the pollen mother cells examined.

TABLE 5. *Interspecific hybridizations involving S. montana and other North American species of Scrophularia.*

SPECIES COMBINATION[1]	FLOWERS POLLINATED	NUMBER OF GOOD SEED SET	NUMBER OF F_1 HYBRIDS OBTAINED
atrata × *montana*	3	108	0
*"californica"** Lake × *montana*	2	0	0
"californica" Marin × *montana*	9	0	0
lanceolata Beech Creek × *montana*	2	0	0
marilandica × *montana*	1	108	0
montana × *atrata*	4	0	0
montana × *"californica"* Lake	1	0	0
montana × *"californica"* Marin	4	0	0
montana × *desertorum* Inyo	1	0	0
montana × *lanceolata* Wellsville	2	0	0
montana × *neomexicana*	1	0	0
montana × *parviflora*	4	0	0
neomexicana × *montana*	3	29	SNT**
parviflora × *montana*	3	0	0

[1] "Female" parent given first.
* *"californica"* = *S. californica* subsp. *californica.*
** Seeds not tested.

TABLE 6. *Interspecific hybridizations between North American species of Scrophularia.*

SPECIES COMBINATION[1]	FLOWERS POLLINATED	NUMBER OF GOOD SEED SET	NUMBER OF F_1 HYBRIDS OBTAINED
atrata × *"californica"** Humboldt	17	608	36
atrata × *"californica"* Lake	5	231	SNT**
atrata × *"californica"* Marin	5	204	SNT
atrata × *"floribunda"** Evey	13	598	SNT
atrata × *"floribunda"* Kern	1	0	0
atrata × *"floribunda"* Silverado	1	26	SNT
atrata × *desertorum* Inyo	8	296	SNT
atrata × *desertorum* Yuba	5	88	SNT
atrata × *lanceolata* Wellsville	6	0	0
atrata × *neomexicana*	8	0	0
atrata × *oregana* Beverly	3	42	SNT
atrata × *parviflora*	8	49	SNT
"californica" Humboldt × *atrata*	12	870	67
"californica" Humboldt × *desertorum* Inyo	4	18	15
"californica" Humboldt × *desertorum* Yuba	3	0	0
"californica" Humboldt × *lanceolata* Wellsville	1	125	31
"californica" Humboldt × *neomexicana*	2	137	SNT
"californica" Humboldt × *parviflora*	2	203	SNT
"californica" Humboldt × *villosa*	2	98	75
"californica" Lake × *atrata*	3	268	41
"californica" Lake × *desertorum* Inyo	2	0	0
"californica" Lake × *desertorum* Yuba	1	0	0
"californica" Lake × *villosa*	2	0	0
"californica" Marin × *atrata*	8	439	SNT
"californica" Marin × *desertorum* Inyo	4	0	0
"californica" Marin × *desertorum* Yuba	3	0	0
"californica" Marin × *lanceolata* Wellsville	1	0	0
"californica" Marin × *marilandica*	1	57	SNT
"californica" Marin × *neomexicana*	4	252	SNT
"californica" Marin × *parviflora*	3	352	SNT
"californica" Marin × *villosa*	1	30	SNT
"californica" Santa Cruz × *villosa*	7	627	75
"floribunda" Evey × *atrata*	5	0	0
"floribunda" Evey × *oregana* Beverly	1	68	2
"floribunda Evey × *villosa*	2	0	0
"floribunda" Kern × *(atrata* × *desertorum)*	1	50	SNT
"floribunda" Kern × *villosa*	1	61	15
"floribunda" Silverado × *atrata*	1	0	0
"floribunda" Silverado × *oregana* Beverly	2	0	0
"floribunda" Silverado × *villosa*	2	153	24
desertorum Inyo × *atrata*	2	0	0
desertorum Inyo × *"californica"* Humboldt	2	0	0
desertorum Inyo × *"californica"* Lake	1	0	0
desertorum Inyo × *"californica"* Marin	5	5	SNT
desertorum Inyo × *"floribunda"* Kern	1	0	0
desertorum Inyo × *lanceolata* Teton	2	0	0
desertorum Inyo × *lanceolata* Wellsville	2	0	0
desertorum Inyo × *marilandica*	5	0	0
desertorum Inyo × *montana*	3	0	0
desertorum Inyo × *neomexicana*	4	0	0
desertorum Inyo × *oregana* Beverly	1	0	0
desertorum Inyo × *parviflora*	2	0	0
desertorum Yuba × *atrata*	1	0	0
desertorum Yuba × *"californica"* Humboldt	2	0	0
desertorum Yuba × *"californica"* Lake	2	0	0

[1]"Female" parent given first.
**"californica"* = *S. californica* subsp. *californica*; *"floribunda"* = *S. californica* subsp. *floribunda*.
***Seeds not tested.

TABLE 6. *Interspecific hybridizations between North American species of Scrophularia.* (continued)

SPECIES COMBINATION[1]	FLOWERS POLLINATED	NUMBER OF GOOD SEED SET	NUMBER OF F_1 HYBRIDS OBTAINED
lanceolata Wellsville × *atrata*	2	90	32
lanceolata Wellsville × *"californica"* Humboldt	1	30	5
lanceolata Wellsville × *"californica"* Lake	1	30	8
lanceolata Teton × *desertorum* Inyo	1	0	0
marilandica × *atrata*	2	0	0
marilandica × *"californica"* Marin	4	22	SNT
marilandica × *neomexicana*	4	288	SNT
marilandica × *parviflora*	3	423	SNT
neomexicana × *atrata*	12	0	0
neomexicana × *"californica"* Humboldt	2	0	0
neomexicana × *"californica"* Marin	2	0	0
neomexicana × *desertorum* Inyo	5	0	0
neomexicana × *marilandica*	2	206	SNT
neomexicana × *oregana* Beverly	4	0	0
neomexicana × *parviflora*	3	266	27
oregana Reedsport × *atrata*	3	58	35
oregana Beverly × *"californica"* Santa Cruz	1	0	0
oregana Beverly × *"floribunda"* Evey	2	142	SNT
oregana Beverly × *"floribunda"* Kern	2	219	3
oregana Beverly × *"floribunda"* Pala	1	108	SNT
oregana Beverly × *neomexicana*	5	0	0
oregana Beverly × *parviflora*	3	0	0
oregana Beverly × *villosa*	2	271	60
oregana Wallapa × *villosa*	1	121	SNT
parviflora × *atrata*	3	0	0
parviflora × *"californica"* Humboldt	2	0	0
parviflora × *"californica"* Marin	3	0	0
parviflora × *desertorum* Inyo	3	0	0
parviflora × *marilandica*	4	232	19
parviflora × *neomexicana*	5	192	0
parviflora × *oregana* Beverly	2	0	0
villosa × *"californica"* Marin	2	0	0
villosa × *desertorum* Inyo	1	0	0

The pollen fertility of six species and twelve interspecific hybrid combinations was determined (table 8). Pollen fertility of the F_1 plants was, in general, nearly as high as that of the species. Yet in one F_2 hybrid examined, the pollen fertility was only four percent, which might suggest a breakdown of hybrid fertility in later generations; further data on this point is necessary.

TABLE 7. *Chromosome numbers of artificially produced hybrids.*

PARENTS	n
S. lanceolata × *S. atrata* (Wellsville)	c. 46
S. californica subsp. *californica* (Humboldt) × *S. lanceolata* (Wellsville)	c. 47
S. atrata × *S. californica* subsp. *californica* (Humboldt)	c. 42

In general, therefore, it may be said that, excluding *S. montana* and possibly *S. desertorum,* the genetic barriers separating western species of *Scrophularia* appear to be weak;

although there is some possibility of the occurrence of breakdown in hybrid fertility in the F_2 and later generations.

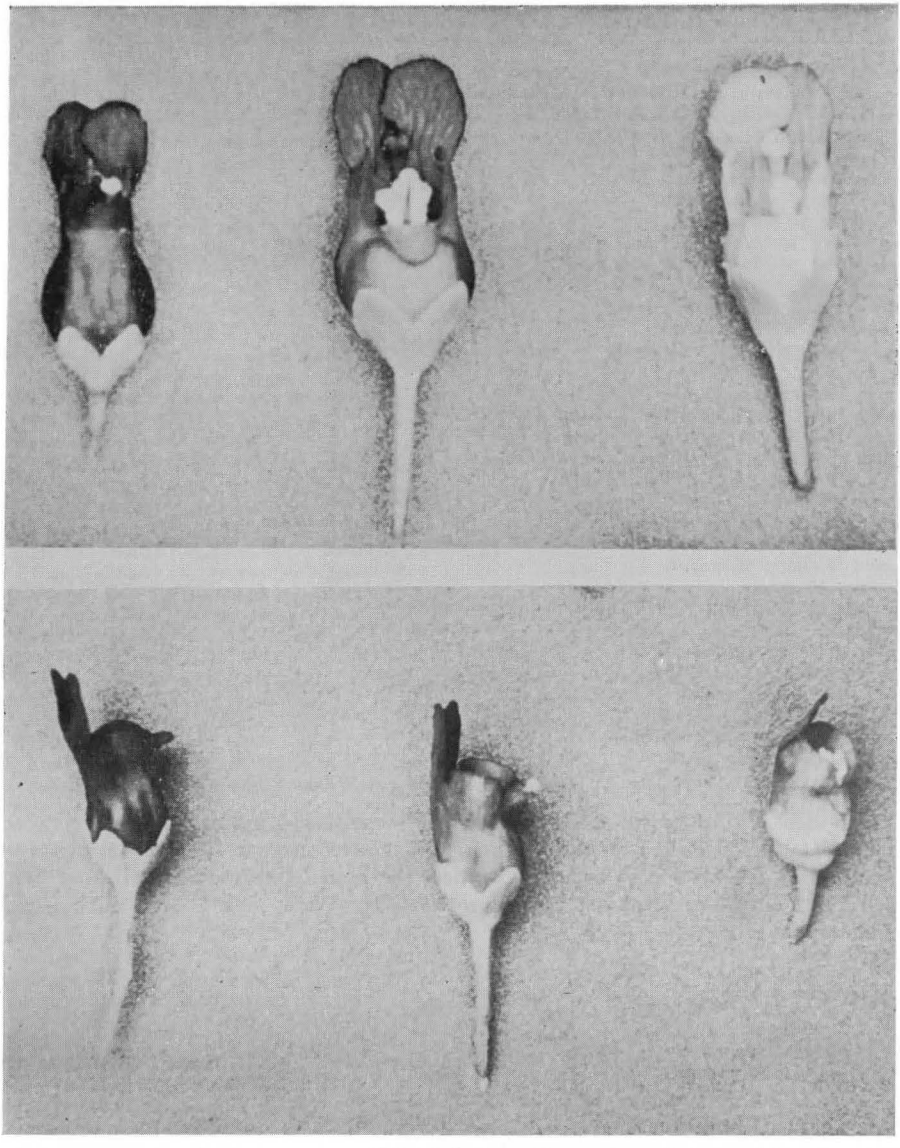

Fig. 8. Flowers of parents and artificial hybrids.—*Upper.*–From left to right: *S. atrata; S. atrata* × *S. californica* subsp. *californica; S. californica* subsp. *californica* (Marin Co.).—*Lower.–S. atrata; S. atrata* × *S. californica* subsp. *californica; S. californica* (Humbolt Co.). × 2.

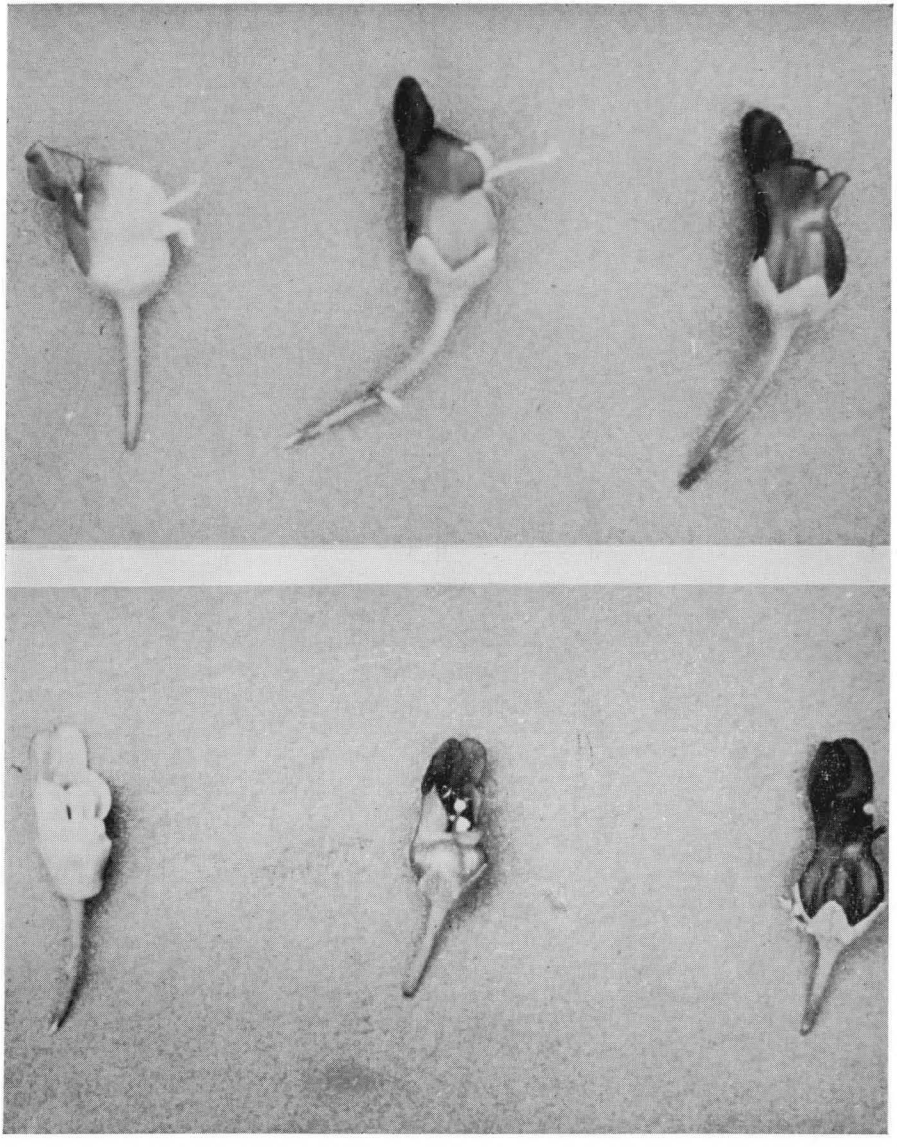

Fig. 9. Flowers of parents and artificial hybrids.—*Upper.*–From left to right: *S. desertorum; S. desertorum* × *S. atrata; S. atrata.*—*Lower.*–*S. californica* subsp. *californica* (Lake Co.); *S. californica* subsp. *californica* × *S. atrata; S. atrata.* ×2.

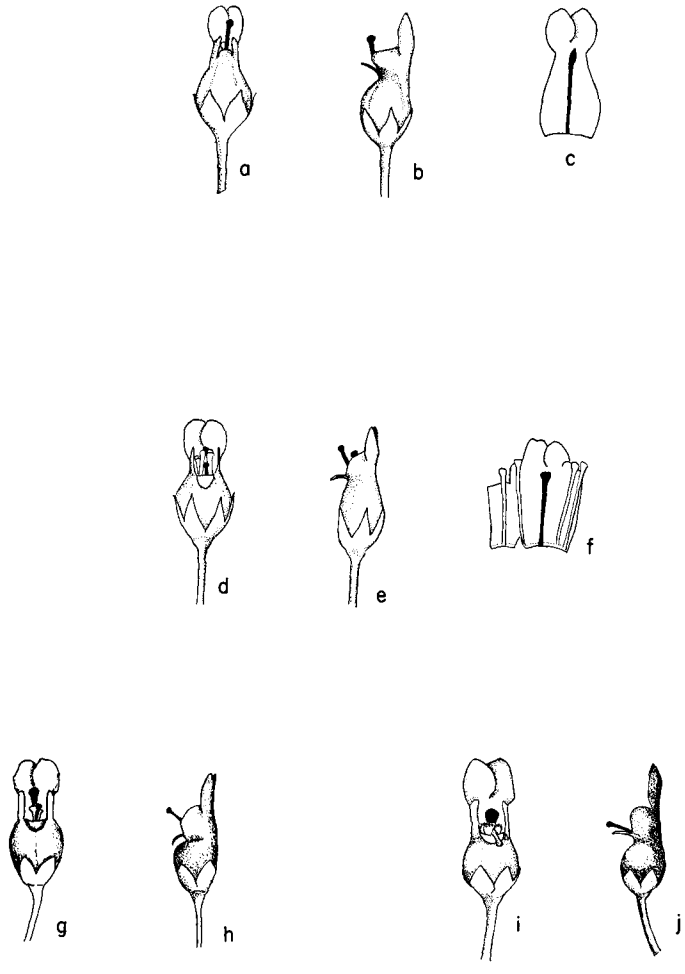

Fig. 10. Flowers of artificial hybrids.—a–c. *S. atrata* × *S. villosa*.—a–b. Face and side views.—c. Sterile filament.—d–f. *S. californica* subsp. *californica* (Humbolt Co.) × *S. villosa*.—d–e. Face and side views.—f. Opened corolla.—g–h. *S. atrata* × *S. californica* subsp. *californica* (Marin Co.), face and side views.—i–j. *S. atrata* × *S. desertorum*, face and side views. All × 1¼.

SPECIFIC CONCEPTS

In the present treatment the natural units of *Scrophularia* have been delimited by the combined information obtained from morphology, cytology, hybridization and geographic distribution. A criterion of strict genetic isolation cannot be used in treating the Nearctic species of *Scrophularia*. If such an approach were used, it would result in the "lumping" of most or all of the species into one. Geographic barriers seem more important in isolating the western North American species. If genetic barriers do exist in the genus within this area, they are probably not strongly expressed in the first hybrid generation (see section on Hybridization).

Fig. 11. Meiotic chromosomes of artificial hybrid, *S. californica* subsp. *californica* (Humbolt Co.) × *S. lanceolata* (Cache Co.); metaphase I. (Camera lucida drawing of PMC.)

TABLE 8. *Pollen fertility record of Scrophularia species and hybrids.*

SPECIES AND HYBRIDS	PERCENT OF GOOD POLLEN	NUMBER OF COUNTS
S. atrata	95	500
S. californica subsp. *californica*	95	542
S. desertorum	95	486
S. montana	95	479
S. neomexicana	95	515
S. parviflora	95	525
S. atrata × *S. californica* subsp. *californica* F_1 (Humboldt)	95	612
S. atrata × *S. desertorum* Inyo F_1	95	612
S. atrata × *S. desertorum* Inyo F_2	4	394
S. atrata × *S. villosa* F_1	95	522
S. californica subsp. *californica* × *S. atrata* F_1 (Marin)	89	453
S. californica subsp. *californica* × *S. lanceolata* F_1 (Humboldt) (Wellsville)	95	573
S. californica subsp. *californica* × *S. villosa* F_1 (Humboldt)	84	506
S. lanceolata × *S. atrata* F_1 (Wellsville)	95	490
S. lanceolata × *S. californica* subsp. *californica* F_1 (Wellsville) (Lake)	95	630
S. neomexicana × *S. parviflora* F_1	95	583
S. parviflora × *S. marilandica* F_1	87	602

KEY TO WESTERN SPECIES OF SCROPHULARIA

A. Inflorescence villous, the hairs tipped with small glands; plants becoming shrubby with age; sterile filament absent or rudimentary. Islands off the coast of southern and Baja California ..... 1. *S. villosa*
AA. Inflorescence puberulent or short-pubescent; stems herbaceous; sterile filament well developed.
B. Sterile filament flabellate, wider than long. Northern half of United States from the Cascade Mountains eastward to the Atlantic Coast ..... 2. *S. lanceolata*
BB. Sterile filament clavate to obovate, sometimes with an acute apex.
C. Corolla bright rose-red, 13–21 mm long. Grant and Sierra counties, New Mexico ..... 3. *S. neomexicana*
CC. Corolla varying from blackish-maroon or garnet-brown to yellowish-green, 5–12 mm long.
D. Corolla dark maroon, the upper half blackish; tube urceolate with a constricted orifice; sterile filament with an acute apex. Santa Barbara County, California ..... 4. *S. atrata*
DD. Corolla varying from dark maroon or garnet-brown to yellowish-green; orifice not constricted.
E. Corolla yellow-green (rarely purplish), 6–10 mm long; leaves lanceolate, with simply serrate margins. Southwestern and central New Mexico ..... 5. *S. montana*
EE. Corolla dark or light maroon, garnet-brown, the ventral portion of the tube often pale brown, yellow or yellow-green.
F. Corolla 5–7 mm long. Arizona and western New Mexico ..... 6. *S. parviflora*
FF. Corolla 7–12 mm long. California, Nevada, Oregon and Washington.
G. Corolla distinctly bicolored; leaf bases cuneate. From the Sierra Nevada to western Nevada ..... 7. *S. desertorum*
GG. Corolla not distinctly bicolored; leaf bases truncate to cordate.
H. Corolla light maroon or garnet-brown; inflorescence narrow and compact to wide and spreading. West of Sierra Nevada, California ..... 8. *S. californica*
HH. Corolla dark maroon, inflorescence narrow. Coast of Oregon and Washington ..... 9. *S. oregana*

1. SCROPHULARIA VILLOSA Pennell, Field Mus. Botan. Ser. 5: 223, 1923.

S. californica var. *catalina* Jepson, Man. Fl. Pl. Calif. 906, 1925.

Glandular-puberulent perennial 12–18 dm tall, becoming shrubby with age; leaf blades ovate, acuminate, sharply and somewhat doubly dentate, truncate to cordate at base, both surfaces puberulent, densely glandular-puberulent on main veins and petioles; larger leaves with blades 10–15 cm long, 8–10 cm wide, on petioles 3–5 cm long; panicle usually glandular-villous, elongate, narrow, of 15–20 or more fascicles; peduncles and pedicels slender, subinflorescence units at 45° angles to each other; sepals 3 mm long, triangular-ovate, acute, glandular-villous, with entire margins; corolla 8–11 mm long, blackish maroon, lowermost lobe recurved, slightly constricted at throat, the tube below the throat covered sparingly with glandular trichomes, nectar inconspicuous; sterile filament absent or a maroon, awn-like rudiment; stigma with two slightly spreading lobes; style 7–9 long, not deflexing; capsule 6–8 mm long; seeds 0.6–0.7 mm long.

Type.—Foot of Equestrian Trail, Santa Catalina Island, Los Angeles County, May 27, 1920, *L. M. Nuttall 162* (F).

Distribution.—Rocky canyons, coastal sage scrub and chaparral. Santa Catalina and San Clemente Islands, California; Guadalupe Island, Baja California (fig. 14).

Representative species.—**CALIFORNIA.** Los Angeles County: Big Wash Canyon, Santa Catalina Island, *Fosberg 8133* (POM); Renton Mine, Santa Catalina Island, *Dunkle 1865* (POM); Cherry

Valley, Santa Catalina Island, *Dunkle 1736* (POM); head of Avalon Valley, *Wolf 10895* (RSA). San Diego County: canyon wall south of Lemon Tank, San Clemente Island, *Munz 6703* (POM); 10 miles southeast of Wilson's Cove, San Clemente Island, *Peirson 3438* (RSA). **MEXICO.** Baja California: canyon about 2 miles south of Northeast Anchorage, Guadalupe Island, *Moran 5970* (RSA).

2. SCROPHULARIA LANCEOLATA Pursh, Fl. Amer. Sept. 419, 1813.

S. pectinata Raf., Autikon Botan. 160, 1840.
S. nodosa var. *occidentalis* Rydb., Contrib. U. S. Nat. Herb. 3: 517, 1896.
S. occidentalis Bickn., Bull. Torrey Botan. Club 23: 315, 1896.
S. lanceolata var. *occidentalis* Pennell, Torreya 22: 82, 1922.
S. leporella Bickn., Bull. Torrey Botan. Club 23: 317, 1896.
S. serrata Rydb., Bull. Torrey Botan. Club 36: 688, 1909.
S. dakotana Lunell, Am. Midland Naturalist 5: 240, 1919.
S. utahensis Gand., Bull. Soc. Botan. France 66: 219, 1919.
S. lanceolata f. *velutina* Pennell, Monog. Acad. Phila. 1: 276, 1935.

Glabrescent perennial 8–15 dm tall, frequently producing several stems; leaf blades lanceolate to lance-ovate, acuminate, simple or sometimes doubly serrate with cuspidate teeth, cuneate, truncate, or cordate at base, both surfaces usually glabrous, but sometimes pubescent along veins and petioles; larger leaves with blades 9–14 cm long and 4–6 cm wide, on petioles 2–4 cm long; panicle glandular-puberulent to villous, elongate, narrow, of 14–20 or more fascicles; peduncles and pedicels relatively stout, subinflorescence units at 45° angles to each other; sepals 2–3 mm long, ovate, rounded, with somewhat scarious, erose margins; corolla 8–14 mm long, greenish-brown, the lowermost lobe recurved, throat slightly constricted, glabrous, nectar inconspicuous; sterile filament flabellate, wider than long, yellow-green, 1–1.8 mm wide; stigma capitate; style 4–6 mm long, not deflexing; capsule 6–8 mm long; seeds 0.8 mm long.

Type.—"In wet meadows and woods: Pennsylvania . . ." Not seen.

Distribution.—Loam or sandy soil along fences, roadsides and in woods. Southern British Columbia to northern California, eastward across the northern United States to the Atlantic Ocean, from sea level to 8,000 feet elevation (fig. 12).

Representative specimens of western United States.—**WASHINGTON.** Clark County: Lacamas Creek, *English 1050* (WTU). Okanogan County: Omak, *Fiker 894* (WTU). Mason County: Schafer State Park, *Freer 34* (WTU). Spokane County: Clark Springs, 10 miles north of Spokane, *Kreager 49* (UTC). Yakima County: Yakima region, *Brandegee* (UC). **OREGON.** Linn County: south end of Fish Lake, *Constance 3440* (ARIZ, UTC). Wallowa County: Cottonwood Creek Canyon, *Sheldon 8123* (RM). Baker County: Camp Creek, *Cusick 2419* (RM). Klamath County: South entrance to Crater Lake National Park, *Baker 6913* (WTU). Lake County: 3-6 miles northwest of Paisley, *Peck 15656* (WTU). Malheur County: 6 miles west of Ironsides, *Shaw 1078* (UTC). **CALIFORNIA.** Siskiyou County: Sisson, *Heller 8059* (GH). Shasta County: Kennet, *Eastwood* (CAS). **IDAHO.** Bannock County: east of Pocatello, *Pennell 6057* (RM). Clearwater County: Shanghai Lookout, *Lingenfelter 487* (RSA). Idaho County: headwaters of Sheep Creek, Seven Devils Mountains, *Ownbey 2073* (RSA). Canyon County: Nampa, *Nelson & Macbride 1073* (POM). Bear Lake County: 5-6 miles east of Montpelier, *Pennell 15143* (RM). Owyhee County: Boulder Creek, *Macbride & Nelson 523* (RM). Adams County: 15 miles south of New Meadows, *Hitchcock & Muhlick 13912* (WTU). Shoshone County: mouth of Shoshone Creek, *Witt 1002* (RSA, UC, WTU). **NEVADA.** Humboldt County: east of McDermitt Indian Reservation, *Train 450* (UC). **UTAH.** Cache County: Logan Canyon, *Smith 1719* (RM). Salt Lake County: reservoir above Salt Lake City, *Benson 4690* (POM). Alta, *Jones 1222* (POM). Utah County: Mt. Timpanogas, *Eastwood & Howell 461* (CAS). Kane County: Navajo Lake, *Harris 29381* (UC). Grand County: LaSal Mountains, *Payson 102344* (RM). San Juan County: southeast part of LaSal Mountains, *Goodman & Hitchcock 1469* (CAS, RM). **MONTANA.** Missoula County: Blackfoot River, 23 miles from Missoula, *Hitchcock 17816* (RSA). Sweet Grass County: Big Timber, *Eggleston 7952* (US). **WYOMING.** Teton County: Waterfall Canyon, Grand Teton National Park, *Shaw 998* (UTC). Lincoln County: 20 miles south of Jackson, Hoback Canyon, *Shaw 925* (UTC). Albany Canyon: Chug Creek, *Nelson 7352* (POM). **COLORADO.** Routt County: 4–5 miles south of Toponas, *Pennell & Schaeffer 22310* (UC). Larimer County: along Masonville Road, west of Fort Collins, *Mathias 368* (POM). Grand County: Middle Peak, near Hot Sulphur Springs, *Ramaley & Robbins* (UC). Fremont County: Grape Creek, Canon City, *Brandegee* (UC). El Paso County: Colorado Springs, *Jones* (POM). Montrose County: Cimarron, *Baker 43* (POM). La Plata County: Parrott Post Office, La Plata Mountains, *Baker 814* (POM). **NEW MEXICO.** Rio Arriba County: Chama, *Greene 606* (GH).

In view of Pennell's (1935) comprehensive study of this species, I accept his synonymy with only minor changes. I have seen type material of *S. serrata, S. leporella* and *S. nodosa* var. *occidentalis*. Pennell was first to recognize that this species occurred from the Atlantic seaboard west to within 50 miles of the Pacific Coast. He pointed out that it is constant in characteristics of the flowers and fruits, yet shows considerable diversity in the shape and margins of leaf blades. The differences in leaf-shape do not appear to be geographically correlated.

3. **Scrophularia neomexicana** Shaw nom. nov.†

S. coccinea A. Gray, Rep. U. S. Mex. Bound, Surv. 2: 111, 1858; non L., 1753.
S. macrantha Greene ex Stiefelhagen, Engl. Botan. Jahrb. 44: 461, 483, 1910. Nomen nudum.

Glabrescent perennial 6–11 dm tall; leaf blades lanceolate to ovate, acute, proximally doubly and distally simply serrate with acute teeth, cuneate at base, glabrous; larger leaves with blades 6–8 cm long and 3–4 cm wide, on petioles 2–4 cm long; panicle glandular-puberulent, elongate, of 12 to 20 fascicles; peduncles and pedicels slender, subinflorescence units at 45° angles to each other; sepals 3–4 mm long, ovate or lance-ovate, with entire margins; corolla 13–22 mm long, rose-red with all lobes erect, antero-lateral onces slightly incurved, tube with slightly constricted orifice, almost entirely covered with glandular trichomes, nectar inconspicuous; sterile filament rounded, longer than broad, cream to rose-red, 1 mm wide; stigma capitate, held 1 mm above the anthers at anthesis, style 10 mm long, not deflexing, capsule 8–11 mm long; seeds 0.7–1 mm long.

Lectotype.—Santa Rita de Cobre, Grant County, New Mexico, Aug. 18, 1851, *C. Wright 281* (GH).

Distribution.—Grant and Sierra Counties, New Mexico (fig. 13).

Representative specimens.—**NEW MEXICO.** Grant County: Santa Rita Mountain, *Metcalfe 1464* (GH, US); west slope of Black Range, *Goodding 6369* (ARIZ, RM); Kneeling Nun Mountain, *Shaw 1147* (RSA). Sierra County: Black Range in transition zone, *Hutchinson 7816* (LA).

Scrophularia neomexicana is extremely rare, having been collected only a few times since is was discovered in 1851. It is one of the most distinct species of the western North American group, with its long rose-red corolla. On September 12, 1959, I found four plants in flower on the sunny talus slopes of Kneeling Nun Mountain above 6,000 feet elevation, overlooking the Santa Rita Copper Mine, Grant County, New Mexico. Associated with it were species of *Cercocarpus, Quercus* and *Yucca*.

4. SCROPHULARIA ATRATA Pennell, Proc. Acad. Nat. Sci. Phila. 99: 172, 1947.

Glabrescent perennial 10–15 dm tall, leaf blades ovate, acute, proximally doubly and distally simply dentate with rounded or broadly acute teeth, cuneate to cordate at base, glabrous except for puberulent main veins; larger leaves with blades 7–10 cm long and 5–8 cm wide, on petioles 2–7 cm long; panicle glandular-puberulent, elongate, of 10–15 or more fascicles; peduncles and pedicels slender, subinflorescence units usually spreading at right angles, the lower peduncles 3–4 cm long; sepals 3 mm long, ovate or lance-ovate, rounded, narrowly scarious margined or slightly erose; corolla 9–11 mm long, dark maroon,

†*Editorial note:* The reviewers of this paper agree that the correct name for the taxon in question is *Scrophularia macrantha* Greene ex Stiefelhagen, which is validly and legitimately published. Stiefelhagen certainly intended to publish it as he recognized the species as No. 53 in his revision (p. 461), and the name is validated by the definition provided in the key (p. 483). Therefore, it cannot be considered a *nomen nudum* under any circumstances. It seems that Stiefelhagen was uncertain whether Greene had already published the species (hence his use of "wo?" following the specific name on p. 461), but this does not invalidate his publication. If he had attributed the name to Greene, "M.S." or "ined.", it would have been the same thing and just as acceptable. In view of Stiefelhagen's description and the locality cited ("Neu-Mexiko, St. Rita-Gebirge Ca. 2100 m."), there appears to be no doubt about the species he had in mind. Thanks are due Mr. J. E. Dandy, Keeper, Department of Botany, British Museum (Natural History), for helpful discussion of this point.

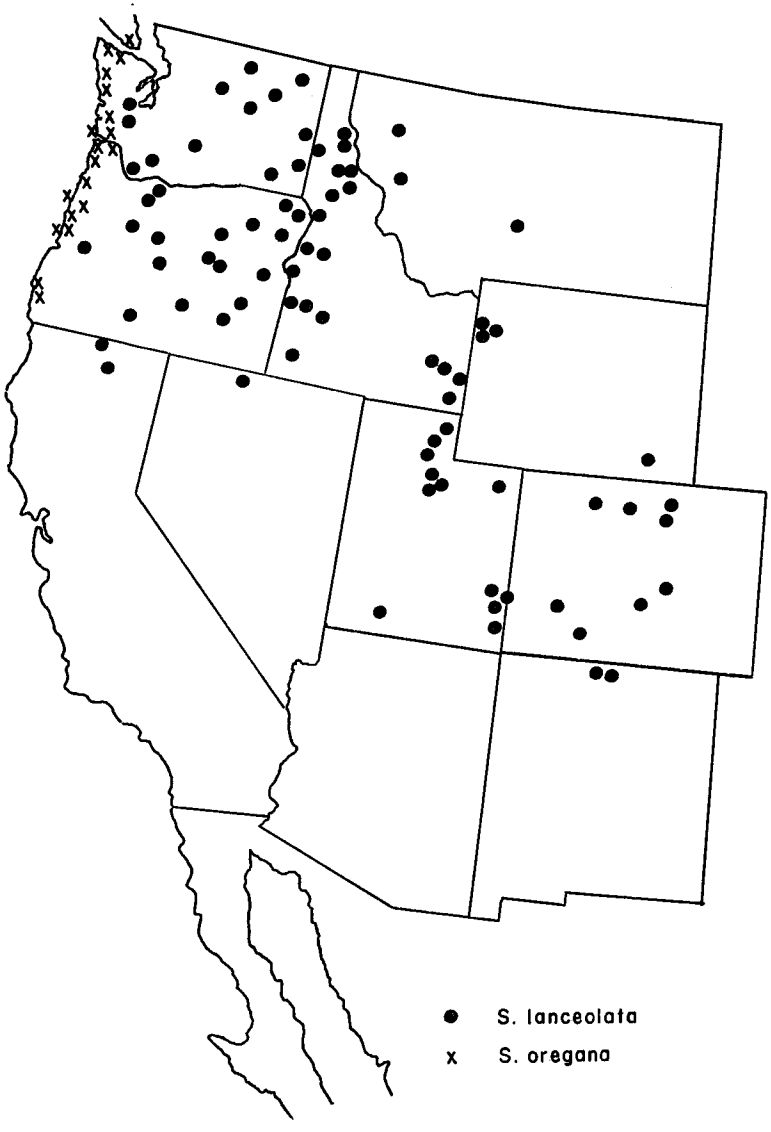

Fig. 12. Distribution of *S. lanceolata* and its geographical relationship to that of *S. oregana*.

dorsal half blackish, lowermost lobe recurved, globular-urceolate with constricted orifice, glabrous, nectar inconspicuous; sterile filament with acute apex, blackish-maroon, longer than broad, 0.5 mm wide; stigma capitate; style 4–6 mm long, not deflexing, maroon; capsule 6–8 mm long; seeds 0.6–0.7 mm long.

Type.—Surf, Santa Barbara County, California, May 8, 1940, *Pennell 25334* (PH).

Distribution.—Vicinity of Lompoc, just north of Point Conception, Santa Barbara County, California (fig. 14).

Representative specimens.—**CALIFORNIA.** Santa Barbara County: San Miguelito Canyon, about 1.5 miles south of Lompoc, *Munz 19433* (RSA); 0.5 mile north of Santa Ynez River, just north of Lompoc, *Munz 19450* (RSA); San Antonio Creek, 4 miles south of Casmalia, *Munz 19455* (RSA); 5 miles north of Lompoc on State Highway 1, *Shaw 1118* (RSA); Oceanside Park turnoff, 0.7 mile inland from Surf, *Shaw 1117* (RSA).

In the vicinity of Lompoc, Santa Barbara County, California, *S. atrata* occurs sympatrically with *S. californica* subsp. *californica*. The co-existence of these two taxa is especially striking in the Miguelito Canyon area, a few miles south of Lompoc. On two separate field trips to this canyon (May, 1954 and May, 1958) blooming colonies of both species were seen in several places along the road. In one site the two species were only a few feet apart. No intermediates were ever encountered. Experimental hybridizations show no genetic barriers between these two taxa, and further study is needed to explain the reproductive isolation observed.

The blackish-maroon corolla, with its globular-urceolate shape and constricted orifice, usually wide-spreading subinflorescence units, and its limited distribution set this taxon apart as a peculiar and local species.

5. SCROPHULARIA MONTANA Wooton, Bull. Torrey Botan. Club 25: 308, 1898.

S. laevis Wooton & Standley, Contrib. U. S. Nat. Herb. 16: 173, 1913.

Glabrescent perennial 10–15 dm tall; leaf blades lanceolate to ovate, acute, simply serrate with cuspidate teeth, cuneate at base, glabrous except for puberulent main veins; larger leaves with blades 15–20 cm long, 5–8 cm wide, on petioles 1–1.5 cm long; panicle glandular-puberulent, narrow, elongate, of 15–30 fascicles; peduncles and pedicels slender, subinflorescence units at 45° angles to each other; sepals 2–3 mm long, triangular-ovate, broadly acute, narrowly scarious margined and sometimes slightly erose; corolla 6–10 mm long, mostly yellow-green, occasionally purplish, the lowermost lobe recurved, the throat only slightly constricted, glabrous, nearly full of nectar at anthesis; sterile filament truncate at apex, yellow-green, about the same length as width, 1–1.2 mm wide; stigma capitate; style 3–5 mm long, not deflexing; capsule 8–11 mm long; seeds 1 mm long.

Type.—Near Gilmour's Ranch, Eagle Creek, White Mountains, Lincoln County, New Mexico, 7,000 feet elevation, August 5, 1897, *E. O. Wooton 280* (US).

Distribution.—Central and southwestern New Mexico (fig. 13).

Representative specimens.—**NEW MEXICO.** San Miguel County: Cowles, 8,200 feet, *Osterhout 4417* (RM). Sandoval County: Lower Tejano Canyon, Sandia Mountains, *Castetter 965* (RM). Lincoln County: Alto, *Fisher 36176* (US); Ruidoso Creek, *Dunn 9014* (RSA); White Mountains, *Eggleston 14459* (US). Otero County: Mescalero Indian Reservation, *Wolf 2829* (GH); 1 mile northeast of Cloudcroft, *Dunn 7560* (RSA); Sacramento Mountains, *Wooton* (RM). Sierra County: Hillsboro Peak, Mimbres Mountains, 8,500 feet, *Diehl 556* (POM). Grant County: Wright's Cabin Forest Camp, Emory Pass, 7,900 feet, *Shaw 1062* (RSA); 10 miles southwest of Kingston, *Cory 33093* (GH).

6. SCROPHULARIA PARVIFLORA Wooton & Standley, Contrib. U. S. Nat. Herb. 16: 173, 1913.

S. glabrata Davidson, Bull. So. Calif. Acad. Sci. 1: 3, 1902, non Ait., 1789.
S. davidsonii Pennell, Not. Nat. Acad. Sci. Phil. 43: 8, 1940.

Glabrescent perennial 4–10 dm tall, frequently producing several stems, some of which become decumbent with age; leaf blades lanceolate to ovate, acute, proximally doubly and distally simply serrate with acute to abruptly acuminate teeth, cuneate to cordate at base, glandular-puberulent on the lower surface; larger leaves with blades 8–11 cm long and 6–7 cm wide on petioles 2–4 cm long; panicle glandular-puberulent, lax, elongate, of 15–25 fascicles; peduncles and pedicels slender, subinflorescence units at 45° angles to each other; sepals 2–3 mm long, triangular-ovate, broadly acute or subacute, narrowly scarious margined and sometimes slightly erose; corolla 5–7 mm long, the proximal half green, the lobes reddish-pink, the lowermost lobe recurved, the throat only slightly constricted, gla-

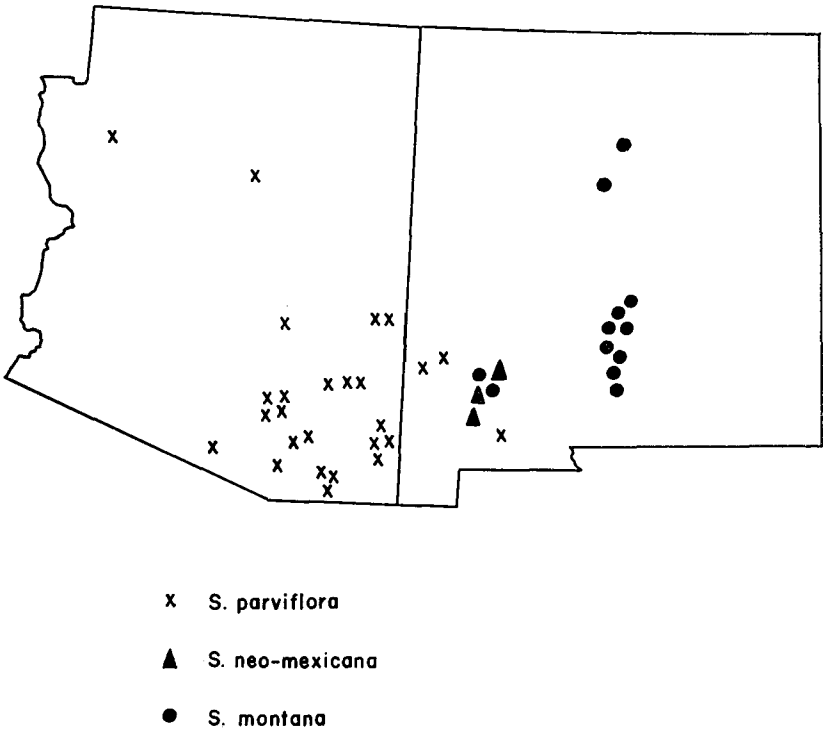

Fig. 13. Distribution of *S. parviflora, S. neomexicana* and *S. montana* in Arizona and New Mexico.

brous, nectar in two drops, inconspicuous; sterile filament rounded, green, longer than broad, 0.8–1 mm wide; stigma capitate; style 6–7 mm long, exserted 1.5 mm beyond the stamens, not deflexing; capsule 5–7 mm long; seeds 1 mm long.

Type.—West Fork of the Gila River, Mogollon Mountains, Catron County, New Mexico, August 2, 1903, *O. B. Metcalfe 345* (US).

Distribution.—Southwestern New Mexico; central and southeastern Arizona (fig. 13).

Representative specimens.—**NEW MEXICO.** Catron County: Mogollon Mountains, *Wolf 2724* (GH); between Mogollon and Mogollon Ranger Station, *Eggleston 16813* (US). Dona Ana County: Organ Mountains, *Wooton* (US). **ARIZONA.** Cochise County: Ramsey Canyon, Huachuca Mountains, *Gould 2468* (ARIZ); Miller Canyon, Huachuca Mountains, *Goodding 233* (RM); Upper Rhyolite Canyon, Chiricahua National Monument, *Clark 8422* (ARIZ); Cave Creek about Portal, Chiricahua National Forest, *Eggleston 11001* (GH). Santa Cruz County: Santa Rita Mountains, *Kearney & Peebles 10561* (US). Pima County: Mount Lemmon, *Shaw 1148* (RSA); Mount Bigelow, Santa Catalina Mountains, *Benson 9026* (ARIZ); Toro Canyon, Baboquivari Mountains, *Gilman 259* (ARIZ). Greenlee County: 33 miles north of Clifton, White Mountains, *Kearney & Peebles 12232* (ARIZ); 20 miles south of Hannigan, Blue Mountains, *Parker & McClintock 7661* (ARIZ). Graham County: Ghost Camp, Pinaleno Mountains, *Shreeve 4379* (ARIZ). Gila County: Pinal Peak, *Smith 14057* (GH); Barnhart Pass, Matzatzal Mountains, *Collom 172* (US); West Fork of Oak Creek Canyon, near Flagstaff, *Deaver 144* (Arizona State Teacher's College). Mohave County: Hualpai Mountain, *Kearney & Peebles 12710* (US).

7. **Scrophularia desertorum** (Munz) Shaw, comb. nov.

S. californica C. & S. var. *desertorum* Munz, Aliso 4: 99, 1958.

Glabrescent perennial 7–12 dm tall, usually producing several stems immediately following seedling stage; leaf blades lanceolate, narrowly acute, doubly serrate with cuspidate teeth, cuneate at base, both surfaces puberulent, glandular-puberulent on main veins and petioles; larger leaves with blades 10–13 cm long and 5–8 cm wide, on petioles 7–10 cm long; panicle glandular-puberulent, elongate, of 15–20 or more fascicles; peduncles and pedicels slender, subinflorescence units at 45° angles to each other; sepals 2–3 mm long, triangular-ovate, acute to obtuse, narrowly scarious margined and slightly erose; corolla 7–9 mm long, conspicuously bicolored, dorsal half maroon, ventral half cream with pinkish edges, lowermost lobe recurved, throat only slightly constricted, glabrous, with two conspicuous nectar drops at the base of the sterile filament, sterile filament clavate, light maroon, longer than broad, 1 mm wide; stigma capitate; style 6–7 mm long, deflexing at anthesis; capsule 6–8 mm long; seeds 0.6–0.9 mm long.

Type.—Dry loose gravelly wash at the lower edge of the pinyon belt, Silver Canyon, 7,500 feet elevation, White Mountains, Inyo County, California, *P. A. Munz 13552* (RSA).

Distribution.—Dry slopes at 400–10,000 feet elevation, from the western slope of the Sierra Nevada eastward to western Nevada (fig. 14).

Representative specimens.—**CALIFORNIA.** Inyo County: 4 miles west of Lone Pine, *Hitchcock 6245* (WTU); Water Canyon, Argus Mountains, *Munz 16490* (WTU); Whitney Portal, *Raven 7432* (CAS); Al Rose Canyon, Inyo Mountains, *Roos 6026* (RSA); west side of Westgard Pass, White Mountains, *V. & A. Grant 9426* (RSA). Tulare County: Monache Meadows near Soda Creek, *Howell 27151* (CAS). Mono County: Virginia Lakes Basin, *Peirson 11226* (RSA); above Chemung Mine, Masonic Mountains, *Munz 21090* (RSA). Tuolumne County: Indian Creek, *Ferris* (DS); Punch Bowl Road near Rawhide, *Stinchfield 80* (DS); 8 miles east of Dardenelles, *Rollins 2976* (DS). Alpine County: Stanislaus River, Middle Fork, *Howell 7603* (CSA). Amador County: Ione, *Eastwood 10158* (CAS); Amador, *Hansen 446* (DS). Calaveras County: Douglas Flat, west of Murphy's, *Pennell 2563* (WTU). Eldorado County: 4 miles from Placerville on road to Kelsey, *Raven 9064* (CAS). **NEVADA.** Washoe County: Truckee Pass, *Kennedy* (CAS); Chocolate Peak east of Mount Rose, *Heller 10657* (CAS); Wimer Reservoir, Mosquito Valley, *Train 2912* (RSA). Mineral County: Wassuck Range, *Archer 6879* (UC). Esmeralda County: 22 miles southeast of Goldfield, *Craig 4130* (POM). Ormsby County: King's Canyon, *Baker 1071* (POM). Nye County: Quinn Canyon Range, *Maguire & Holmgren 25552* (WTU).

Munz (1958) was the first to recognize this taxon which extends from the western slope of the Sierra Nevada into western Nevada. Noting its wider, bicolored corolla and the lighter green foliage he proposed the varietal name *S. californica* var. *desertorum.*

In the course of this investigation several additional facts were brought to light concerning this taxon. As the plants grew in the greenhouse, they formed several compact rosettes of leaves much sooner than any other western species. Consistently cuneate leaf bases and two conspicuous nectar drops are additional morphological features which set them apart. On the western slope of the Sierra Nevada this species comes in contact with *S. californica* subsp. *floribunda;* however, no natural hybrids were encountered. Hybridization studies in the greenhouse indicate *S. desertorum* has limited crossibility with many other western species, crossing readily only with *S. atrata.*

Out of 30 attempts at hybridization involving two populations of *S. desertorum* and several populations of *S. californica,* only 23 seeds were formed. In view of these facts, I feel justified in elevating Munz's variety to the rank of species.

8. SCROPHULARIA CALIFORNICA Cham. & Schlecht., Linnaea 2: 585, 1827.

Glabrescent perennial 8–12 dm tall; leaf blades ovate or triangular-ovate, acute, simply or somewhat doubly crenate, dentate, serrate or laciniate, truncate or cordate at the base, both surfaces usually glabrous, but glandular-puberulent on lower surface of main veins; larger leaves with blades 7–19 cm long and 6–15 cm wide, on petioles 3–7 cm long; panicles

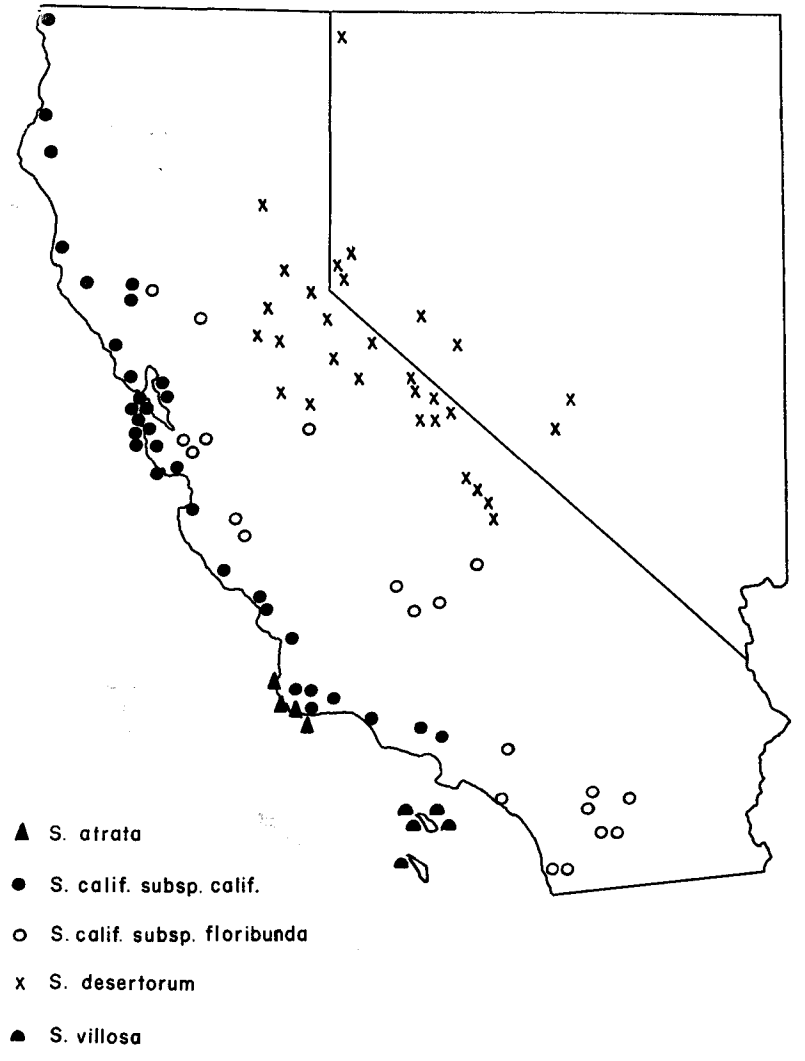

Fig. 14. Distribution of *S. californica* and its geographical relationship to that of *S. villosa, S. atrata,* and *S. desertorum.*

glandular-puberulent, narrow and compact to wide and spreading, of 12–30 fascicles; peduncles and pedicels slender, subinflorescence units at 45° angles to each other; sepals 3–4 mm long, acuminate to rounded-obtuse, narrowly scarious margined or slightly erose; corolla 8–12 mm long, dorsally garnet-brown to maroon, ventrally paler or yellowish-green, the lowermost lobe recurved, the throat slightly constricted, glabrous, nectar inconspicuous; sterile filament clavate to obovate, brown to light maroon, longer than broad 0.8–1 mm wide; stigma capitate; style 4–6 mm long, deflexing at anthesis; capsule 6–8 mm long; seeds 0.6–0.8 mm long.

This is the most confusing and difficult western North American species. It is extremely variable and widespread, occurring all along the coast of California and on both sides of the Great Valley of California. It is found in a variety of habitats, especially on roadside cuts and in the chaparral, from sea level to 3,300 feet elevation (fig. 14).

The variability is most striking in the nature of the inflorescence, color of the corolla, and margin of the leaf. Of these three kinds of variability, only leaf margin seems to be correlated with geographical distribution. The treatment herein included is based upon morphological and distributional studies of herbarium material and field observations. It recognizes two subspecies, *S. californica* subsp. *californica* and *S. californica* subsp. *floribunda*. The former occupies the coastal region from the Santa Monica Mountains, Los Angeles County, north to Del Norte County, while the latter inhabits the inner Coast Ranges and the lower western slope of the Sierra Nevada of central California. Finally it replaces the subsp. *californica* in coastal southern California.

Some intermediates with regard to leaf margin are found where the two subspecies meet in the inner Coast Ranges of Santa Clara and Monterey counties.

KEY TO THE SUBSPECIES

Leaf blades slightly crenate or serrate to coarsely dentate. Coast Ranges of California.....8a. *S. californica* subsp. *californica*

Leaf blades deeply cut into laciniate divisions, these sharply serrate to dentate. Inner Coast Ranges and lower western slope of Sierra Nevada of central California to San Diego.....8b. *S. californica* subsp. *floribunda*

8a. SCROPHULARIA CALIFORNICA Cham. & Schlecht. subsp. CALIFORNICA

S. nodosa var. *californica* M. E. Jones, Contrib. W. Botan. 12: 67, 1908.

Type.—San Francisco, California, October, 1816, *A. von Chamisso* (not seen).

Distribution.—Coastal California from Santa Monica Mountains, Los Angeles County, north to Del Norte County, occasionally as far inland as the east slope of the Coast Ranges (fig. 14).

Representative specimens.—**CALIFORNIA.** Los Angeles County: Mandeville Canyon, Santa Monica Mountains, *Clokey 4573* (UTC). Ventura County: 1 mile south of Mussel Shoals, *Shaw 1112* (UTC). Santa Barbara County: South base of San Marcos Pass, about 7 miles below summit, *Munz 19429* (RSA); 1 mile north of Lompoc, *Munz 19445* (RSA); first tunnel on Gaviota Pass along U. S. Highway 101, *Shaw 1113* (UTC). San Luis Obispo County: State Highway 166 about 15 miles east of Santa Maria, *Munz 19456* (RSA); 4 miles north of Morro Bay, *Wolf 3615* (WTU). Monterey County: 3 miles east of Monterey on road to Salinas, *Shaw 1094* (UTC); Salmon Creek crossing along State Highway 1, *Shaw 1091* (UTC). Santa Cruz County: State Highway 9, north of Felton, *Pennell 25406* (CAS); Santa Cruz, *Jones 2225* (UTC). San Mateo County: north end of Searsville Lake, *Wolf 416* (WTU); 2 miles back of Stanford University, *Wolf 287* (WTU); San Bruno Hills, *Heller 8457* (DS). Alameda County: Oakland Hills above Mills College, *Howell 19414* (CAS); Niles Canyon, *Constance 23* (WTU). San Francisco County: Mountain Lake, *Ewan 10400* (WTU); 1 mile east of Mount Davidson, *Raven 9283* (CAS); above Baker's Beach, Presidio, *Rubtzoff 955* (CAS). Sonoma County: Bodega Bay Road, 2 miles west of Bodega, *Ewan 9220* (WTU). Lake County: Kelsey Creek, 1 mile north of Kelseyville, *Benson 15305* (POM); Barlettt Mountain, southeast of Bartlett Springs, *Pennell & Mason 25526* (WTU). Mendocino County: Hare Creek, 5 miles south of Noyo, *Constance 2501* (UTC). Humboldt County: Samoa, *Munz 19878* (RSA); 1 mile west of Bridgeville, *Munz 19866* (RSA).

8b. **Scrophularia californica** Cham. & Schlecht. subsp. **floribunda** (Greene) Shaw, comb. nov.

S. californica var. *floribunda* Greene, Man. Bay Reg. Botan. 273, 1894.
S. floribunda Heller, Muhlenbergia 2: 46, 1906, non Boiss. & Bal., 1856.
S. californica var. *laciniata* Jepson, Man. Fl. Pl. Calif., 906, 1925, non. *S. laciniata* Waldst. & Kit., 1805.
S. multiflora Pennell, Proc. Acad. Nat. Sci. Phila. 99: 173, 1947.

Type.—Not seen.

Distribution.—Coast Ranges and western slope of the Sierra Nevada, replacing subsp. *californica* in coastal southern California (fig. 14).

Representative specimens.—**CALIFORNIA.** San Diego County: Banner Grade, 3 miles from Julian,

Shaw 800 (RSA); San Felipe Creek, Sentenac Canyon, *Shaw 802* (RSA); Balboa Park, San Diego, *Shaw 799* (RSA); valley east of San Diego, *Pennell & Epling 25157* (WTU); 5 miles south of Temecula, *Shaw 1086* (RSA). Riverside County: Gavilan Peak, *Clokey 4635* (WTU); San Juan Canyon, on road to Santiago Peak, *Everett 7172* (RSA, WTU); 5 miles from Banning on road to Idylwild, *Shaw 1107* (RSA). Orange County: 2 miles above Ranger Station, Silverado Canyon, *Shaw 1085* (RSA). Los Angeles County: Evey Canyon, north of Claremont, *Shaw 778* (RSA). Kern County: 5 miles east of Bakersfield, Kern Canyon, *Shaw 816* (RSA); Keene, *Pennell 25101* (CAS). Santa Clara County: foothills west of Los Gatos, *Heller 7336* (DS); Tuff Hill, *Cannon* (DS). Monterey County: Mansfield Ranch, King City, *Eastwood 4038* (CAS); Hastings Reservation, Santa Lucia Mountains, *Cook et al. 88* (CAS). Tulare County: Upper Tule River, road to Camp Nelson, *Wolf 4615* (CAS, WTU); Ground Hog Meadow, Sequoia National Forest, *Ferris & Lorraine 10721* (WTU); 1.5 miles north of Woodlake, *Bacigalupi & Ferris 3252* (DS). Mariposa County: Blockman Ranch, *Eastwood 4226* (CAS). Yolo County: Davis, *Miller 43* (UTC). Lake County: Kelseyville, *Blankinship* (CAS).

9. SCROPHULARIA OREGANA Pennell, Bull. Torrey Botan. Club 55: 316, 1928.

Glabrescent perennial 10–18 dm tall; leaf blades ovate or triangular-ovate, acute, simply or somewhat doubly serrate or dentate, truncate or cordate at base, glandular-puberulent on lower surface; larger leaves with blades 12–20 cm long and 6–12 cm wide on petioles 2–4 cm long; panicles glandular-puberulent, narrow and compact, of 5–25 fascicles; peduncles and pedicels relatively stout, subinflorescence units at 45° angles to each other; sepals 3–4 mm long, ovate or triangular-ovate, acute or acuminate, narrowly scarious margined or slightly erose; corolla 8–12 mm long, dorsally blackish maroon, ventrally paler, slightly green beneath lowermost recurved lobe, the throat slightly constricted, glabrous, nectar inconspicuous; sterile filament clavate to obovate, apex sometimes broadly acute, maroon, longer than broad, 1–1.2 mm wide; stigma capitate; style 5–6 mm long, not deflexing, capsule 7–9 mm long; seeds 0.8 mm long.

Type.—From dry open area, surrounded by dense Sitka spruce forest, Newport, Lincoln County, Oregon, May 4–5, 1927, *E. M. Harvey 57* (PH).

Distribution.—Coastal region of Oregon, Washington and southern British Columbia (fig. 12).

Representative specimens.—**OREGON.** Curry County: Humbug Mountain, *Thompson 12807* (WTU); Goldbeach, *Thompson 463* (WTU). Douglas County: Winchester Creek, 4–5 miles south of Reedsport, *Pennell 15666* (ARIZ, WTU); Winchester Bay, 5 miles south of Reedsport, *Shaw 1077* (RSA). Lincoln County: Yachats River (sec. 26 T. 14 S., R. 12 W.) *Detling 4061* (WTU); Beverly Beach State Park, *Shaw 1076* (RSA). Clatsop County: Astoria, *Morrill 68* (WTU); U. S. Highway 101, 3 miles south of Seaside, *Shaw 1075* (RSA). Columbia County: Upper Clatskatie Creek, *Thompson 2428* (WTU). Benton County: Boldgett, *Harvey 32* (PH). **WASHINGTON.** Pacific County: 2 miles north of Megler Ferry along U. S. Highway 101, *Shaw 1074* (RSA); Port of Wallapa Harbor, *Shaw 1073* (RSA). Grays Harbor County: 1.6 miles north of Moclips, *Jones 6542* (WTU); 10 miles south of Queets, *Hitchcock 19888* (WTU). Jefferson County: Island at Ruby Beach, 5–6 miles north of Kalalock, *Pennell 21204* (WTU). Clallam County: Clallam Bay, *Jones 5966* (WTU); Neah Bay, *Thompson 9441* (WTU). **BRITISH COLUMBIA.** Vancouver Island, *Rosendahl & Grand 55* (PH).

In 1928, Pennell was emphatic about the distinctness of this taxon from *S. californica,* but in 1947, he changed his opinion and considered *S. californica* as ranging from Vancouver Island to southern California. After studying *S. oregana* in the field and growing it for two years in the greenhouse, I am convinced that morphologically and geographically it is worthy of specific rank. The large, open throat of the blackish-maroon corolla, the narrow, ascending inflorescence, and the tendency for the corollas to persist on developing fruits are characteristics which readily set *S. oregana* apart from *S. californica.*

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