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Author(s): Duncan M. Porter
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THE GENUS KALLSTROEMIA (ZYGOPHYLLACEAE)

Duncan M. Porter[1]

My interest in the *Zygophyllaceae* dates from 1959 (at Stanford University), when I began a taxonomic study of the family as it occurs in Baja California, Mexico. As I became more familiar with the family, it became increasingly obvious that the genera under investigation were badly in need of taxonomic revision, although their species in Baja California were relatively distinctive. I chose to study *Kallstroemia* because it appeared to be the New World genus most in need of revision. In addition, it is the largest genus of the *Zygophyllaceae* in the New World, elsewhere being surpassed in number of species only by *Fagonia, Tribulus,* and *Zygophyllum.*

Such statements as: "Será necessario hacer una revisión minuciosa de las especies centro y norteamericanos para establecer el valor de ellas." (It will be necessary to do a thorough revision of the Central and North American species in order to establish their validity.) (Descole, *et al.,* 1939, p. 221); "There is some difference of opinion as to how the species of this genus should be defined, and the characters for separating them are usually rather vague and unsatisfactory." (Standley & Steyermark, 1946, p. 397); and ". . . revision of the genus is needed." (Macbride, 1949, p. 397), showed a realization of the need for revision. In the following study, I have attempted to do my part in reducing the taxonomic chaos hitherto present in *Kallstroemia.*

The conclusions arrived at are based on the examination of herbarium specimens, and the collection and field observation of about half the species. The observations of wild populations throughout much of the range of the genus have yielded valuable information. In addition, four of the species were studied in greenhouse plantings, which provided information as to seed germination, seedling morphology, and compatibility relationships involving the breeding system.

At the beginning of the investigation, it was planned to obtain chromosome numbers for as many of the species as possible, and to attempt crossing experiments between different species. Unfortunately, these goals proved to be impossible to achieve, be-

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[1] Present address: Missouri Botanical Garden, St. Louis, Mo.

cause most of the preserved cytological material did not contain the requisite meiotic stages. In addition, there was an inadequate amount, and only sporadic flowering, of the greenhouse material. Chromosome numbers for species of the genus remain unknown, as no countable configurations were found in approximately 250 field collections of buds examined for meiosis.

Although morphological analyses provided a basis for interpreting certain natural relationships between the species, the information at hand is not adequate to provide more than the barest outline of phylogenetic relationships within the genus. Future studies utilizing additional field observations, breeding experiments on a large scale, and information regarding chromosome numbers, while perhaps not changing the basic concepts regarding the species of the genus, undoubtedly will permit a more natural classification of *Kallstroemia* than is given in the present work.

GENERIC RELATIONSHIPS

The most recent synopsis of the *Zygophyllaceae* (Scholz, 1964) follows Engler's (1890, 1915, 1931) placement of *Kallstroemia* in the tribe *Tribuleae* Rchb. of the subfamily *Zygophylloideae* along with *Kelleronia* Schinz, *Neoluederitzia* Schinz, *Sisyndite* E. Mey. ex Sond., and *Tribulus* L. Engler (1931) further divided the *Tribuleae* into two subtribes, the *Neoluederitziinae* Engl. (including *Neoluederitzia* and *Sisyndite*) and the *Tribulinae* (with *Kallstroemia, Kelleronia,* and *Tribulus*). These five genera were considered to be closely related and to have arisen from a "single primitive stock" (Engler, 1915, 1931). Comparative morphology and palynology, however, indicate that whereas *Kallstroemia, Kelleronia,* and *Tribulus* form a natural group, *Neoluederitzia* and *Sisyndite* have affinities elsewhere in the family.

In addition to the differences segregating the *Tribulinae,* stated by Engler and others (e.g., herbs versus shrubs or trees; indehiscent mericarps versus dehiscent capsules; lack of endosperm versus its presence; lack of staminal appendages versus their presence), pollen grain morphology has been utilized more recently as an additional criterion of separation. Descole, *et al.,* (1940) were the first to distinguish the *Tribuleae* from the *Zygophylleae* on the basis of polyforate versus tricolporate pollen, and Erdtman (1952) and Agababian (1964), in surveys of pollen grain morphology in the family, have indicated the homogeneity of the *Tribulinae* and the lack of similarity to the rest of the family. The latter author concludes (p. 44) that, "the determination of the relationships of this group of genera appears to be difficult" [translation by Dr. G. K. Brizicky].

Another genus that should be included in this assemblage is *Tribulopis* R. Br., which some consider to be a synonym of *Kallstroemia,* while others include it in *Tribulus. Kallstroemia, Kelleronia* and *Tribulopis* have each, at one time or another, been considered synonyms of *Tribulus,* but there is good evidence supporting their position as separate genera, which constitute a natural group deserving recognition as a major subdivision of the family.

Kallstroemia is composed of 17 species native to the New World: *Kelleronia* has about ten species in Ethiopia, the Hadhramaut, and Somaliland; *Tribulopis* some half-dozen species in tropical and subtropical Australia; and *Tribulus* a number of species native to the Old World. Like most members of the family, they are to be found mainly in arid and semiarid areas.

Specimens of *Tribulopis* and *Tribulus,* as well as *Kallstroemia,* have been examined morphologically and anatomically. However, no material of *Kelleronia* has been seen. Morphological details of the latter genus have been taken from Schinz (1895), Baker (1898), Engler (1915, 1931), Chiovenda (1916, 1917, 1929), Erdtman (1952), and Agababian (1964).

These four genera differ from other *Zygophyllaceae* in that they are mostly prostrate to ascending annual herbs, with opposite, even-pinnate leaves and inequilateral, ovate (rarely linear) leaflets. They have ten stamens with unappendaged filaments in two unequal series, and each filament of the outer whorl is adnate at the base to the basal portion of the petal opposite. Nectariferous tissue is present between the stamens and perianth, pollen is polyforate, and they all have indehiscent mericarps. Vegetatively, the members of this alliance are rather similar, differing mainly in details of flowers and fruits.

The five sepals are herbaceous, more or less ovate, concave, pubescent, and scarious-margined in all, deciduous in *Kelleronia, Tribulopis,* and *Tribulus,* being persistent in all species of *Kallstroemia* except *K. californica.* The five petals are free, white to orange, obovate to truncate, as long as to longer than the sepals, prominantly veined, and hemispherically spreading. They are marcescent only in *Kallstroemia.*

All four genera have five bilobed, nectariferous glands between each of the inner whorl of stamens and the sepals. These glands project downward and outward between the adjacent petals into the concave sepal base. In addition, *Tribulopis* and *Tribulus* have a second whorl of nectaries between stamens and ovary opposite the outer whorl of stamens. It is unknown whether *Kelleronia* has this second set of nectaries, but they are absent from *Kallstroemia.* In *Tribulus,* the interior nectaries are triangular and free [*T. alatus* Del., *T. macropterus* Boiss., *T. terrestris* L. (Schweickerdt, 1937)], or connate into a five-lobed urceolate ring surrounding the base of the ovary [*T. cristatus* Presl, *T. excrucians* Wawra, *T. pterocarpus* Ehrenb., *T. pterophorus* Presl, *T. zeyheri* Sond. (Schweickerdt, 1937); *T. cistoides* L. (Brown, 1938)]. They are bilobed and connate at the base in *Tribulopis solandri* R. Br.

The ovary is five-carpellate in the four genera and is five-lobed and five-loculed in *Kelleronia, Tribulopis,* and *Tribulus.* In *Kallstroemia* it is ten-lobed and ten-loculed. Locule number is mirrored by the style and stigma, both being respectively five-ridged and five-lobed in *Kelleronia, Tribulopis,* and *Tribulus,* and ten-ridged and ten-lobed in *Kallstroemia.*

There is a single ovule per locule in *Kallstroemia* and *Tribulopis,* while *Kelleronia* has two or more, and *Tribulus* has two to five, arranged in two vertical rows on the placentae. In the two latter genera, each locule becomes two- to five-compartmented through the formation of transverse septae between the ovules. Therefore, in all four genera the ovules originally are pendulous, but ontogenetically they become horizontally arranged one above the other in *Kelleronia* and *Tribulus.* Consequently, *Kallstroemia* forms ten one-seeded mericarps, *Tribulopis* five one-seeded mericarps, and *Kelleronia* and *Tribulus* five two- to five-seeded mericarps in which the seeds are separated by transverse partitions. In *Kelleronia* and *Tribulus* the seeds are depressed and nearly horizontal, while those of *Kallstroemia* and *Tribulopis* are pendulous and obovoid. The number of seeds formed has been used in the separation of *Tribulopis* from *Tribulus,* but abortive ovules, resulting in reduced seed formation, are present in species of both these genera and in *Kallstroemia,* and probably result from inadequate pollination.

When the mericarps separate in *Kallstroemia,* they leave a persistent, styliferous axis that is topped by the persistent style, which forms a beak on the fruit. In *Tribulus* this axis is absent, and the style does not persist. It does persist to form a beak on the fruit of *Tribulopis,* but whether it does so following separation of the mericarps is unknown. Likewise, the situation in *Kelleronia* is unknown.

Virtually nothing is known of the reproductive biology of *Kelleronia* and *Tribulopis,* but there are some basic differences between *Kallstroemia* and *Tribulus.* In *Kallstroemia* individual flowers open for only a part of one day. Pollen and the stigma mature simultaneously. The petals are marcescent and fold convolutely together around the style following anthesis, appressing the anthers to the stigma and effecting self-pollination in all species but *K. perennans.* In *Tribulus,* flowers usually last about two days. *Tribulus cistoides* is protandrous (Robertson & Gooding, 1963), with pollen shed the first day and the stigma receptive the second, while *T. terrestris* is protogynous (Goldsmith & Hafenrichter, 1932), with the stigma receptive the first day and pollen shed the second. Self-pollination may take place, and it occurs most frequently by the stamens curving upward and appressing their anthers to the stigma unaided by the petals. It is probable also that insects aid in some selfing.

Certain differences in seed germination are found between *Kallstroemia* and *Tribulus.* In the former, germination is epigeal, the entire mericarp being carried upward by the expanding cotyledons. In *Tribulus* the cotyledons force their way upward to above ground level, but the mericarp remains in the ground. Usually only one seed germinates, but more than one may do so in some cases (Johnson, 1936). Cotyledons in *Kallstroemia* are bright green, simple, entire, concave on the abaxial surface, and have three well-marked palmate veins. They are ovate in outline and pubescent. Those of *T. cistoides* and *T. terrestris* differ in being rectangular, shiny-green, slightly tinged with yellow, parallel veined and glabrous.

It can be seen from the above discussion that evidence from comparative morphology supports the recognition of four genera in this alliance. However, evidence for the elucidation of phylogenetic relationships is lacking. More information is needed regarding the morphology of *Kelleronia,* and cytological and genetical data are needed before one can knowingly discuss the natural relationships of *Kallstroemia, Kelleronia, Tribulopis,* and *Tribulus.*

MORPHOLOGY

This section contains a general review of vegetative, floral, fruit, and seed morphology in *Kallstroemia.* A more detailed comparison of morphological differences between species will be found in the section titled morphological characters and taxonomic criteria.

VEGETATIVE MORPHOLOGY

Habit. The diffusely branching herbaceous to suffrutescent stems of *Kallstroemia* spread radially from a stout, annual (perennial in *K. boliviana* and *K. perennans* and perhaps occasionally so in *K. hintonii* and *K. rosei*) root and branch primarily from the basal nodes. In most species, stems are prostrate to decumbent in mature plants, but in *K. grandiflora, K. parviflora,* and *K. perennans* they may be ascending. Stems of seedlings and young individuals of most species also are upright at first, but they soon fall over from their own weight and become prostrate or decumbent. Occasional individuals of *K. grandiflora* growing under exceptionally favorable conditions (e.g., along roadsides and in low places where rainwater has collected) may reach a height of one meter and a diameter of several meters. Size ranges from these large globose individuals of *K. grandiflora,* which may cover 16 square meters or more (Cannon, 1911), down to prostrate plants of *K. curta* and *K. hirsutissima* with a diameter of one to two feet.

Roots. The root system consists of a thick, fibrous, deeply penetrating, conical tap root with a relatively stout crown, that may reach a length of several decimeters. The slender, filamentous lateral roots are mainly parallel and close to the soil surface. In the Sonoran Desert near Tucson, Arizona, Cannon (1911) found that roots of *Kallstroemia grandiflora* may penetrate as deeply into the ground as those of some perennials in the same area, with the tap root reaching a length of 22 centimeters, and the longest lateral root being over 21 centimeters long. This deeply penetrating root system enables *Kallstroemia* to resume growth following the normal growing season if an unseasonal rain should occur before the plant succumbs during the dry season.

Stems. Stem growth is sympodial, the apical meristem changing from a vegetative to a floral meristem at each successive node. Therefore, a flower terminates the stem, further growth taking place from a vegetative bud in the axil of one of the pair of leaves at the last node. This new stem axis crowds the terminal flower of the preceding axis aside, so that the stem has a characteristic zig-zag appearance with seemingly axillary flowers on alternate sides at the usually more or less swollen nodes. Branching occurs when the axillary bud of the opposite leaf grows out as well. This type of growth is characteristic of the *Zygophyllaceae* (Engler, 1890).

When fresh, the stems are terete, somewhat succulent, flexible, fibrous, and tough. Upon drying, they shrink in diameter and become brittle and striate, the striations being outward manifestations of a ring of cortical fibers. They are green, yellow-green, or reddish, drying to yellow.

Like the foliage, the stems usually are densely covered with unbranched, white, gray, or yellow nonglandular trichomes. These are unicellular outgrowths of epidermal cells which may be bulbously swollen basally. They are especially prevalent at the nodes. Trichomes are appressed toward the stem apex and usually also spreading in all species except *Kallstroemia peninsularis* and a few individuals of *K. pubescens* from Peru, where they are retrorse. There is a correlation between amount, but not type, of pubescence and various climatic and edaphic factors. The specimens from drier situations are the most pubescent, while at the other extreme individuals growing under mesophytic conditions are almost glabrous. Also, specimens from alkaline soils are much more pubescent than the average.

Stipules. A pair of free stipules is found on the stem at the base of the petiole. They are foliaceous, ciliate, persistent, narrowly to broadly falcate, acuminate, erect or spreading from the stem, and shorter than the petioles. The pubescence is the same as that on the stems.

Leaves. Vernation is imbricate, and the leaves are opposite, one of each pair alternately smaller than the other or sometimes abortive. They are slightly succulent and abruptly even-pinnate, with the petioles usually shorter than the leaflets. Seedling leaves are less divided than those of the mature plant and grade gradually into them. Both petiole and rachis have the same type of pubescence as the stem, and the rachis is terminated by a foliaceous, subulate, pubescent, and apiculate mucro about one millemeter long.

Leaflets vary in number from two to ten pairs. They are usually somewhat unequal in size, those on one side of the rachis being slightly smaller than the other. The basal pair are markedly unequal, and the terminal pair more falcate and pointed forward than the lower pairs. The leaflets are opposite, basally oblique to inequilateral, entire, acute to obtuse, mucronate, apiculate, pubescent to glabrate, ciliate, and their margins may be flat or inrolled. Venation is reticulate.

Pubescence varies from heavy (especially on younger leaflets) to almost glabrate. Trichomes are similar to those on the stem. They are appressed toward the leaf apex and are found on both abaxial and adaxial surfaces of the blade and along its margins, being more numerous on the abaxial surface. Marginal trichomes may be so profuse as to give leaflets a whitish outline. Likewise, the petiole and rachis usually appear whitish because of numerous trichomes.

The leaves show marked nyctotropic movements, the leaflets rising soon after dark and adpressing their adaxial surfaces together. They return to their normal horizontal position before dawn. This movement is also readily observable within a short time after the plant is pulled from the ground. Nyctotropic movements have been observed to occur in all species of *Kallstroemia* grown in the greenhouse (*K. grandiflora, K. maxima, K. pubescens,* and *K. rosei*), and also in *Tribulus cistoides* and *T. terrestris*. Under very hot and dry conditions, the leaves will fold up during the day.

FLORAL MORPHOLOGY

Peduncles. The peduncles are pseudo-axillary, shorter to longer than the leaves, more or less thickened distally (becoming more so in fruit), and have the same type of pubescence as the stems and leaves. They are reflexed in bud, and erect during anthesis. Following anthesis, they usually elongate and recurve under the leaves, becoming curved, straight, or sharply bent at the base and straight above.

Flowers. Flowers are solitary, pentamerous (occasionally hexamerous in *Kallstroemia tribuloides*), polypetalous, syncarpous, perfect, regular, and hypogynous. They appear to be alternate, but through sympodial branching of the stem they are borne terminally. Because of this seemingly alternate arrangement, the genus has been described as having a cincinnus as an inflorescence, but this is not the case. The flowers occasionally have been described as being tetramerous, but specimens of this type have not been seen.

Calyx. The five sepals are imbricate in bud. They are concave, free, lanceolate to broadly ovate in flower, foliaceous, pubescent, acute, apiculate, scarious margined, and inserted at the base of the receptacle. Trichomes may be the same or different from the type on the vegetative parts. They are not found on the scarious margins, but only on the green central portion of the abaxial surface, and occasionally on the adaxial surface. However, sepal margins usually appear ciliate, because the scarious margins nearly always fold involutely inward following anthesis, whether the remainder of the sepal does so or not. After anthesis the sepals may appear subulate or linear-lanceolate due to the involutely inward folding of their margins. They are persistent in all species except *Kallstroemia californica*.

Corolla. The five petals are convolute in bud. They are free, alternate with the sepals, elliptical to broadly obovate, rounded or truncate, and irregularly notched to entire at the apex, glabrous, as long or usually longer than the sepals, fugaceous, and usually marcescent. They have prominent veins, spread hemispherically, and are inserted at the base of a fleshy, obscurely ten-lobed disc. At the base, each petal is adnate to the base of the filament of the stamen in the outer whorl opposite it. Petal color varies from white through yellow to bright orange, and also may be basally green to red, the base being darker than the remainder of the petal.

Androecium. The androecium is obdiplostemonous, there being two whorls of five stamens each. Filaments are inserted in the disc; they usually are filiform to subulate, but are winged at the base in *Kallstroemia hintonii*. Those of the two whorls are of different lengths, the ones opposite the petals being longer than the inner whorl, but shorter than the petals. Filaments are the same color as the base of the petal, varying from green to red. They are generally long enough to reach the top of the style, but in *K. perennans* they are only about two-thirds the length of the style. The connectives often contain druses that are presumably composed of calcium oxylate. Between the base of each filament of the inner whorl and the opposite sepal is a small, ovoid, bilobed nectary. It projects downward and outward between the bases of the adjacent petals into the concave sepal base.

The anthers are globose to ovoid or occasionally linear, yellow to red, bilobed, bilocular, tetrasporangiate, sub-basifixed to versatile, introrse, and longitudinally dehiscent. Those of the inner whorl occasionally are small and sterile.

The pollen grains are spherical, yellow to red, and have a polyforate exine. They are shed singly.

Gynoecium. The superior, sessile, ten-lobed, ten-loculed, globose to ovoid or occasionally conical ovary is glabrous to sparsely or densely pubescent with straight to curved, white or gray, unicellular trichomes. Placentation is axile, and the ovules are one per locule, pendulous, and anatropous, with a superior micropyle. Sometimes one or more is abortive, especially in individuals which have been self-pollinated.

The gynoecium has been described as five-carpellate, with two ovules per carpel which spuriously are divided in ontogeny by a vertical septum, thus only being secondarily ten-loculed with a single ovule per locule (Wight & Arnott, 1834; Torrey & Gray, 1838). However, ten locules are present throughout the growth of the ovary, and the change to this condition is not only ontogenetical, but is an evolutionary culmination of a phylogenetical trend.

The style arises from the summit of the ovary and is cylindrical or conical, with a more or less conical base. It varies from glabrous to variously pubescent, is more or less ten-ridged, and terminates in as many stigmatic bands as there are locules. It persists to form a beak on the mature fruit.

The clavate to capitate stigma is papillose (coarsely pubescent in *Kallstroemia perennans*), silvery, simple and basally lobed, or with distinct ridges. In *K. peninsularis* the stigmatic surfaces extend downward almost to the base of the style, but in all other species the stigma is terminal.

FRUIT AND SEED MORPHOLOGY

Fruit. The fruit is a ten-lobed, glabrous or variously pubescent, ovoid or occasionally conical to pyramidal capsule which, upon maturation, septicidally divides and separates into ten unilocular, one-seeded mericarps. However, there may be fewer than ten through abortion of some ovules. Both the beak (the persistent style) and the styliferous axis persist on the peduncle following this separation.

Mature mericarps are hard and nut-like, obliquely triangular, broadly wedge-shaped, and vary from whitish to black. The glossy, variously pitted lateral faces slope into a thin straight, curved, or angled adaxial edge. The abaxial surface is rounded and thicker, may be slightly keeled or cross-ridged, and usually bears a series of rounded to elongate tubercles. This surface varies from thickly pubescent to glabrous.

Seed. The oblong-ovoid seed is obliquely pendulous from the apex of the central angle of the mericarp and lacks endosperm. The testa is smooth, white, and membranaceous. It completely surrounds the embryo at maturity and is free from the mericarp wall.

The embryo is straight, with ovoid, foliaceous cotyledons, a superior, conical radicle, and a rudimentary epicotyl. The only information concerning embryology in the genus is Mauritzon's (1934) observation in "*Kallstroemia maxima*" that the suspensor consists of a single row of cells.

REPRODUCTIVE BIOLOGY

This section discusses general aspects of flowering, pollination, and seed germination in the genus. An account of suspected interspecific hybridization will be found in the section on interspecific relationships.

FLOWERING

Prior to anthesis, the peduncle in *Kallstroemia* is reflexed, with the developing bud lying beneath the herbage. As the flowering period is approached, it becomes erect, carrying the bud into an upright position. Following pollination, the peduncle elongates and usually once more becomes reflexed, forcing the developing fruit back below the leaves. This takes place in a single day.

Pollen is fully formed by the time the bud is about one millimeter in diameter, when the anthers are essentially still sessile and before filament elongation has taken place. Meiosis in the microsporocyte is of the simultaneous type, no wall forms after the first division and the two divisions are almost simultaneous. Therefore, four free nuclei are found in the microsporocyte protoplast before cytokinesis takes place. This is followed in the developing pollen grains by the formation of a tetrahedral tetrad. The microsporocyte cell wall disappears late in pollen maturation, and the polyforate nature of the grains can be seen prior to the disintegration of this wall.

By the time the pollen grains are fully formed, the petals still consist only of primordial bumps on the receptacle. Their principal period of growth takes place after the anthers reach mature size. Both the petals and filaments accelerate their growth rate immediately prior to anthesis, exceeding the sepals only at this time.

Flowers in most species usually open only in the morning, closing about midday, except in cloudy weather, when they open later or remain closed. Flowering is accomplished by the convolute petals unfolding, spreading hemispherically, and forcing the sepals backward.

Sloane (1696, 1707), Don (1831), and Macfadyen (1837) have commented on the floral fragrance of *Kallstroemia maxima*. However, I have not detected any odor in the flowers myself. This trait is not reported for any other species of the genus.

POLLINATION

Species of *Kallstroemia* so far examined in the field or grown in the greenhouse are not self-pollinated prior to anthesis. Pollen is shed after the flower has opened, at which time the stamens are appressed to, or very near the spreading petals, and the stigma is held erectly above them. The stigma is receptive to pollen at this time. Although the stamens are differentiated into two series, the anther size is only exceptionally different in the two whorls, and all ten anthers dehisce more or less simultaneously.

The genus appears to be one which is pollinated promiscuously, being visited by various Diptera and Hymenoptera for pollen, and by these and Lepidoptera for nectar. Very few reports of the types of insects visiting the flowers have been recorded. According to notations accompanying herbarium specimens, *Kallstroemia* *grandiflora* is visited by "bees and wasps" in Sonora and Colima, Mexico, and *K. maxima* by "honeybees and small flies" in Costa Rica. In Jamaica the latter species is sought out by small butterflies for its nectar.

The only pollinators of *Kallstroemia* to have been positively identified are bees of the genus *Perdita*, usually found in the deserts of the southwestern United States and northwestern Mexico on various *Compositae*. *Perdita pectidis* has been taken from "*Tribulus maximus*" (*Kallstroemia californica* or *K. parviflora*) in New Mexico (Cockerell, 1896). *P. echinocacti* has been found a number of times on *K. grandiflora* in Arizona and Sonora (Timberlake, 1954, 1960), and *P. euphorbiae* is known from the same species in Sonora (Timberlake, 1960).

When a honeybee lands on a flower of *Kallstroemia maxima*, it thrusts aside the stamens, while standing over them and the style in order to reach the nectar at the bases of the sepals. In this way pollen is transferred from the anthers to the bee, and from the bee to the stigma. The bee circles clockwise on the flower until it has sampled all the nectaries, then moves on to another flower, not uncommonly returning later to the original flower, either to repeat the previous performance or to reject the flower. The bee, therefore, may act not only as an agent in cross-pollination, but also may effect self-pollination by transferring pollen from anthers to stigma in the same flower. This is accomplished in either the initial visit or upon return of the bee to a flower previously visited.

Self-pollination also takes place through the following novel method. During the flowering period the filaments slowly curve upward, moving the anthers upward and appressing them to the style and stigma just before the petals close, which further appresses the anthers to the stigmatic surface. The clockwise, convolute twisting of the petals around the style as they close helps insure self-pollination in the absence of insect visitors. Although the petals are fugaceous, they usually are marcescent also and may persist twisted around the style until the fruit is mature. Greenhouse plantings of *Kallstroemia grandiflora, K. maxima, K. pubescens*, and *K. rosei* all have exhibited this phenomenon, and they have set seed following it as well. Most of the remaining species display this behavior also, for herbarium specimens of all species but *K. perennans* have revealed anthers appressed to stigmas and marcescent petals. In *K. perennans* the stamens are only two-thirds as long as the style and do not reach the stigma, and the petals are fugaceous but not marcescent. The only other member of the *Zygophyllaceae* known to be self-compatible is *Larrea tridentata* (DC.) Cov. (Raven, 1963).

SEED GERMINATION

Seeds of *Kallstroemia* are viable for at least three years, and Ernst (1876) claimed that seeds of *K. maxima,* among those of other weeds, retained their viability after having lain dormant in the soil for more than 30 years. However, there is some question as to whether the seeds were acually *in situ* for such a time, or whether they were introduced later upon exposure of the surface during excavation of the area in Caracas, Venezuela, where his observations were made.

Germination of the seeds proved difficult when mericarps were placed on moist filter paper in petri dishes and these placed in the dark at room temperature. Even if the mericarp wall was broken, germination was virtually nil. These mericarps also were more liable to fungal attack than those planted in three-inch pots in a 1:1 mixture of loam and peat-moss. Here the percentage of germination was high, regardless of whether the mericarp wall was broken or not. The percentage of germination was much lower for mericarps placed in pure sand, probably because it dried out much faster than the above mixture.

Germination takes place through the abaxial surface of the mericarp, which splits vertically down the center. It is epigeal, the entire mericarp being carried up into the air by the unfolding cotyledons. Following germination, rapid elongation of the primary root takes place, with the aerial parts growing more slowly. The first leaves, other than the cotyledons, have two pairs of leaflets, and a gradual increase in leaflet number takes place until that of the mature plant is reached. Flower buds generally begin to appear with the fifth or sixth leaf.

The pattern of germination exhibited by *Kallstroemia maxima, K. pubescens,* and *K. rosei* in greenhouse plantings is that termed "intermittent" by Salisbury (1961). Here the seeds germinate at irregular intervals. Following an initial burst of germination during the second week after the mericarps had been sown and first watered, seeds of a given planting were still intermittently germinating over one year later. This pattern was independent of whether or not the mericarp wall had been broken, although seedlings from scarified mericarps did begin to sprout on the ninth day following planting, one day before those from non-scarified mericarps.

According to Salisbury, intermittency is frequently caused by diversity in the permeability of the seed coat. Whether this is true for *Kallstroemia* can be determined only through further experimentation. Another possible explanation is that growth inhibitors may be present in the seed coat or mericarp which must be leached out by rainwater or soil moisture. A water-soluble inhibitor of germination has been found in the fruit wall of *Zygophyllum dumosum* Boiss. (Koller, 1955), and the seeds of *Larrea tridentata* (Runyon, 1930) and of *Tribulus terrestris* (Johnson, 1936) exhibit dormancy, a phenomenon frequently caused by growth inhibitors (Evenari, 1949).

DISTRIBUTION AND ECOLOGY

Fossils of plants purported to belong to the *Zygophyllaceae* have been reported a number of times in the literature. However, with the exception of a single instance, all of these fossils are of extant shrubby genera with no discernable close relationships to *Kallstroemia*. The exception (Martin, 1963) is a report of pollen of *Kallstroemia* itself from southeastern Arizona, southwestern New Mexico, and northeastern Chihuahua. All of the localities from which *Kallstroemia* pollen was reported were alluvial deposits of less than 10,000 years of age. Unfortunately, the only information this gives us is that the genus was present at that time in an area in which it is still to be found.

Spatial Distribution

There are four species of *Kallstroemia* in North America that, with justification, can be termed primarily of the warm desert, even though three of them also occur outside the desert proper. These four species are *Kallstroemia californica, K. grandiflora, K. hirsutissima,* and *K. perennans.* The first three may at times be found growing in the same locality.

Of the four, *Kallstroemia perennans* has the most restricted distribution *(Map 15).* This rare perennial of the Chihuahuan Desert is known only from Brewster, Presidio, and Val Verde counties in southwestern Texas. It appears to be the only species of the genus to be confined to a single type of substratum, having been collected only on limestone soils. Rainfall occurs mainly from June to September in the Chihuahuan Desert (Shreve, 1942), and *K. perennans* is known to flower in May, June, and September. It is found at elevations from about 650 to 1000 meters.

The most common *Kallstroemia* in the North American deserts is *K. grandiflora (Map 14),* which is found throughout the Sonoran and Chihuahuan deserts except in Baja California, Mexico. It occurs also in the mesquite-grassland formation[1] between these two warm deserts, as do *K. californica* and *K. hirsutissima. Kallstroemia grandiflora* ranges south of the desert proper along the west coast of Mexico from southern Sonora to the valley of the Río Balsas and in northern Guerrero as well. In its southern extension, this species is found in thorn forest and tropical deciduous forest from southern Sonora to Colima and in arid tropical scrub in Michoacán and Guerrero. This area is characterized by arid vegetation types and marked wet and dry seasons (Shelford, 1963). *Kallstroemia grandiflora* is a typical summer annual over most of its range. It flowers mainly from July through October, following the heavy summer rains that usually fall during this time in the Sonoran and Chihuahuan deserts (Shreve, 1942, 1951), and south along the semiarid west coast of Mexico (Shelford, 1963). Flowering may take place sporadically at other times if conditions are adequate for seed germination and plant growth. Further south, from Jalisco to Guerrero, the scanty information available indicates that growth and flowering takes place sporadically from August to March, presumably following fall and winter rains, although Shelford (1963) states that most of the precipitation in this area falls from June to September. The species occurs from sea level to about 2000 meters and is found mainly on sandy soils, being particularly common on the sandy expanses of the Sonoran Desert. A number of specimens from the easternmost part of its range in Texas and Mexico have been collected on limestone and gypsum soils.

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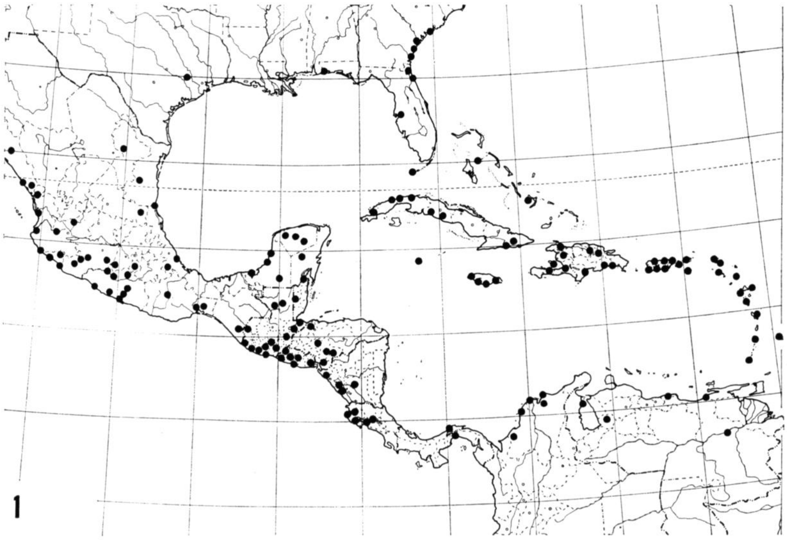
[1] Except where noted, the terms used for Mexican vegetation types are those of Leopold (1950).

Kallstroemia californica (Map 10) is another primarily warm desert species. It occurs over much of the same area as *K. grandiflora,* but is distributed more widely in all directions except toward the south. Like that species, it continues in the thorn forest southward along the Mexican west coast. However, it extends only as far south as southern Sinaloa. Unlike *K. grandiflora, K. californica* is found in the westernmost extension of the Sonoran Desert in Baja California, where it also ranges southward into the tropical deciduous forest of the Cape Region. It occurs in the Mojave Desert of California as well, where, similar to *K. grandiflora* in the Sonoran and Chihuahuan deserts, it "may carpet the desert for miles after a rainy summer" (Munz, 1962, p. 97). *Kallstroemia californica* is found eastward through the mesquite-grassland formation and across the northern sections of the Chihuahuan Desert, where its distribution is rather spotty, to southern Texas and northeastern Mexico. In the northern area of its distribution and east of the desert, this species becomes more abundant in the various arid grassland formations it inhabits. It is common within the mesquite-grassland of southern Texas, and occurs less frequently in the *Acacia*-grassland (*fide* Shelford, 1963) both in Texas and the south and southwest in the Mexican states of Coahuila, Nuevo León and Tamaulipas. Throughout most of its range, *K. californica* grows and flowers from July through October, following the summer rains. Exceptions are in Texas, where flowering may begin in May or occasionally as early as March, and in Baja California. In the latter area, the plants behave as winter annuals, growing and flowering from August through March, following fall and winter rains. Such a growth cycle is unusual for the genus, but it is not particularly so for the area, as the Sonoran Desert in Baja California is extremely poor in summer annuals (Shreve, 1951). Like *K. grandiflora, K. californica* is to be found mainly in sandy disturbed areas, where it occurs mainly at lower elevations, but extends from sea level to about 1600 meters. This species apparently has increased its range eastward in recent times, concomitant with the invasion of the grasslands by arid scrub.

The fourth species of the warm desert group, *Kallstroemia hirsutissima (Map 7),* is distributed most commonly in the Chihuahuan Desert, but it extends northwestward through the mesquite-grassland formation to that portion of the Sonoran Desert



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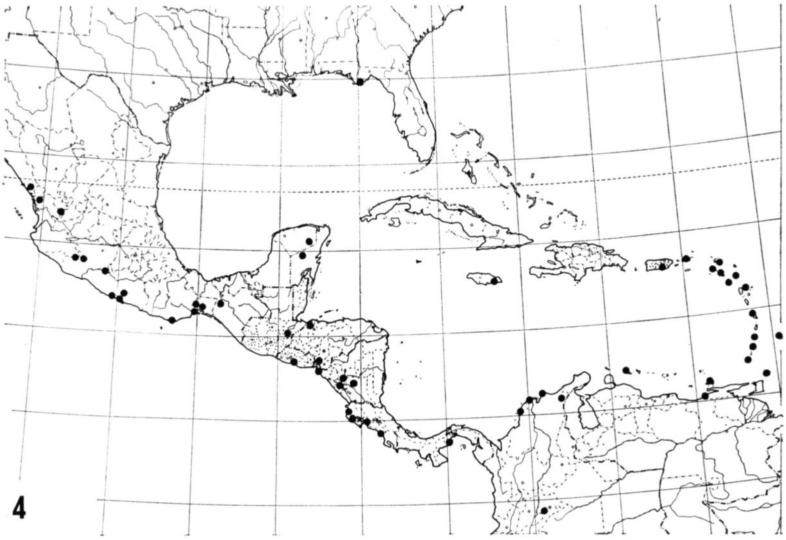

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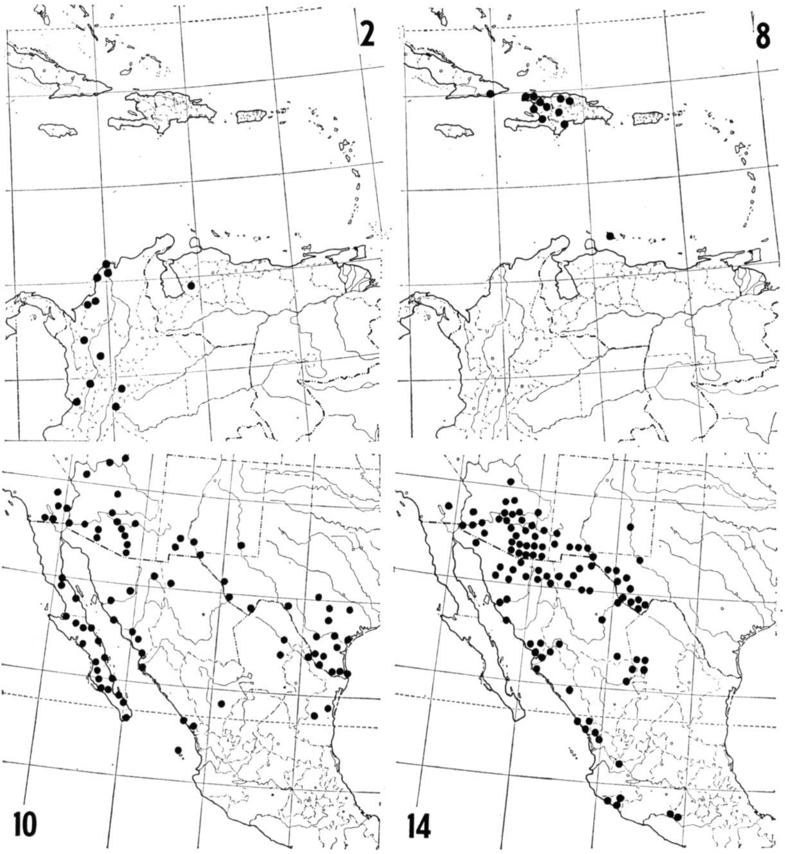
MAP 1. Distribution of *Kallstroemia maxima.* MAP 4. New World distribution of *Kallstroemia pubescens,* exclusive of Ecuador and Perú (see MAP 5).

in southeastern Arizona that Shreve (1951) has called the Arizona Upland. As is true of *K. californica, K. hirsutissima* occurs to the east in the mesquite-grassland and *Acacia*-grassland formations of southern Texas and northeastern Mexico. However, it has not been collected often in the latter area. It is a summer annual, known to germinate, grow, and flower only from June to October, but mostly from July through September. *Kallstroemia hirsutissima* is found from sea level to about 1700 meters, mainly at higher elevations. Perhaps, as is suggested for *K. californica,* it has recently spread eastward into the semiarid grasslands.

There is a fifth species which ranges to some extent into the North American warm deserts, but in contrast to the others, it appears to be the only *Kallstroemia* that is indigenous to areas characterized by various grassland formations. *Kallstroemia parviflora (Maps 5, 16)* has been collected from Illinois south to the central Mexican states of Guanajuato, Querétaro, and Hidalgo. It occurs from California east to Mississippi and has been introduced into Peru as well. In Mexico, *K. parviflora* is almost entirely confined to the mesquite-grassland, but it has been collected sporadically in the Chihuahuan Desert also. To the northwest, it has been found occasionally in the United States in the Sonoran and Mojave deserts and beyond. The species is most common in Texas, from whence it ranges northward through New Mexico and Oklahoma to Colorado and Kansas, mainly occurring west of 96° longitude. *Kallstroemia parviflora* occurs sporadically to the east into Missouri and Illinois, where it has been introduced along the railroads, and it is also known from a single collection in Mississippi. In the United States this species is to be found mainly in the mesquite-grassland, and the different grasslands characterized by short-grass, mixed-grass, and tall-grass (*fide* Shelford, 1963). It occurs sporadically outside of these areas. Flowering is mainly from July to September throughout this vast range. Germination and growth follow the summer rains, which decrease in amplitude toward the north. However, growth and flowering may take place at other times as well if conditions of moisture and temperature are adequate. It is interesting to note that this species remains a summer annual where it has been introduced in Peru, flowering from November through April. There it has been collected in localities characterized by different communities of subtropical scrub receiving summer rainfall (Tosi,



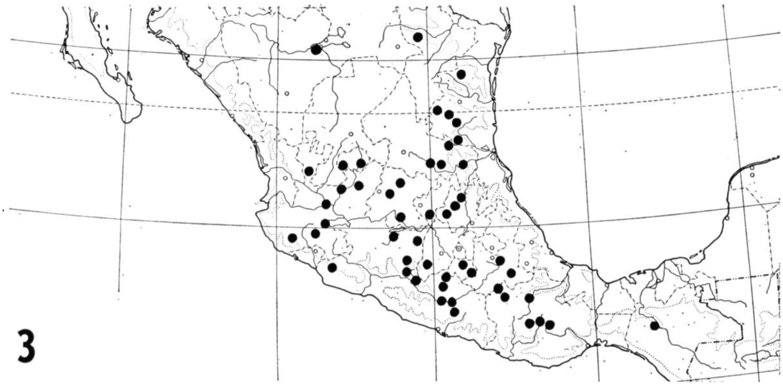
MAP 2. Distribution of *Kallstroemia maxima* × *K. pubescens*?. MAP 8. Distribution of *Kallstroemia curta*. MAP 10. Distribution of *Kallstroemia californica*. MAP 14. Distribution of *Kallstroemia grandiflora*.

1960). *Kallstroemia parviflora* is to be found usually in sandy disturbed areas, but in a report on the desert gypsum flora of western Texas and adjacent New Mexico, Waterfall (1946) indicated that this species (reported as *K. brachystylis*) grew well on gypsum. However, he thought that the plants observed were probably gypsum tolerant, rather than gypsophilous.

There are six species of *Kallstroemia* that occur in Mexico in addition to three of the four species discussed above. Of the six, four are endemic to Mexico, and three of these endemics have a restricted distribution. *Kallstroemia standleyi* appears to have the narrowest distribution of the Mexican endemics, but further investigation will undoubtedly prove it to have a wider range than is known at present. *Kallstroemia standleyi* has been collected only at the type locality, on sand dunes near the beach, one-half mile east of Salina Cruz, Oaxaca *(Map 11)*. Leopold (1950) and Shelford (1963) characterize the vegetation of this general area as savannah, but from personal observation I would say that the coastal area in the immediate vicinity of Salina Cruz is better termed arid tropical scrub. It is possible that the presence there of a xerophytic vegetation type may be a secondary phenomenon due to man's interference through cutting and grazing. This species is known to flower in July.

The second Mexican endemic with a restricted distribution is *Kallstroemia hintonii,* known only from elevations of from 300 to 400 meters in the general region of Apatzingán, Michoacán *(Map 11)*. Although *K. hintonii* has been collected only a half-dozen times, it does not appear to be rare where it is found. Leavenworth (1940) states that it may be seen "coloring whole fields at times," and I have found a population which stretched for about two miles along both sides of the road between Apatzingán and Aguililla, Michoacán. The vegetation of the Apatzingán area is tropical deciduous forest and arid tropical scrub. Summer rains predominate and occur from June to September (Shelford, 1963). *Kallstroemia hintonii* is known to flower in August, September, and December.

The southern part of the Mexican territory of Baja California Sur contains the endemic *Kallstroemia peninsularis (Map 15)*. This species is found mainly in low sandy areas and sandy beaches in the tropical deciduous forest of the Cape Region, but it also occurs occasionally to the west and north in the Sonoran Desert.



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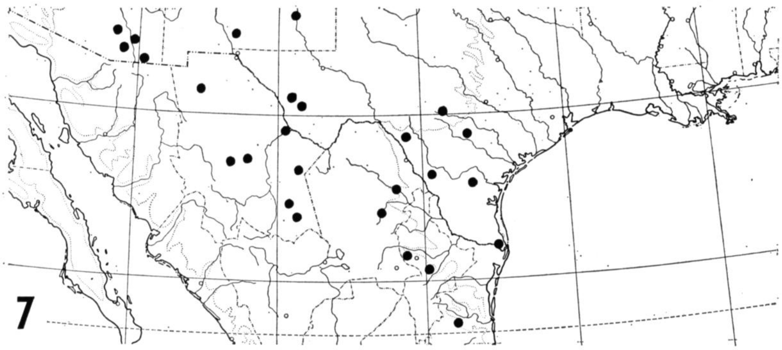

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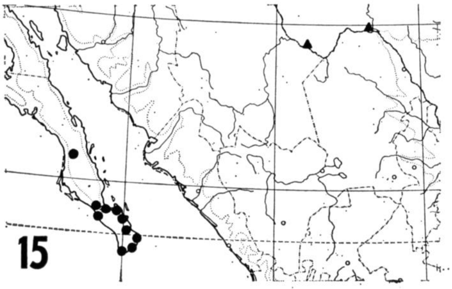

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Map 3. Distribution of *Kallstroemia rosei*. Map 7. Distribution of *Kallstroemia hirsutissima*. Map 11. Distribution of *Kallstroemia standleyi* (triangle) and *K. hintonii*. Map 15. Distribution of *Kallstroemia peninsularis* and *K. perennans* (triangles).

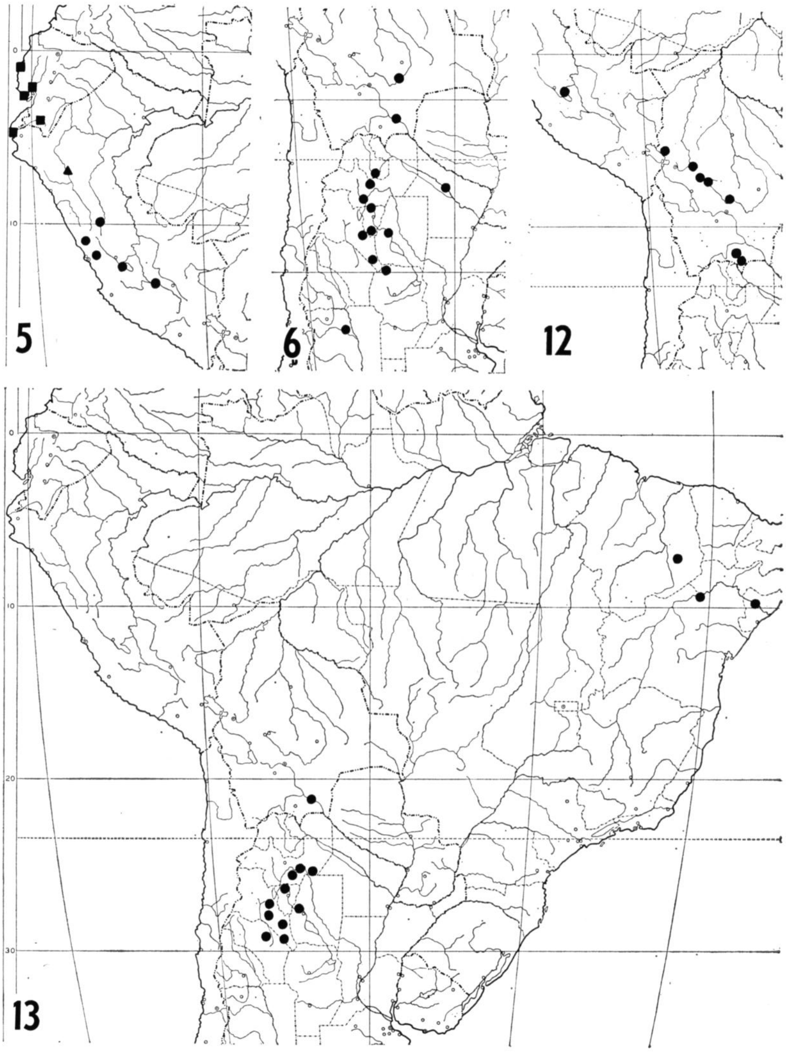
The Cape Region of Baja California differs from the adjacent desert area in that the more copious rains usually fall during the summer months, although winter rains are not unknown (Shreve, 1937). *Kallstroemia peninsularis* is known to flower from August through March, following both summer and winter rains.

The most widespread *Kallstroemia* endemic of Mexico is also the one found in the most mesophytic vegetation type. *Kallstroemia rosei (Map 3)* appears originally to have been restricted to open disturbed sites in the pine-oak forest of central and northeastern Mexico, but man has distributed it into lower and more xerophytic habitats, especially Guerrero and Michoacán. At present, it occurs from 200 to 3150 meters, mainly at higher elevations. *Kallstroemia rosei* ranges from the Sierra Madre Oriental in Nuevo León to the Sierra de Oaxaca and Sierra Madre del Sur in central Oaxaca, and from Jalisco to Puebla in the mountains of central Mexico. It is very common also in the Río Balsas basin and is found sporadically at lower elevations elsewhere. The pine-oak forest area of Mexico has a rainy season that generally extends from June through September (Shelford, 1963), and *K. rosei* usually flowers during this time, although scattered instances of flowering until March are known.

The Caribbean region has three species of *Kallstroemia,* two of which have a very wide distribution, both occurring outside of this area. In contrast to their more temperate congeners, these more tropical species may be found flowering thoughout the year. Seed germination and growth appear to be almost wholly dependent upon the presence of adequate moisture—at least this appears to be true in their native habitats.

The island of Hispaniola seems to be the original area occupied by *Kallstroemia curta.* It has probably been introduced into Cuba and the Netherlands Antilles islands of Aruba, Bonaire, and Curaçao *(Map 8).* This species is the most restricted of the Caribbean members of the genus. It occurs from sea level to 1300 meters but is found mainly at lower elevations.

One of the most widespread species of *Kallstroemia* is *K. maxima (Map 1).* It is commonest in the islands of the Caribbean and in western Central America. This species also ranges across northern South America and northward along both coasts of Mexico to the Tropic of Cancer and beyond. In the southeastern United States it occurs as far north as South Carolina, and it has

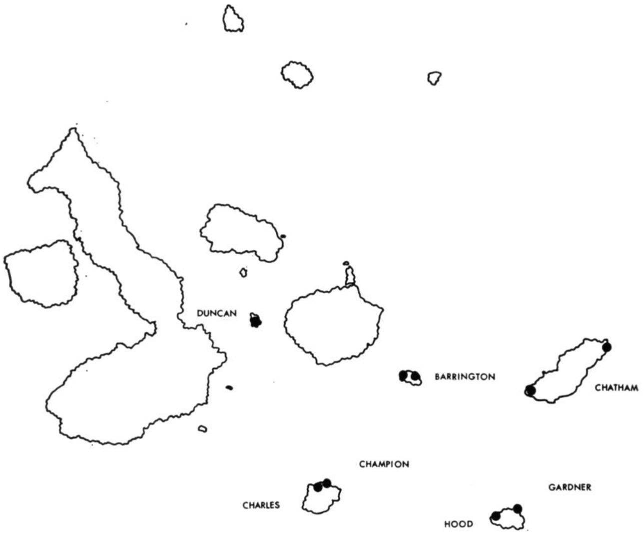


Map 5. Distribution of *Kallstroemia pubescens* (squares) in Ecuador and Peru, *K. pennellii* (triangle) and *K. parviflora* in South America. Map 6. Distribution of *Kallstroemia tucumanensis*. Map 12. Distribution of *Kallstroemia boliviana*. Map 13. Distribution of *Kallstroemia tribuloides*.

been introduced into Brenham County, Texas, where it persists. This weedy species of sandy disturbed soils has been collected at elevations ranging from sea level to about 1350 meters, but it is especially prevalent along roadsides and in cultivated areas at lower elevations. *Kallstroemia maxima* rarely is to be found outside of areas that are frost-free the year around.

A species that occurs sympatrically with *Kallstroemia maxima* over much of its range is *K. pubescens (Maps 4, 5).* Although the two are found growing in the same locality occasionally, they appear to be at least partially isolated ecologically. *Kallstroemia pubescens* tends to be found in sandier situations at slightly higher elevations than *K. maxima.* It occurs from sea level to 1400 meters, being most common at lower elevations. It is commoner than *K. maxima* in the Lesser Antilles and is almost completely absent from the Greater Antilles. *Kallstroemia pubescens* is found in disturbed areas through western Central America as far north as Yucatán on the southeastern coast of Mexico, while on the west coast it reaches southern Sinaloa. It is less common through this area than *K. maxima.* However, *K. pubescens* ranges further south than the latter species, occurring in the xerophytic coastal area (*fide* Svenson, 1946a) of Ecuador and northern Peru. It is also known from a single locality in western Florida. This species flowers the year around, except in Ecuador and Peru, where it flowers during the rainy season from February to April. It is the only *Kallstroemia* known outside of the New World, having been introduced to coastal Ghana and Nigeria (Keay, 1955) and West Bengal, India (Bennet, 1965).

Five species of *Kallstroemia* are endemic to South America. Of these, two have been found growing in the same localities, and mixed collections of herbarium specimens are sometimes found. These two species, *K. tribuloides* and *K. tucumanensis,* have the southernmost distributions in the genus *(Maps 6, 13).* Both of them are native to a region characterized by xerophilous scrublands (Cárdenas, 1945; Cabrera, 1951) which stretch along the eastern base of the Andes from southern Bolivia to central Argentina. They have been collected at elevations from 300 to 1800 meters in this area. This arid and semiarid region is similar to those of North America where the genus is found, and summer rain predominates (Cabrera, 1951). Seed germination and plant growth take place following these rains. *Kallstroemia tucuman-*



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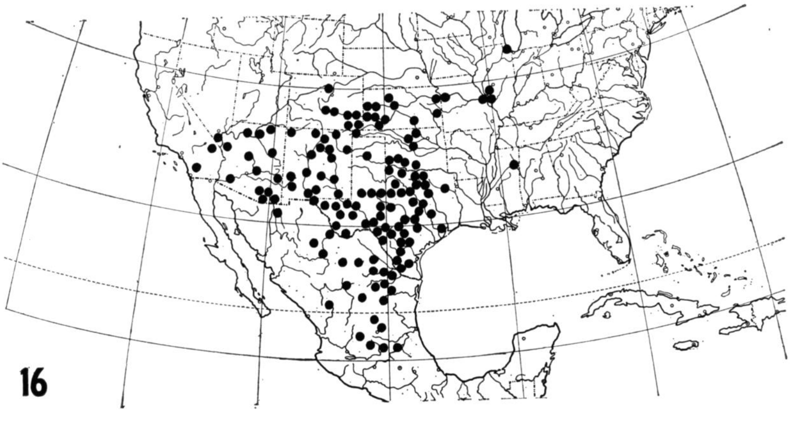

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Map 9. Distribution of *Kallstroemia adscendens*. Map 16. Distribution of *Kallstroemia parviflora* in North America (see Map 5 for South American distribution).

ensis flowers from November to April, and *K. tribuloides* from November to May. The former has been found farther north and south than *K. tribuloides,* but the latter also is known from northeastern Brazil *(Map 13)* in an area dominated by deciduous scrub forest (Smith & Johnston, 1945). *Kallstroemia tribuloides* is thought to have been introduced to Brazil from Argentina (Descole, *et al.,* 1939). The Brazilian collections that I have seen were mainly from sandy places along the Rio São Francisco, the largest river in the area. This species is also found in similar situations in Argentina.

Another species which occurs in Bolivia is *Kallstroemia boliviana.* It is found in the semiarid valleys of the eastern slopes of the Cordillera Oriental at elevations from about 1100 to 2800 meters *(Map 12).* A single Peruvian collection is known from a comparable area at an elevation of 1300 to 1400 meters where the vegetation is subtropical spiny shrubland (Tosi, 1960). *Kallstroemia boliviana* flowers from October through April. The interandean region of Bolivia, where it is to be found generally, receives summer precipitation from November through April (Franze, 1927).

The Peruvian *Kallstroemia pennellii* is known only from the type locality along the Río Marañon above Balsas, Cajamarca, at an altitude between 700 and 900 meters *(Map 5).* The vegetation of this area is tropical spiny forest (Tosi, 1960), a hot semiarid formation of northern Peru. This locality is characterized by summer rains and very high temperatures. The single collection known flowered in April.

The fifth, wholly South American *Kallstroemia,* is *K. adscendens,* an endemic of the Galápagos Islands, Ecuador *(Map 9).* It is known from the islands of Charles, Chatham, Duncan, Gardner, and Hood. It has been collected on beaches and lower slopes of the arid coastal zone, where the vegetation is predominantly xerophytic shrubs and subshrubs (Robinson, 1902). According to Svenson (1946a), sporadic rains occur in the islands from February to June. Flowering of *K. adscendens* is known to take place from April through June.

Based on a broad scope of information, a certain correlation may be seen between the occurrence of *Kallstroemia* and regions with high summer temperatures and summer precipitation, although the genus is by no means restricted to such areas. Those tropical species occurring in regions where rainfall and high temperatures may be found throughout the year grow and flower at any time. However, where the tropical representatives of the genus are encountered in areas with definite wet and dry seasons, they show the same periodicity in seed germination and plant growth as the temperate species found under similar circumstances.

HABITAT

Species of *Kallstroemia* are invariably found in open, disturbed habitats. These habitats may be natural, as in desert areas, or artificial, such as those provided by man in his rapid destruction of the natural vegetation. Plants of open natural habitats in deserts and sparsely occupied sand dunes, beaches, etc., have the greatest facility for spreading into and colonizing artificially created habitats (Salisbury, 1942, 1961). Open desert land, sand dunes, and beaches were undoubtedly the prime habitats of *Kallstroemia* prior to the invasion of the New World by European man. Since then, and perhaps to a limited extent even before, the resulting deterioration of the natural vegetative cover and the concomitant increase of disturbed habitats have provided numerous new areas into which species of *Kallstroemia* could migrate. At present, the most common situations where species of the genus are to be found as weeds are roadsides and cultivated areas. Clements (1920) has stated that the presence of *K. californica* (listed as *K. brachystylis), K. grandiflora, K. hirsutissima,* and *K. parviflora* is an indication of overgrazing in the arid grasslands of the southwestern United States. *Kallstroemia parviflora* became a troublesome weed in southern Kansas soon after the beginning of cultivation in that area (Carleton, 1892; Holzinger, 1892).

DISPERSAL MECHANISMS

Species of the genus inhabiting desert areas probably are dispersed through the action of rain wash. However, sea water dispersal probably does not take place in *Kallstroemia.* I have observed that the mericarps of two Caribbean species, *K. maxima* and *K. pubescens,* like those of *Tribulus cistoides* (Guppy, 1906), will not float in sea water. Unlike most of *Tribulus,* the mericarps of *Kallstroemia* lack appendages that would allow them to cling to the outer surface of an animal, with the exception of those with rough tubercles as in *K. californica* and *K. standleyi,* and those with hispid trichomes as in *K. perennans.* However, animal dispersal may take place because of the mucilaginous sheath secreted by the mericarps when they are wet. This sheath could allow them to adhere to an animal and in drying bind them temporarily to skin, fur, or feathers. Mucilage produced by the wetted mericarps may not only increase chances of dispersal, but it could act to anchor the mericarps to the soil, providing a decided advantage for the small disseminules of species growing in open situations. Dispersal of disseminules through formation of an adherent mucilage is well documented (e.g., Salisbury, 1961).

The hard pericarp of the mericarps also may allow them to be eaten and passed through the digestive tract of an animal unharmed. This ingestion could act to break seed dormancy as well. There is no concrete evidence for internal transport by animals, but it is known that in Arizona *Kallstroemia grandiflora* seeds are fed upon by quail (Griner, 1940) and the herbage is eaten by herbivores (McGinnies, 1922). In Peru, *K. parviflora* is browsed by livestock (Macbride, 1949). Similarly, *K. tribuloides* and *K. tucumanensis* are browsed in Argentina (Ruíz Leal, 1947, 1951).

Today the animal most important in dispersal of the genus is man. The southward spread of *Kallstroemia tucumanensis* has been facilitated through man's action, probably by the mericarps being imbedded in mud attached to vehicles (Ruíz Leal, 1951). Undoubtedly, man has been instrumental in carrying *K. maxima* to Texas, *K. parviflora* to Peru, and *K. pubescens* to West Africa and India. In the latter case, *K. pubescens* was discovered along a railroad right-of-way (Bennet, 1965). Railroads appear to have played a leading role in the spread of *K. parviflora* north and east from its presumed original area of occupation in North America. Early collections show this species to have advanced mainly along railroad rights-of-way. But now, like most other species in the genus, it is primarily dispersed by the automobile. This is so often the case that species of *Kallstroemia* are frequently to be found in disturbed areas along roads and highways.

Vegetative dispersal probably does not take place. There is no evidence for vegetative reproduction in the genus. This is not unexpected in a group of plants that mostly are ephemeral annuals.

DISTRIBUTION AND SELF-COMPATIBILITY

The prevelance of self-compatibility in desert annuals and particularly in weedy plants is well documented (cf., Stebbins, 1950; Baker, 1955; Salisbury, 1961). From observations on the reproductive biology of *Kallstroemia,* it can be inferred that all species of the genus, with the probable exception of *K. perennans,* are self-compatible. There are three situations under which self-compatibility proves to be advantageous in the survival and spread of a species: (1) Individuals may resort to self-pollination if conditions are unfavorable for outcrossing, as in the absence of pollinators (Stebbins, 1950)—this situation also could arise where individuals are so widely spaced that the frequency of outcrossing is restricted (Fryxell, 1957); (2) In cases of long distance dispersal, only a single disseminule is necessary for the establishment of a new colony if the species is self-compatible (Baker, 1955); (3) In the colonization of temporary habitats, such as those inhabited by weeds, there is a premium placed on species that can rapidly build up populations of individuals that are as well adapted as their parents to these temporary situations (Stebbins, 1950). This can be accomplished most successfully by relatively homozygous individuals belonging to self-fertilizing lines (Stebbins, 1957).

The above processes undoubtedly have occurred in the past and are presently ocurring in *Kallstroemia.* Absence of pollinators and wide separation of individuals (i.e., as weeds along roadsides) are surmounted through selfing. Isolated individuals invariably set seed in the field. The presence of self-compatibility has probably been a factor in the introduction and persistence of *K. maxima* in Texas, *K. parviflora* in Peru, *K. pubescens* in West Africa and India, and *K. tribuloides* in northeastern Brazil. In addition, it has aided in the rapid spread of most species to disturbed environments. Direct evidence for rapid build-up through preadaptation is lacking because nothing is known concerning the genetics of the genus.

Self-compatibility permits self-fertilization, but it does not insure it. This insurance is provided in *Kallstroemia* by the stamen and petal movements which act to appress pollen to the receptive stigma. However, self-fertilization is facultative, and outcrossing probably predominates under many circumstances. Stamen and petal movement occur whether outcrossing has taken place or not.

It would be interesting to know whether there is any differential pollen tube growth between selfed and crossed pollen.

Biotic Relationships

Occasional individuals of *Kallstroemia hirsutissima, K. maxima, K. parviflora,* and *K. tucumanensis* have been encountered in which the nodes or fruits had been attacked by insect larvae. Some Central American populations of *K. maxima* examined in the field were highly infested with these larvae to the extent that practically every fruit had been attacked. A small black aphid is commonly found on the herbage of many species of *Kallstroemia.* North American specimens of the introduced *Tribulus terrestris* commonly are covered with a similar aphid.

Two insects that have been introduced into the western United States for the biological control of *Tribulus terrestris* may prove harmful to indigenous species of *Kallstroemia,* and perhaps to *Larrea tridentata,* also. It has been reported by Andres and Angalet (1963) that adults of these insects will feed on the leaves and stems of *Kallstroemia californica, K. grandiflora, Larrea tridentata,* and *Zygophyllum fabago* (an introduced weed in California), as well as *Tribulus terrestris. Microlarinus lareynii* (Jacquelin du Val), a seed weevil, will oviposit on fruits of both *K. californica* and *K. grandiflora,* but larvae develop to maturity only in the latter. *Microlarinus lypriformis* (Wollaston), a stem weevil, will not oviposit on *Kallstroemia.*

A discussion of insect pollen vectors of *Kallstroemia* is found above in the section on reproductive biology.

At least two species of *Kallstroemia* are parasitized by other plants. I have seen specimens of *K. grandiflora* from Arizona and Sonora, Mexico, and *K. maxima* from Puerto Rico and Yucatán, Mexico, that were host to *Cuscuta umbellata* HBK. *Tribulus terrestris* is commonly parasitized by this species, also. Yuncker (1965) reports *C. erosa* Yunck., a species of southern Arizona and northern Mexico, on an unidentified species of *Kallstroemia.*

MORPHOLOGICAL CHARACTERS AND TAXONOMIC CRITERIA

The only previous work of a revisional nature on the genus is that of Rydberg (in Vail & Rydberg, 1910). In this and subsequent publications, the main criteria used in species delimitation were flower size, sepal shape, type and distribution of ovary and fruit pubescence, shape and length of the persistent style, and amount and type of pubescence on the herbage. These characters were not consistently given the same importance in every case. In the present study, it has been found that such additional characters as spatial relationship of the persistent sepals to the mature fruit, mericarp morphology, stigma shape, and leaf shape are important also. The criteria utilized by Rydberg were found in the main to be useful, albeit not always in the same context that he had used them. The fallacies of relying on single characters or those of a purely vegetative nature in classification have been clearly indicated (Rollins, 1952, 1957). Accordingly, the species are delimited herein by constellations of character combinations (*fide* Rollins, 1957). As may be seen in the following discussion, these character combinations provide the basis for a certain number of inferences concerning natural relationships in the genus.

There is a great deal of variation in the absolute size of the vegetative structures in plants of *Kallstroemia.* Size and the amount of pubescence on these parts appear to depend mainly upon the conditions under which the plants have developed. A high degree of variation in the vegetative parts is encountered frequently in plants of arid and semiarid regions. This in turn can be attributed to concomitant variation in climatic and edaphic conditions (e.g., Schweickerdt, 1937). There is also a certain amount of variation in flower and fruit size in species of *Kallstroemia* that appears to be somewhat influenced by conditions during the growth of the plant. Robust individuals have longer internodes, stems, and peduncles, and larger leaves, leaflets, flowers, and fruits, in comparison with depauperate individuals which grew under conditions of inadequate moisture, excessive disturbance, or highly alkaline soils. The latter are much smaller in all aspects, both vegetative and floral. However, the quantitative differences traceable to the influences of local environmental factors do not transcend the qualitative differences that serve to distinguish the species.

VEGETATIVE CHARACTERS

Stems. The stems of most species of *Kallstroemia* are prostrate to decumbent in mature individuals. Exceptions are the ascending stems of occasional plants of K. *grandiflora* and K. *parviflora* and most individuals of K. *perennans*. In K. *curta* and K. *hirsutissima* the stems are prostrate only. The taxonomic value of the stem habit itself is limited, but it can be utilized in concert with other morphological traits. Lengths of the stems and internodes at times have been used to help delimit species, but these characters, like most others of a quantitative nature, may be very variable within a species. Presence, absence, or amount of stem striation are frequently given in taxonomic descriptions for each species, but striate stems are found throughout the genus. Striations are due to a ring of cortical fibers and are not seen in the somewhat succulent stems of living plants. They become evident only after the stem has dried and shrunk.

The most useful taxonomic character of the stems is found in their pubescence. The trichomes are antrorse (directed apically) in all species but *Kallstroemia peninsularis* and a few specimens of K. *pubescens* from Peru, where they are retrorse. In most species, the stems are hirsute and sericeous, but exceptions are to be found in K. *californica* (hirsute and strigose), K. *peninsularis* (hirsute and hirtellous), K. *perennans* (hispid and strigose), K. *pennellii* (strigose), and K. *tribuloides* (sericeous). The same type pubescence as that of the stem is to be found on stipules, peduncles, petioles, and rachises.

Stipules. There is little difference in the stipules from species to species. Whether they are persistent or deciduous in mature individuals has been used in some taxonomic descriptions, but the stipules are absent only if they have been lost in the process of collecting, drying, and mounting the herbarium specimens.

Leaves. There are two distinct shapes of leaves in the genus. In one type, the terminal pair of leaflets is the largest, consequently the leaf shape is obovate. This leaf type is found in *Kallstroemia boliviana* (Fig. 10b), K. *curta* (Fig. 6b), K. *hirsutissima* (Fig. 5b), K. *maxima* (Fig. 1b), K. *pubescens* (Fig. 3b), K. *rosei* (Fig. 2b), and K. *tucumanensis* (Fig. 4b). In the second type, one of the lower pairs of leaflets is the largest, and leaf shape is elliptical. This type is found in K. *adscendens* (Fig. 7b), K. *californica* (Fig. 8b), K. *grandiflora* (Fig. 13b), K. *hintonii* (Fig. 17b), K. *parviflora* (Fig. 16b), K. *peninsularis* (Fig. 14b), K. *pennellii* (Fig. 12b), K. *perennans* (Fig. 15b), K. *standleyi* (Fig. 9b), and K. *tribuloides* (Fig. 11b). The species with obovate leaves have fewer leaflets, on the average, than the species with elliptical leaves. This difference in leaf shape does not indicate the presence of two basic groups of related species in the genus, however. Several closely related species of *Kallstroemia* differ in leaf shape, and *K. californica* usually has elliptical leaves, but individuals occasionally are partially or wholly obovate-leaved.

Leaf size may vary more within some species following changed environmental conditions than it does between the species. Also, there is no correlation between flower size and leaf shape or leaflet number. Leaflet number differs somewhat from species to species, but in several instances (i.e., *Kallstroemia californica, K. grandiflora, K. maxima, K. parviflora,* and *K. tribuloides)* there may be a sizeable difference in number from individual to individual within a species. Leaflet number in depauperate specimens is lower than usual. There is insufficient difference in leaf or leaflet size from species to species for either to play a major role in the discrimination of taxa within the genus.

Leaflet pubescence in most species is appressed-hirsute on both surfaces of the blade. The abaxial surface is usually more pubescent than the adaxial surface. The main vein and margins are usually sericeous. Exceptions are *Kallstroemia boliviana, K. pennellii,* and *K. standleyi,* in which the pubescence of the leaflets is entirely sericeous, and *K. hintonii,* where it is wholly appressed-hirsute.

Floral Characters

Flowers. There are substantial differences in flower size and color between different species of the genus. Flower size and color are relatively stable characters in some species, while in other species they may be quite variable. Depending upon the situation, they may be of more or less diagnostic value. There are certain correlations between flower color and size in that those species with small flowers, less than one centimeter in diameter *(Kallstroemia adscendens, K. californica, K. curta,* and *K. hirsutissima)* always have yellow petals. But petal color in the larger-flowered species varies from white through yellow to bright orange with the basal portion varying from green to red. In these latter species the petal base is usually somewhat darker than the distal portion. In some populations of *K. grandiflora, K. hintonii,* and *K. maxima* the base is a bright red.

Calyx. Following anthesis, there are three basic configurations

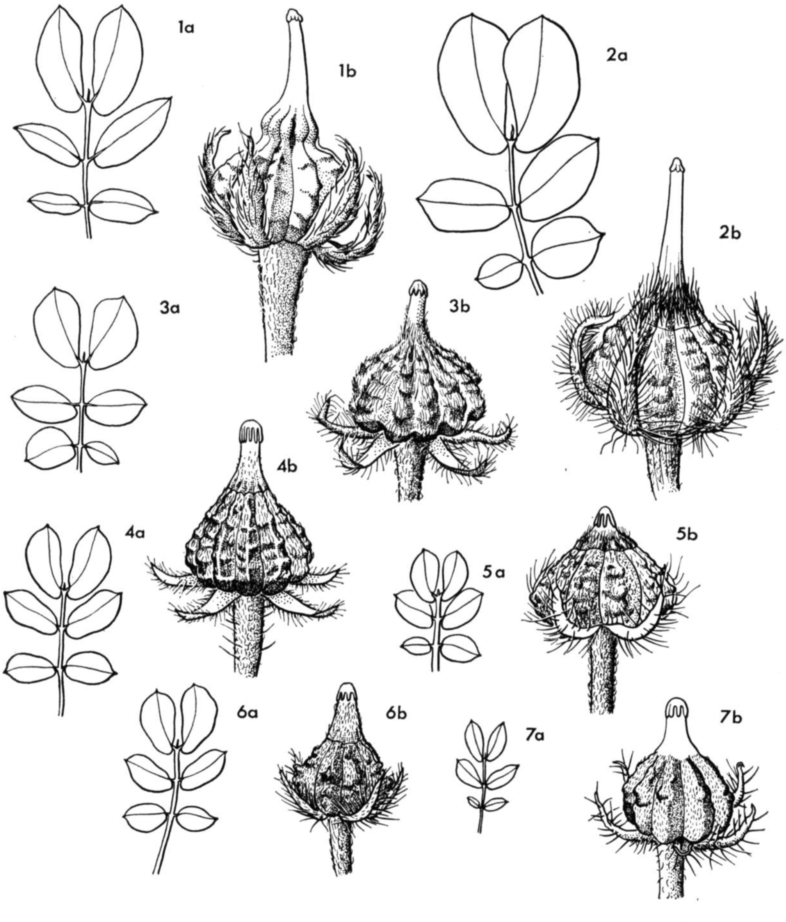

FIG. 1. *Kallstroemia maxima: a,* leaf, *b,* fruit, of *Porter 1035.* FIG. 2. *Kallstroemia rosei: a,* leaf, *b,* fruit, of *Porter 1375.* FIG. 3. *Kallstroemia pubescens: a,* leaf, *b,* fruit, of *Porter 1214.* FIG. 4. *Kallstroemia tucumanensis: a,* leaf, *b,* fruit, of *Pflanz 4041.* FIG. 5. *Kallstroemia hirsutissima: a,* leaf, *b,* fruit, of *Stewart 1166.* FIG. 6. *Kallstroemia curta: a,* leaf of *Leonard & Leonard 13322; b,* fruit of *Ekman 15981.* FIG. 7. *Kallstroemia adscendens: a,* leaf, *b,* fruit, of *Snodgrass & Heller 756.*

of the sepals which are very useful taxonomically. They may clasp the base of the mature fruit, with only the scarious margins folding involutely under, if at all, as in *Kallstroemia boliviana* (Fig. 10a), *K. hintonii* (Fig. 17a), *K. hirsutissima* (Fig. 5a), *K. maxima* (Fig. 1a), *K. pennellii* (Fig. 12a), and *K. tribuloides* (Fig. 11a). They may spread from the base of the mature fruit, occasionally curving upward, with the margins sharply folding involutely upon one another and making the sepals appear linear or linear-lanceolate to the naked eye, as in *K. adscendens* (Fig. 7a), *K. californica* (sepals usually deciduous; Fig. 8a), *K. curta* (Fig. 6a), *K. pubescens* (Fig. 3a), *K. rosei* (Fig. 2a), *K. standleyi* (Fig. 9a), and *K. tucumanensis* (Fig. 4a). Instead of spreading, the sepals may curve upward around the mature fruit, shriveling and turning brown, as in *K. grandiflora* (Fig. 13a), *K. parviflora* (Fig. 16a), *K. peninsularis* (Fig. 14a), or *K. perennans* (Fig. 15a).

A further character is the type of pubescence present on the sepals (see above figures). The indument may be hirsute (*Kallstroemia curta, K. hintonii, K. hirsutissima,* and *K. maxima*), hirsute and strigose (*K. adscendens, K. boliviana, K. rosei,* and *K. tribuloides*), hispid and strigose (*K. grandiflora, K. parviflora,* and *K. perennans*), hispid and hirtellous (*K. peninsularis*), hispidulous (*K. pubescens* and *K. tucumanensis*), sericeous (*K. pennellii* and *K. standleyi*), or strigose to hirsutulous and strigillose (*K. californica*). There is an evident correlation between the presence of hispid and strigose pubescence and the upwardly turned sepals which ultimately shrivel and turn brown.

Corolla. See the discussion above under flowers.

Androecium. The filaments are filiform or subulate in all species except *Kallstroemia hintonii,* where they are winged at the base. They are sufficiently long to extend the anthers upward and appress them to the stigma except in *K. perennans,* where the filaments reach only two-thirds up the length of the style. Filament color is correlated with the color of the petal base. Because the colors of the two are always the same, they are assumed to be genetically linked.

In a given flower, anther and pollen color are the same. However, the color may differ both between and within species. The color range is from yellow to red. In *Kallstroemia adscendens, K. californica, K. curta, K. hirsutissima, K. parviflora, K. peninsularis, K. standleyi,* and *K. tucumanensis* the color is yellow; in *K. boliv-*

iana, K. hintonii, K. perennans, and *K. tribuloides* it is orange or red. In the remaining species, populations of individuals may have anthers and pollen that are some shade of either yellow, orange, or red. *Kallstroemia maxima* and *K. pubescens* may be either yellow or red; *K. grandiflora* and *K. rosei* usually are orange or red, rarely yellow. The anther and pollen color of *K. pennellii* is unknown. Yellow-flowered individuals usually have yellow anthers and pollen as well, but this is not invariably the case (e.g., as in *K. hintonii*). There is a correlation and presumably genetic linkage between a red petal base and red anthers and pollen in *K. grandiflora, K. hintonii,* and *K. maxima.* These color differences usually are reliable criteria only in fresh material, because of fading and color changes which accompany the drying of specimens.

Anthers in *Kallstroemia standleyi* and *K. tribuloides* are regularly linear-oblong; otherwise they are ovoid or globose throughout the remainder of the genus. However, occasional specimens of *K. grandiflora, K. maxima, K. parviflora, K. rosei,* and *K. tribuloides* have been seen in which one whorl of stamens has linear anthers. Occasionally, one whorl of stamens has abortive anthers.

Gynoecium. The ovary is ovoid or globose in most species of *Kallstroemia,* but in *K. boliviana, K. rosei,* and *K. tribuloides* it is conical, and pyramidal in *K. pubescens.* It is almost always pubescent, being glabrous only in *K. hintonii, K. maxima,* and *K. tribuloides,* but it is occasionally strigose in *K. maxima.* As with all other floral structures, ovary size varies with overall flower size, being correspondingly large or small.

Style length, like ovary size, differs with the flower size, smaller-flowered species having shorter styles. There may be a certain amount of variation of style length within a species, but in *Kallstroemia grandiflora, K. hintonii, K. maxima, K. parviflora, K. peninsularis, K. pennellii, K. perennans, K. rosei, K. standleyi,* and *K. tribuloides* it is nearly always longer than the ovary. In the other species, it is equal to or shorter than the ovary. Style shape in the genus is mostly cylindrical above and conical below, but *K. adscendens, K. boliviana, K. californica, K. curta, K. hirsutissima, K. pubescens* (rarely cylindrical above), *K. rosei,* and *K. tucumanensis* all have more or less stout conical styles. Therefore, one can see a definite correlation between style length and

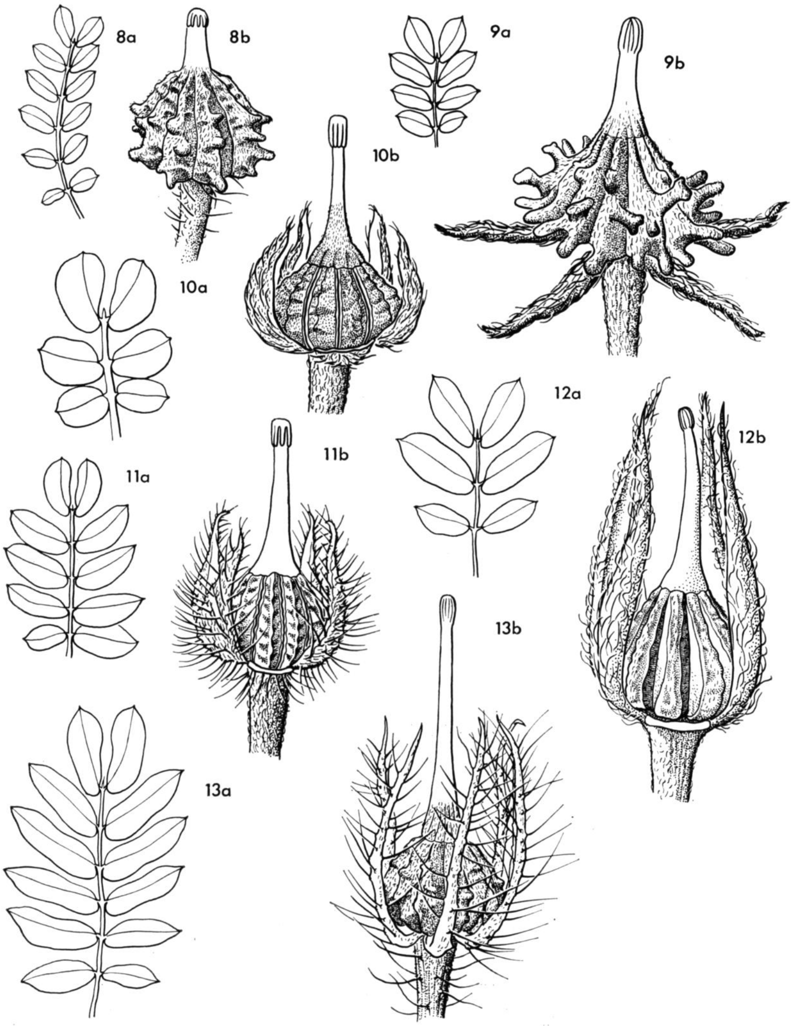

Fig. 8. *Kallstroemia californica: a,* leaf, *b,* fruit, of *M. E. Jones 24963.* Fig. 9. *Kallstroemia standleyi: a,* leaf, *b,* fruit, of *Morley 861* (type). Fig. 10. *Kallstroemia boliviana: a,* leaf, *b,* fruit, of *Cárdenas 3860.* Fig. 11. *Kallstroemia tribuloides: a,* leaf, *b,* fruit, of *Schreiter s. n.* Fig. 12. *Kallstroemia pennellii: a,* leaf, *b,* fruit, of *Pennell 15185* (type). Fig. 13. *Kallstroemia grandiflora: a,* leaf, *b,* fruit, of *Gentry 1667.*

shape, stout, conical styles generally being shorter than the ovary. There are differences in the amount, type, and distribution of stylar pubescence. Most species are glabrous to strigose in this character, but the style is hirsute in *K. perennans.* In *K. hirsutissima* and *K. rosei* it is surrounded at the base by a ring of hirsute pubescence, a feature that is especially pronounced in the latter species.

There appear to be three fundamental stigma types in *Kallstroemia.* The stigma may be capitate and obscurely ten-lobed, as in *K. maxima* (Fig. 1a), *K. pubescens* (Fig. 3a), and *K. rosei* (Fig. 2a). The stigma may be oblong and ten-ridged, as in *K. boliviana* (Fig. 10a), *K. parviflora* (Fig. 16a), *K. pennellii* (Fig. 12a), *K. perennans* (Fig. 15a), *K. standleyi* (Fig. 9a), *K. tribuloides* (Fig. 11a), or *K. tucumanensis* (Fig. 4a). It may be clavate and ten-ridged, as in *K. adscendens* (Fig. 7a), *K. californica* (Fig. 8a), *K. curta* (Fig. 6a), *K. grandiflora* (Fig. 13a), *K. hintonii* (Fig. 17a), *K. hirsutissima* (Fig. 5a), and *K. peninsularis* (Fig. 14a). There are no general correlations between stigma type and flower size or style length.

The stigmatic surface is papillose in all species but *Kallstroemia perennans,* where it is coarsely canescent (Fig. 15a). It extends downward almost to the stylar base in *K. peninsularis* (Fig. 14a) but is terminal in all other species.

Fruit Characters

Peduncles. The length of the peduncle in fruit is of some taxonomic significance. In *Kallstroemia californica, K. curta, K. hirsutissima, K. perennans, K. pubescens, K. rosei,* and *K. tucumanensis* it is usually shorter than the subtending leaf. In all other species, with the exception of *K. peninsularis,* it is usually longer. The fruiting peduncle of *K. peninsularis* may be longer or shorter than its subtending leaf.

Shape of the peduncle in fruit differs from species to species. In *Kallstroemia boliviana, K. rosei, K. standleyi,* and *K. tribuloides* it is curved. In *K. adscendens, K. californica, K. grandiflora, K. peninsularis,* and *K. perennans* the fruiting peduncle is bent sharply at the base and is straight above. *Kallstroemia parviflora* may be as the latter species, or the peduncle is completely straight. It is straight in *K. hintonii* and *K. pennellii* and may be

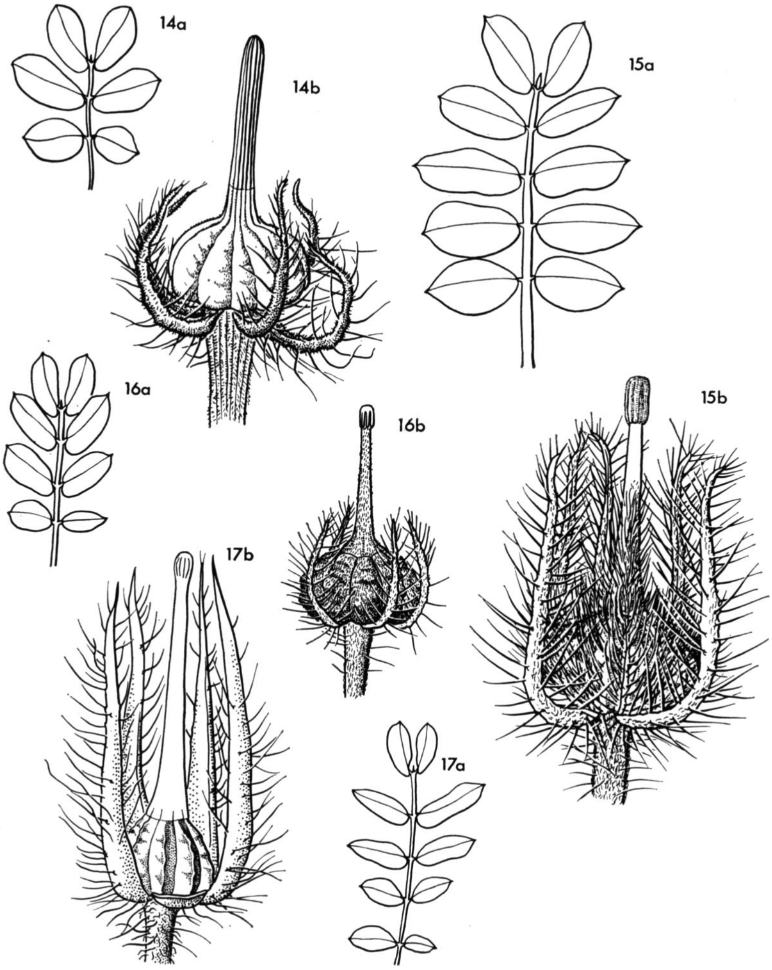

FIG. 14. *Kallstroemia peninsularis: a,* leaf of *Porter 341; b,* fruit of *Wiggins 14454.* FIG. 15. *Kallstroemia perennans: a,* leaf of *Turner 3779; b,* fruit of *McVaugh 8226A.* FIG. 16. *Kallstroemia parviflora: a,* leaf of *Cory 4968; b,* fruit of *Pollard 1295.* FIG. 17. *Kallstroemia hintonii: a,* leaf, *b,* fruit, of *Hinton 12106* (type).

either straight or curved in *K. curta, K. hirsutissima, K. maxima, K. pubescens,* and *K. tucumanensis.*

Fruit. The body of the fruit in most species of the genus is ovoid and three to six millimeters in diameter, but it is broadly ovoid in *Kallstroemia hintonii* (Fig. 17a), *K. hirsutissima* (Fig. 5a), *K. perennans* (Fig. 15a), and *K. standleyi* (Fig. 9a), being four to six millimeters high and six to ten wide. It ranges from glabrous [*K. hintonii* (Fig. 17a), *K. maxima* (Fig. 1a), and *K. tribuloides* (Fig. 11a)] to strigillose [*K. californica* (Fig. 8a), *K. curta* (Fig. 6a), *K. hirsutissima* (Fig. 5a), *K. peninsularis* (Fig. 14a), and *K. pennellii* (Fig. 12a)] or strigose [*K. adscendens* (Fig. 7a), *K. boliviana* (Fig. 10a), *K. grandiflora* (Fig. 13a), *K. parviflora* (Fig. 16a), *K. rosei* (Fig. 2a), *K. standleyi* (Fig. 9a), and *K. tucumanensis* (Fig. 4a)], to occasionally appressed short-pilose [*K. pubescens* (Fig. 3a)], or both hispid and strigose [*K. perennans* (Fig. 15a)].

The length and shape of the beak on the fruit (the persistent style) differs greatly between species. In *Kallstroemia adscendens* (Fig. 7a), *K. curta* (Fig. 6a), *K. hirsutissima* (Fig. 5a), and *K. tucumanensis* (Fig. 4a) the beak is conical and shorter than the fruit body, and in *K. californica* (Fig. 8a) and *K. standleyi* (Fig. 9a) it is cylindrical above with a conical base, but it is shorter than the body. In all other species [*K. boliviana* (Fig. 10a), *K. grandiflora* (Fig. 13a), *K. hintonii* (Fig. 17a), *K. maxima* (Fig. 1a), *K. parviflora* (Fig. 16a), *K. peninsularis* (Fig. 14a), *K. pennellii* (Fig. 12a), *K. perennans* (Fig. 15a), *K. pubescens* (Fig. 3a), *K. rosei* (Fig. 2a), and *K. tribuloides* (Fig. 11a)], it is cylindrical above with a more or less conical base and as long as to longer than the body. Species such as *K. grandiflora, K. hintonii, K. parviflora, K. peninsularis, K. perennans,* and *K. rosei* may have the beak becoming two to three times the length of the fruit body. There is a rough correlation between beak length and flower size.

Pubescence of the beak of the fruit mostly is glabrous or strigose, being usually the same as that on the body of the fruit. *Kallstroemia hirsutissima* and *K. rosei* are unique in that there is a ring of hirsute pubescence surrounding the base of the beak. This pubescence is quite marked in *K. rosei.* The entire beak is hirsute in *K. perennans.*

Another taxonomically useful character of the fruit is the mericarp. In most species the mericarps are three to five millimeters high and about one millimeter wide, but in *Kallstroemia hintonii, K. perennans,* and *K. standleyi* they may reach a width of from two to two-and-one-half millimeters. The most useful characteristic of the mericarps is in the differences found in their abaxial surfaces. This surface differs from tubercled [*K. curta* (Fig. 6a), *K. grandiflora* (Fig. 13a), *K. hirsutissima* (Fig. 5a), and *K. peninsularis* (Fig. 14a)] to tubercled or rugose [*K. parviflora* (Fig. 16a)], tubercled or rugose, and cross-ridged [*K. pubescens* (Fig. 3a)], tubercled and cross-ridged, [*K. adscendens* (Fig. 7a) and *K. rosei* (Fig. 2a)], tubercled, cross-ridged and slightly keeled [*K. maxima* (Fig. 1a)], cross-ridged and more or less keeled [*K. hintonii* (Fig. 17a), *K. pennellii* (Fig. 12a), and *K. perennans* (Fig. 15a)], tubercled and laterally grooved [*K. tucumanensis* (Fig. 4a)], rugose and margins flattened [*K. boliviana* (Fig. 10a)], or rugose and margins flattened and slightly keeled [*K. tribuloides* (Fig. 11a)]. Four to five oblong, blunt or fungoid tubercles are present in *K. californica* (Fig. 8a) and *K. standleyi* (Fig. 9a) which may become one-and-one-half to two millimeters long and become more prominent as the fruit matures. The pubescence of the abaxial surface is the same as that of the fruit body.

The amount and pattern of pitting on the sides of the mericarp is variable even within the same specimen and is of no diagnostic value. However, there is a certain amount of difference in the shape of the adaxial edge of the mericarp, mirroring the shape of the styliferous axis which persists on the peduncle after the mericarps have fallen. This edge is straight in *Kallstroemia perennans* and *K. standleyi,* curved in *K. tribuloides,* and more or less angled in all the remaining species but *K. pennellii,* where it has not been seen.

HYBRIDIZATION, INTERSPECIFIC RELATIONSHIPS, AND EVOLUTION

Hybridization

In addition to comparative morphology, a commonly used criterion to discern natural relationships in plants is that of hybridization between taxa. Such hybridization may occur in the field, or it may be artificially induced, through crosses in the experimental garden. The latter type of experimentation has not been done in *Kallstroemia*, but there are two cases of suspected interspecific hybridization in the genus. Evidence for this hybridization occurs in areas where man has transported the parent species and has modified the environment to create new habitats that can be utilized by any resulting hybrids. The majority of instances in which hybridization and introgression have been discovered in plant populations have been detected under such circumstances (Stebbins, 1950).

The first case involves *Kallstroemia maxima* and *K. pubescens*. These two species are sympatric over a wide area of their ranges *(Maps 1 and 4)*, but they appear to be at least partially isolated ecologically. *Kallstroemia pubescens* usually is found at slightly higher elevations and in sandier soils than *K. maxima*, but mixed populations of them have been seen. There is evidence for hybridization between the two only in their southernmost region of overlap, in Colombia and Venezuela *(Map 2)*. Certain herbarium specimens (cited under *K. maxima*) from this area appear to be intermediate between the above species in sepal and fruit characteristics (the two species are very similar vegetatively), and I suspect that these specimens are of hybrid origin.

Examination of the sepals and fruits of *Kallstroemia maxima* and *K. pubescens* with magnification shows these structures to be quite different in the two species (Fig. 1b and 3b). The sepals of *K. maxima* are ovate and clasp the mature fruit, only the scarious margins becoming involute. The sepal trichomes are hirsute, of one length, and usually are appressed toward the sepal apex. The fruit in this species is ovoid and usually is glabrous, occasionally being strigose with short, rigid, curved trichomes. By contrast, in *K. pubescens* the sepals spread from the base of the mature fruit, the margins become sharply involute, and consequently the sepals appear to be linear or linear-lanceolate. The sepal trichomes are hispidulous, spreading stiffly, and of two lengths. They are much finer than those of *K. maxima*. The fruit of *K. pubescens* is more pyramidal than in *K. maxima*, and it is densely pubescent with fine, straight, appressed-pilose trichomes.

These sepal and fruit characters are more or less intermediate in the suspected hybrids. In the latter specimens, the sepals either clasp the mature fruit or spread from it. The amount of involution of the sepal margins is moderate, but it does not reach either extreme found in one species or the other. Trichomes are variable in length on the same sepal and usually are spreading, not appressed. The sepal trichomes are not as fine or as short as those of *Kallstroemia pubescens,* and not as stout as those of *K. maxima,* but they may be as long as those of the latter species. The shape and tuberculation of the fruit approaches that of *K. maxima,* but fruit pubescence is of the same type as that found in *K. pubescens.* This pubescence is much denser than that sometimes found in *K. maxima.* Microscopic examination of pollen grains stained with acetocarmine following removal from unopened flowers of both the species and the suspected hybrids revealed less than nine per cent malformed grains in collections of each of the three from the same general area. When the pollen was treated with methylene blue, all of the grains were stained, even if malformed. Specimens of the putative hybrids are listed in the taxonomy section following the discussion of *K. maxima.*

In contrast to the above situation where hybridization only is suspected, there is evidence of both hybridization and introgression between *Kallstroemia maxima* and *K. rosei* where their ranges overlap in southwestern Mexico *(Maps 1 and 3).* However, no plants that could be considered intermediates between the two species have been seen. *Kallstroemia maxima* and *K. rosei* both apparently have been transported to this area during historical times. This introduction, at least in the case of *K. rosei,* presumably is still taking place. The latter species is native to open, disturbed habitats in the pine-oak forests of central Mexico at elevations above about 1000 meters, while *K. maxima* is a more tropical species from the lower elevations of the Caribbean and Central American region. The two species have been brought together mainly in the region of the Río Balsas Basin, where increased cultivation and other disturbances have provided suitable habitats for these species to overlap in their distributions. Before man's intervention, they undoubtedly were allopatric.

The two species are rather similar vegetatively, differing mainly in flower and fruit characters, although *Kallstroemia rosei* tends to be larger in vegetative characters. Characteristically, the fruits of the latter (Fig. 2b) are densely pubescent, the fruit body being strigose with short curved trichomes and with longer, stouter, straight trichomes forming a ring of white, hirsute pubescence around the base of the beak. This ring may be quite striking to the naked eye. In specimens from this area of overlap, however, the fruits on some individuals are almost glabrous. On others, the fruits vary markedly in the amount of pubescence on the same individual, a situation unknown elsewhere in the range of *K. rosei.* There is also some variation in the amount of involution of the sepal margins in these specimens. Following anthesis, the sepals usually spread from the base of the fruit, and their margins become sharply involute. However, in the suspected introgressants, the margins may fold under, but not nearly to the extent normal for the species. The sepals also occasionally clasp the mature fruit, rather than spread from it.

The fruits of *Kallstroemia maxima* (Fig. 1b) are almost always glabrous, but most of the collections of this species, from its area of overlap with *K. rosei,* are strigose to a greater or lesser extent. However, none of these specimens has the ring of hirsute pubescence surrounding the base of the beak that is found in *K. rosei.* The sepals of *K. maxima* in this area also vary toward those of *K. rosei.* They generally fail to extend beyond the mature mericarps, but here they may reach to the top of the beak. The sepal margins are more involute in these specimens than is true elsewhere, usually only the scarious margins become involuted. However, involution of the sepal margins in *K. maxima* never reaches the extreme of that found in *K. rosei.*

Although the information summarized above suggests the presence of interspecific hybridization in the genus, experimental proof of its existence is lacking. Such proof concerning the compatibility of these species and the isolating mechanisms present between them is desirable, as is more information concerning the geographical relationships of both the species and their suspected hybrids. This vital information, along with cytological studies, undoubtedly will help in interpreting the morphological data at hand. In the absence of genetical evidence, it is thought best to consider these individuals only as suspected hybrids.

INTERSPECIFIC RELATIONSHIPS

The geographical distribution of the genus suggests that it has arisen somewhere in North America, probably Mexico, which is its present center of diversity and abundance. However, with almost complete lack of a fossil record, it cannot be certain that the genus did not originate in an area where it is now absent. Although all known members of the *Zygophyllaceae* now inhabit arid or semiarid habitats, it does not necessarily follow that the ancestors of *Kallstroemia* did so as well. It is still open to question whether the ancestors of the present-day species ranged throughout the tropics, evolving species independently in North and South America, or whether they gradually adapted to more arid conditions in the north and have since invaded both arid South America and dry, open, disturbed habitats in the tropics. This question is complicated not only by a lack of knowledge of the genetics and cytology of the genus, but also by the lack of a species or a group of species that can be definitely regarded as primitive. Comparative morphology reveals that the species of North America are more closely related to each other than to any species of South America. Each continental grouping of species shows certain relationships to those of the tropics.

The evidence derived from comparative morphology regarding species relationships in the genus discussed above may be summarized as follows. In North America, *Kallstroemia grandiflora, K. parviflora, K. peninsularis,* and *K. perennans* form a group of closely interrelated species. *Kallstroemia hirsutissima, K. californica,* and *K. standleyi* make up another group in which the latter two species appear to be most closely related. However, *K. hirsutissima* shows close relationships to the Caribbean *K. curta,* and *K. californica* to *K. adscendens* of the Galápagos Islands. The Mexican *K. rosei* is closest to the Caribbean *K. maxima,* while *K. hintonii* does not appear to be closely related to any other species. In South America, *K. boliviana* and *K. tribuloides* are closely related to one another and show relationships to *K. pennellii.* On the other hand, *K. tucumanensis* is very close to the Caribbean *K. pubescens.* The morphological bases for these relationships are discussed under the relevant species.

EVOLUTION

There is paleobotanical evidence for the presence of semiarid vegetation in both the northern and southern hemispheres of the New World during the late Eocene and early Oligocene, but evidence for desert floras in North America before the Pliocene is lacking (Axelrod, 1950, 1958). Desert vegetation types appear to have developed during the latter epoch through the appearance of more arid communities in the rain shadows of the rising mountain systems in the western area of the continent. Likewise, the desert vegetation of Argentina is surmised to have developed late in the Cenozoic, concomitant with the elevation of the Andean system (Berry, 1928, 1932). The ecological effects of the Andean orogeny began in the Miocene and reached their present maximum in the Quaternary (Simpson, 1965).

A rapid evolution of herbaceous plants during the late Tertiary and Quaternary has coincided with this differentiation and spread of arid and semiarid communities (Stebbins, 1947, 1949; Axelrod, 1950). This great expansion and diversification of herbs appears to have been a direct response to the factors causing a comparatively rapid change toward a warmer, drier climate. Modern desert species have been derived by the gradual adaptation of more mesic ancestors to lowered yearly rainfall, shifting seasonal distribution of rain, and increasing ranges and extremes of temperature (Axelrod, 1950). As has been the case with a number of herbaceous genera, the ancestors of the present-day species of *Kallstroemia* adapted to this increasingly more xerophytic environment by evolving annuals which inhabit areas marked by high summer temperatures and summer rainfall. A principal advantage of the annual habit for these plants has been their ability to pass through the dry season unfavorable to growth as drought-resistant seeds.

The rapid evolution associated with these large climatic changes has involved not only the development of adaptations to drier conditions and the rise of the annual habit, but also has been greatly aided and diversified by the alternate isolation and merging of populations, providing opportunities for increase in genetic diversity through hybridization and introgression (Stebbins, 1949, 1952). Furthermore, the population structure of species in arid and semiarid regions is likely to be more favorable for evolution than that of species in more mesic habitats (Stebbins, 1952). The frequent isolation of small populations offers many situations for genetic change through natural selection and chance fixation. Occasional migration between populations further increases their genetic diversity and offers new gene combinations to the selective action of the environment. Such a population structure is that most favorable to rapid evolution (Wright, 1940).

Populations of *Kallstroemia* characteristically are local and discontinuous. They rarely cover extensive areas, although individuals usually are numerous where found. Exceptions to this pattern are at times found in *K. californica, K. grandiflora* and *K. hintonii,* but such extensive masses of the plants are exceptional. This population structure helps to explain the small amount of phenotypic diversity to be found in most local populations, and the perceptible differences seen between such populations. The genetic makeup of the seed or seeds founding a new population, random genetic drift, and chance interpopulational hybridization, along with vigorous environmental selection, have all acted to produce these differences. On a larger scale, they have led to speciation.

ECONOMIC IMPORTANCE

Although by no means a genus of great economic importance, *Kallstroemia,* and especially *K. maxima,* finds many uses in the native *materia medica* of the areas where it is to be found. It is also a minor forage plant.

In Sonora, Mexico, *Kallstroemia californica* (presumably the herbage) is used in the cure of insect and reptile bites (Rose, 1891).

According to McGinnies (1922), the forage value of *Kallstroemia grandiflora* is excellent, and it is chiefly grazed in the summer. However, another source (Anonymous, 1963, p. 72) states that, it "has very little forage value due to its rough foliage," but it "is a good summer cover crop." The seeds are eaten by quail in the summer and fall (Griner, 1940). These reports are from Arizona. Watson (1889, p. 43), writing of specimens from Sonora, Mexico, states that the pollen of this plant is injurious to the eyes, and therefore the plant is called *Mal de Ojos* (bad for the eyes).

Kingsbury (1964) cites a report of *Kallstroemia hirsutissima* poisoning cattle under natural conditions, and sheep and goats under experimental conditions. The toxic principle is unknown.

As mentioned above, *Kallstroemia maxima* has a number of medicinal uses throughout its range. In Jamaica, a salve is made of the plant by mixing it with suet, which is effective against ringworm (Sloane, 1707). A poultice is used for various cutaneous afflictions in Cuba (Baillon, 1875; Gomez de la Maza, 1889) and Surinam (Westroüen van Meetenen, 1883). In Venezuela (Perez Arbeláez, 1956) and Costa Rica, this is used also to bring boils and similar sores to a head. In the latter country, the infusion and decoction purportedly is effective against paralysis, tetanus, and spasms (Pittier, 1957), and in Colombia the infusion is used as a diuretic (Perez Arbeláez, 1956).

Kallstroemia maxima is eaten by herbivores in Jamaica (Browne, 1756) and Cuba (Richard, 1845) and is the only species in the genus reported to be eaten by man. According to Standley (1928), the plant sometimes is cooked and eaten as a potherb in El Salvador, and Perez Arbeláez (1956) reports this use in Colombia. This may be the case, but it probably results from the close resemblance of *K. maxima,* at least to the native user, to *Portulaca oleracea* L. *(Portulacaceae),* a common potherb throughout Latin America. These plants grow under the same conditions and are found together. They superficially resemble one another vegetatively, and are known universally throughout their ranges in Latin America by the same common name, *Verdolaga.*

In New Mexico, "the Spanish New Mexicans say that the powdered roots [of *Kallstroemia parviflora*—reported as "*K. brachystylis*"], when soaked in warm water, make a good wash for sore eyes and swollen gums. Also if taken as a tea it is an excellent remedy for fever, stomach trouble and dysentary" (Anonymous, 1963, p. 72). Perhaps the root infusion would be efficacious in the case of *K. grandiflora* pollen in the eyes! Lopez (1948), writing from Chihuahua, Mexico, states that this species "es buena para el estomago" (is good for the stomach). In Peru *K. parviflora* is used as forage by stock (Macbride, 1949).

According to Standley (1940), *Kallstroemia pubescens* in Guatemala is utilized as a remedy for kidney stones. The species also is appreciated in Ghana, Africa, where it was long ago introduced: "The leaves are used to cure constipation. They are powdered in a morter with palm nuts and drunk as soup in 3 doses. This is also believed to induce conception. The leaves are put into water, salt is added, and when they have been boiled, the liquor is drunk as another cure for constipation" (Irvine, 1930, p. 419).

In Argentina both *Kallstroemia tribuloides* and *K. tucumanensis* are eaten by herbivores (Ruíz Leal, 1947, 1951). The former species apparently is the only one in the genus, except perhaps for *K. grandiflora,* which has been raised as an ornamental: "The seeds of this plant may be raised on a hot-bed, and when the plants have grown 2 or 3 inches, they may be planted out in the open border in a sheltered situation, in the month of May" (Don, 1831, p. 769).

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TAXONOMIC HISTORY

Since the the foundation of the genus by Scopoli in 1777, most of the published material on *Kallstroemia* has been concerned with either distributional and ecological information or the description of new species. The most recent work of a revisional nature was done by Rydberg in 1910 and covered North America only. It is now very much out of date.

The following list is a chronological taxonomic history of the genus.

1696: Sloane published the first notice of the plant later to be called *Kallstroemia maxima,* "Tribulus terrestris major flore maximo odorato." Thus, the epithet *maxima* is based not on floral size, as many have assumed (e.g., Macfadyen, 1837), but on floral odor.

1707: The first illustration of a *Kallstroemia (K. maxima)* was published by Sloane.

1753: Linnaeus described *Tribulus maximus* (= *Kallstroemia maxima)* from Jamaica, citing Sloane in the protologue.

1777: Scopoli published *Kallstroemia,* basing it on "*Tribulus maximus* Loefl." (= *Tribulus maximus* L.). The derivation of the name was never explained. Some authors suggest it was compounded from "Greek Kallos, beautiful, and Stroemia, a genus of Capparidaceae" (Jepson, 1936, p. 437), while others believe it to be "in honor of *Kallstroem,* obscure contemporary of Scopoli" (Munz, 1959, p. 159). Scopoli made no combinations in the genus.

1818: Nuttall described *Tribulus trijugatus* (= *Kallstroemia maxima)* from Georgia.

1825: The fundamental differences between fruits of *Tribulus maximus* and those of the other known species of *Tribulus* were recognized by A. Jussieu. He stated that perhaps a new genus should be based on the former species, apparently unaware that Scopoli already had done so on the same basis 48 years previously.

1826: The genus *Ehrenbergia* was described by von Martius from Brazil.

1827: Von Martius published *Ehrenbergia tribuloides* (= *Kallstroemia tribuloides),* correctly recognizing its affinities with *Tribulus,* but apparently he was unaware that it was actually the second known species of *Kallstroemia.*

1827: Sprengel published *Tribulus brasiliensis* (= *Kallstroemia tribuloides)* from Brazil, basing it on *Ehrenbergia tribuloides. Ehrenbergia* Mart. is a later homonym for a genus erected by Sprengel in the Rubiaceae.

1828: Reichenbach was the first to recognize and use the name *Kallstroemia* since its publication.

1831: George Don described *Tribulus pubescens* (= *Kallstroemia pubescens)* from the "Cape Coast," now Ghana. This is the only species of *Kallstroemia* known to occur outside the New World, also being introduced to Nigeria and India.

1834: Wight and Arnott indicated that *Kallstroemia* was distinct from *Tribulus,* but they made no new combinations in the genus.

1835: The genus *Heterozygis* was erected by Bunge, who based it on *Tribulus maximus.* He published no new combinations.

1836: The first combination was made in *Kallstroemia, K. cistoides,* by Endlicher. However, the species is actually a *Tribulus, T. cistoides.*

1837: Macfadyen published *Tribulus decolor* (= *Kallstroemia maxima)* from Jamaica.

1837: Meisner published *Kallstroemia tribulus* (= *Kallstroemia maxima),* basing it on *Tribulus maximus.*

1838: Hooker and Arnott were the first to correctly place a species, *K. maxima,* in *Kallstroemia.*

1840: Rafinesque published *Tribulus dimidiatus* (= *Kallstroemia maxima),* based on *T. trijugatus.*

1840: The combination *Kallstroemia tribuloides* was published by Steudal, who wrongly attributed it to Wight and Arnott.

1841: Steudal published *Tribulus trijugus,* an orthographic error for *T. trijugatus.*

1849: Robert Brown recognized the basic differences in the fruits of *Kallstroemia, Tribulopis,* and *Tribulus.*

1849: J. D. Hooker published *Kallstroemia minor* (=*K. pubescens)* from Ghana, basing it on the same type as *Tribulus pubescens.*

1852: Gray described *Kallstroemia grandiflora* from Arizona and *K. grandiflora* var. *detonsa* (= *K. grandiflora)* from New Mexico.

1854: *Tribulus adscendens* (= *Kallstroemia adscendens)* was described from the Galápagos Islands, Ecuador, by Andersson.

1859: Grisebach divided *Tribulus* into two sections, *Eutribulus* and *Kallstroemia,* basing the division on characters of the fruit.

1861: Andersson published the combination *Tribulus maximus* var. *adscendens* (= *Kallstroemia adscendens).*

1862: J. D. Hooker treated *Kallstroemia* and *Tribulopis* as subgenera of *Tribulus.*

1867: Hooker now placed *Kallstroemia* and *Tribulopis* as sections of *Tribulus.*

1868: *Tribulus maximus* var. *minor* (= *Kallstroemia pubescens)* was described by Oliver.

1872: Baillon argued that the differences between *Kallstroemia* and *Tribulus* were not sufficient to warrant the separation of the former from *Tribulus.*

1876: *Tribulus californicus* (= *Kallstroemia californica)* was described by Watson from Baja California, Mexico.

1876: Brewer and Watson published the combination *Tribulus grandiflorus* (= *Kallstroemia grandiflora)* erroneously ascribing it to Bentham and Hooker.

1877: Kellogg described *Tribulus fisheri* (= *Kallstroemia grandiflora)* from Sonora, Mexico.

1887: After long treating them as genera separate from *Tribulus,* Gray now indicated that *Kallstroemia* and *Tribulopis* should be considered as synonyms of the former because of the supposed close resemblances between species of *Tribulus* and *Kallstroemia californica.*

1890: Engler divided *Kallstroemia* into two sections, *Eukallstroemia* and *Thamnozygium,* the former with nine species, the latter with two species. He also placed *Tribulopis* as a synonym of *Kallstroemia,* and seven of the species in *Eukallstroemia* and both those in *Thamnozygium* were new combinations from this genus and *Tribulus.* The remaining two species in section *Eukallstroemia, Kallstroemia maxima* and *K. tribuloides,* are the only ones at present considered actually to belong in the genus.

1894: Sessé and Mociño's *Tribulus tuberculatus* (= *Kallstroemia maxima)* was described from Cuba.

1895: Vail published the combination *Kallstroemia californica.*

1897: *Kallstroemia brachystylis* (= *K. californica)* was described by Vail from New Mexico.

1897: Gray recognized three sections in *Tribulus,* two of which constituted *Kallstroemia,* the other being *Tribulus s. str.*

1897: Robinson published the combination *Tribulus brachystylis* (= *Kallstroemia californica).*

1898: Kuntze described *Tribulus maximus* var. *roseus* (= *Kallstroemia boliviana)* from Bolivia.

1898: *Kallstroemia parviflora* was described from Texas by Norton.

1900: Cockerell described *Kallstroemia grandiflora* var. *arizonica* (= *K. grandiflora)* from Arizona.

1902: The combination *Kallstroemia adscendens* was published by Robinson, reversing his previous belief that *Kallstroemia* should be considered a synonym of *Tribulus*.

1903: Vail described *Kallstroemia hirsutissima* from New Mexico.

1910: Rydberg, in the most complete revision of *Kallstroemia* to date, described six new species in the genus. These were *K. canescens* (= *K. maxima)* from Sinaloa, Mexico; *K. caribaea* (=*K. pubescens)* from Montserrat, West Indies; *K. glabrata* (= *K. pubescens)* from Guerrero, Mexico; *K. intermedia* (= *K. parviflora)* from Texas; *K. longipes* (= *K. pubescens)* from Sinaloa; and *K. rosei* from Morelos, Mexico.

1913: Britton and Brown chose *Tribulus maximus* as the lectotype species of *Kallstroemia.*

1913: *Kallstroemia laetevirens* (= *K. parviflora)* was described from New Mexico by Thornber.

1913: Rydberg described *Kallstroemia curta* from Curaçao, West Indies.

1924: *Kallstroemia incana* (= *K. curta)* was described by Rydberg from Hispaniola, West Indies.

1931: Engler maintained his subgeneric classification of *Kallstroemia,* with the exception that 18 species were now included in section *Eukallstroemia* and two in section *Thamnozygium.*

1935: L. O. Williams described *Kallstroemia hirsuta* (=*K. perennans)* from Texas, not realizing that the name was a later homonym of a combination made by Engler in 1890.

1936: Standley described *Kallstroemia boliviana* from Bolivia. Although Standley was considered to be an expert on the *Zygophyllaceae,* this was the only species he ever published in this genus.

1939: *Kallstroemia tucumanensis* was described from Argentina by Descole, O'Donell, and Lourteig.

1939: Kearney and Peebles published the combination *Kallstroemia californica* var. *brachystylis* (= *K. californica).*

1950: Turner published *Kallstroemia perennans,* a new name for William's *K. hirsuta.*

1955: The combination *Kallstroemia pubescens* was published by Dandy.

MATERIAL EXAMINED

The first set of my collections has been deposited in the Gray Herbarium of Harvard University. Specimens from 31 institutions have been studied and many of them are cited by herbarium abbreviations under each taxon. These are the standardized abbreviations of Lanjouw and Stafleu (1964), except for the following, which are not included in their publication:

ENAG	Escuela Nacional de Agricultura y Ganadería, Managua, Nicaragua.
MAGN	Ministerio de Agricultura y Ganadería, Managua, Nicaragua.
USMG	Universidad de San Marcos, Guatemala City, Guatemala.

TAXONOMIC TREATMENT

Kallstroemia Scop., Introd. 212. 1777. TYPE SPECIES: *Tribulus maximus* L. [*Kallstroemia maxima* (L.) Hook. & Arn.].

Ehrenbergia Mart., Nov. Gen. Sp. Brasil. 2:72. 1826. Not *Ehrenbergia* Spreng., Neue Entdeck. 2:129. 1821. TYPE SPECIES: *Ehrenbergia tribuloides* Mart. [*Kallstroemia tribuloides* (Mart.) Spreng.].

Heterozygis Bunge, Mem. Acad. Sav. Etr. St. Petersb. 2:82. 1835. TYPE SPECIES: *Tribulus maximus* L.

Annual or occasionally perennial herbs. *Stems* herbaceous to suffrutescent, diffusely branched, prostrate to decumbent or ascending; spreading radially from a thick, fibrous central tap root to 1 m or more long and about 1 m high, branching primarily from basal nodes; terete, somewhat succulent, becoming striate on drying, yellow-green to reddish, drying yellow, fibrous, tough, nodes somewhat swollen; densely pubescent to glabrate, hirsute or hispid and sericeous, rarely only sericeous and strigose, trichomes white, gray, or yellow, directed apically or rarely retrorse. *Stipules* 2, interpetiolar, foliaceous, narrowly to broadly falcate, 3–10 mm long, 1–3 mm wide; acuminate, ciliate, pubescent, trichomes as on stem; erect to spreading, persistent. *Leaves* opposite, elliptical to broadly obovate, 1–8.5 cm long, 1.5–5 cm wide, slightly succulent, one of each pair alternately smaller or sometimes abortive; abruptly even-pinnate, petiole usually shorter than leaflets; rachis terminating in a foliaceous, subulate, apiculate, pubescent mucro ca. 1 mm long; petiole and rachis pubescence as on stem. *Leaflets* 2–10 pairs, opposite, entire, elliptical to broadly oblong or obovate, apex acute to obtuse, mucronate, apiculate, base oblique to inequilateral; 3–29 mm long, 1.5–17 mm wide, somewhat unequal in size, those on one side of rachis slightly smaller, lowest pair markedly unequal, terminal pair pointed forward and more falcate; pubescent to glabrate, appressed-hirsute or rarely hispid or sericeous, margins and veins more or less sericeous, usually ciliate; margins flat to occasionally inrolled; venation reticulate; petiolule 1 mm long or less. *Peduncles* pseudoaxillary, more or less thickened distally, pubescence as on stems; erect at anthesis, reflexed in bud and following anthesis; longer or shorter than subtending leaves, 2–105 mm long in flower and fruit; curved, straight, or bent sharply at base and straight above in fruit. *Flowers* solitary, hypogynous, pentamerous or rarely hexamerous, perfect, regular, polypetalous, syncarpous, 7–60 mm in diameter, appearing alternately on stem. *Sepals* 5(–6), foliaceous, free, inserted at base of receptacle, imbricate in bud; lanceolate to broadly ovate, 2–16 mm long, 1–4 mm wide, concave, margins scarious, apex acute, apiculate; pubescent, hirsute or hispid and strigose, or occasionally sericeous or hirsute; scarious margins or entire sepal usually becoming involute, occasionally shriveling and turning brown; clasping or spreading from base of mature fruit; persistent or rarely caducous. *Petals* 5(–6), free, convolute in bud, alternating with and as long or usually longer than sepals, 3–34 mm long, 1.5–20 mm wide, white to bright orange, base same or green to red, drying white to orange; elliptical to broadly obovate, apex rounded or truncate, entire to irregularly notched, veins prominent; spreading hemispherically, fugaceous, usually marcescent. *Disc* fleshy, obscurely 10(–12)-lobed. *Stamens* 10(–12), inserted in 2 whorls in disc; 5 opposite petals exterior, somewhat longer, adnate basally to petals; 5 opposite sepals shorter, subtended to exterior by a small bilobed gland; shorter than petals, 2/3 as long to slightly longer than style. *Filaments* filiform, subulate, or rarely winged at base, same color as petal base. *Anthers* globose or ovoid to linear-oblong or rarely linear, bilobed, sub-basifixed to versatile, yellow through orange to red, less than 1–2 mm in diameter, or 2–4 mm long; longitudinally dehiscent, introrse, those opposite sepals rarely abortive. *Pollen* spherical, polyforate, yellow through orange to red. *Ovary* superior, sessile, 10(–12)-lobed and -loculed, globose or ovoid and 1–3 mm in diameter, or occasionally conical or pyramidal and 2–4 mm high; glabrous to pubescent, strigose, strigillose, or rarely short-pilose or hispid and strigose. *Ovules* 1 per locule, pendulous, anatropous, placentation axile, sometimes 1 or more aborting. *Style* 1, cylindrical to broadly conical, less than 1–8 mm long, more or less 10(–12)-ridged, persisting to form beak on fruit. *Stigma* capitate, oblong, or clavate, less than 1–7 mm long, terminal or rarely extending down almost to base of style, 10-ridged or -lobed, papillose or rarely coarsely canescent, silvery. *Fruit* 10 (–12)-lobed, ovoid, occasionally conical, or rarely pyramidal, 3–6 mm in diameter or 3–6 mm high and 3–10 mm wide; glabrous to pubescent, strigose, strigillose, or rarely short-pilose or hispid and strigose; at maturity dividing septicidally and separating from a persistent styliferous axis into 10(–12) or occasionally fewer mericarps. *Beak* cylindrical to conical, base more or less conical, 1–18 mm long, glabrous to pubescent. *Mericarps* unilocular, 1-seeded, obliquely triangular, laterally wedge-shaped, 3–5 mm high, 1–2.5 mm wide; abaxially more or less tuberculate or rugose, occasionally also cross-ridged or keeled, glabrous to pubescent; sides glossy, more or less pitted; adaxial edge straight to conspicuously angled. *Seeds* oblong-ovoid, obliquely pendulous from apex of central angle, germination epigeal; testa smooth, white, membranaceous; embryo straight, cotyledons ovoid, radical conical, superior, epicotyl rudimentary; endosperm none.

KEY TO THE SPECIES OF KALLSTROEMIA[1]

[1] Information concerning geographical distribution is approximate only and is included primarily for the convenience of the user of the key. The pubescence types as used in the key are defined as follows: hirsute (trichomes long, coarse, spreading, and moderately stiff), hispid (trichomes long, stiff, spreading, and rigid), hispidulous (trichomes very short, stiff, spreading, and rigid), sericeous (trichomes long, fine, appressed, and slightly wavy), short-pilose (trichomes short, soft, and straight), strigose (trichomes short, slightly curved, appressed, and rigid), and strigillose (trichomes very short, slightly curved, appressed, and rigid).

1. Leaves obovate, terminal leaflets of mature leaves largest.
   2. Mature mericarps with 4–5 blunt elongate tubercles to 1.5 mm long; sepals usually deciduous; stems hirsute and strigose (southwestern United States and northern Mexico; Fig. 8a, 8b) .... 8. *K. californica.*
   2. Mature mericarps rugose to tubercled, cross-ridged, or keeled, tubercles never elongate; sepals persistent; stems hirsute and sericeous.
      3. Ovary and fruit body glabrous or rarely strigose, style and beak glabrous, stigma capitate; sepals hirsute (Caribbean region, southeastern coastal United States, tropical Mexico to northern South America; Fig. 1a, 1b) .... 1. *K. maxima.*
      3. Ovary and fruit body pubescent, style and beak glabrous to pubescent, stigma clavate, oblong, or if capitate then style hirsute at base or fruit body appressed short-pilose; sepals hirsute and strigose, or hispidulous.
         4. Flowers 2–3.5 cm in diameter, style as long or longer than conical ovary, beak as long or longer than fruit body.

    5. Sepals clasping and almost entirely covering mature mericarps, only scarious margins becoming involute; beak ca. as long as fruit body, strigose; stigma oblong; peduncles longer than subtending leaves; leaflets sericeous (Bolivia and Peru; Fig. 10a, 10b) .... 10. *K. boliviana.*
    5. Sepals spreading from base of mature fruit and curving upward, margins becoming strongly involute; beak ca. twice as long as fruit body, base hirsute; stigma capitate; peduncles usually shorter than subtending leaves; leaflets appressed-hirsute and sericeous (Mexico; Fig. 2a, 2b) .... 2. *K. rosei.*
  4. Flowers 1.5 cm or less in diameter, style as long or usually shorter than globose, ovoid, or pyramidal ovary, beak shorter than fruit body.
    6. Sepals clasping mature fruit, only scarious margins becoming involute; fruit broadly ovoid, 4–5 mm high, 6–8 mm wide, beak hirsute (southwestern United States and northern Mexico; Fig. 5a, 5b) .... 5. *K. hirsutissima.*
    6. Sepals spreading from base of mature fruit, margins becoming strongly involute; fruit ovoid, 3–6 mm in diameter, beak strigose, appressed short-pilose, or glabrous.
      7. Sepals hirsute and strigose; stigma clavate; fruit strigillose, beak 1.5–2 mm long and widely conical (Cuba, Hispaniola, and Netherlands Antilles; Fig. 6a, 6b) .... 6. *K. curta.*
      7. Sepals hispidulous with trichomes of two lengths; stigma capitate; fruit appressed short-pilose or strigose, beak narrowly conical or cylindrical above.
        8. Flowers 9–15 mm in diameter, petals 6–11 mm long and 5–8 mm wide; ovary pyramidal, 3–5 mm long including style; fruit densely appressed short-pilose, beak 5–8 mm long (Caribbean region, tropical Mexico to Peru, West Africa, India; Fig. 3a, 3b) .... 3. *K. pubescens.*
        8. Flowers 4–8 mm in diameter, petals 3–5 mm long and 2–3 mm wide; ovary ovoid, ca. 1 mm in diameter, style 1 mm long; fruit strigose, beak 2–3.5 mm long (Argentina and Bolivia; Fig. 4a, 4b) .... 4. *K. tucumanensis.*

1. Leaves elliptical, middle leaflets of mature leaves largest.
  9. Stem pubescence retrorse; stigma extending from along upper 1/3 to ca. entire length of style, surface papillose (southern Baja California, Mexico; Fig. 14a, 14b) .... 14. *K. peninsularis.*
  9. Stem pubescence antrorse; stigma usually terminal and surface papillose, but if extending along upper 1/3 of style then surface coarsely canescent with short gray trichomes.
    10. Flowers 1 cm or less in diameter, style stout, conical, shorter than ovary.
      11. Leaflets 2–3 pairs; sepals persistent; peduncles longer than subtending leaves in fruit; stems hirsute and sericeous (Galápagos Islands, Ecuador; Fig. 7a, 7b) .... 7. *K. adscendens.*
      11. Leaflets 3–7 pairs; sepals usually deciduous; peduncles shorter than subtending leaves in fruit; stems hirsute and strigose (southwestern United States and northern Mexico; Fig. 8a, 8b) .... 8. *K. californica.*

10. Flowers 1 cm or more in diameter, style conical to cylindrical, longer than ovary.
    12. Ovary and fruit glabrous.
        13. Flowers 3–6 cm in diameter; petals white, aging yellow, base yellow-green or rarely red; filaments winged at base; stems hirsute and sericeous, leaflets 5–7 pairs (Michoacán, Mexico; Fig. 17a, 17b) .... 17. *K. hintonii.*
        13. Flowers 1.5–2.5 cm in diameter; petals orange, base sometimes darker; filaments filiform to subulate; stems sericeous, leaflets 3–6 pairs (Argentina, Bolivia, and Brazil; Fig. 11a, 11b) .... 11. *K. tribuloides.*
    12. Ovary and fruit pubescent.
        14. Sepals sericeous, spreading from base of mature fruit, margins becoming strongly involute; beak from ca. 1/2 as long to as long as fruit body; mature mericarps with several elongate blunt or slightly fungoid tubercles to 2 mm long (Oaxaca, Mexico; Fig. 9a, 9b) .... 9. *K. standleyi.*
        14. Sepals hispid and strigose, or if sericeous then clasping mature mericarps and margins not becoming involute; beak from as long as fruit body to three times as long; mature mericarps rugose to tuberculate or cross-ridged and keeled, tubercles never elongate.
            15. Fruit densely hispid and strigose; stigma extending along upper 1/3 of style, surface coarsely canescent with short gray trichomes (southwestern Texas; Fig. 15a, 15b) .... 15. *K. perennans.*
            15. Fruit strigose or strigillose; stigma terminal, papillose, silvery.
                16. Sepals sericeous, clasping mature mericarps, margins not becoming involute; stems strigose (Peru; Fig. 12a, 12b) .... 12. *K. pennellii.*
                16. Sepals hispid and strigose, extending upward beyond mericarps, shriveling and turning brown, margins becoming strongly involute; stems hirsute and sericeous, or hispid and strigose.
                    17. Flowers 2–6 cm in diameter, petals 10–34 mm long and 7–22 mm wide; stigma clavate, 2–3 mm long; peduncles 3–10.5 cm long in fruit (southwestern United States, northwestern and western Mexico; Fig. 13a, 13b) .... 13. *K. grandiflora.*
                    17. Flowers 1–2.5 cm in diameter, petals 5–11 mm long and 3.5–6 mm wide; stigma oblong, ca. 1 mm long; peduncles 1–4 cm long in fruit (central and southwestern United States, northeastern and central Mexico, Peru; Fig. 16a, 16b) .... 16. *K. parviflora.*

1. **Kallstroemia maxima** (L.) Hook. & Arn., Bot. Beechey 282. 1838

The author combination usually is attributed to "Torr. & Gray," Fl. N. Amer. 1:213. 1838. Publication of the latter's Part 2, pp. 185–360, however, took place in October, 1838 (Jackson, 1893), while Part 6, pp. 241–288, of Hooker and Arnott was published before August, 1838 (Marshall, 1950). The combination also occasionally is attributed to "Wight & Arn., Prodr. 1:145. 1834." However, Wight and Arnott never made this combination. They wrote, "*Kallstroemia,* Scop. (containing *Trib. maximus,* Lin. and *Ehrenbergia tribuloides,* Mart. . . .", thus recognizing *Kallstroemia* as distinct from *Tribulus,* but not proposing any new combinations in the genus.

Tribulus maximus L., Sp. Pl. **1**:386. 1753. TYPE: According to Fawcett and Rendle (1920, p. 166), "Specimen from Hort. Cliff. in Herb. Mus. Brit., and from Browne in Herb. Linn., the latter named by Linnaeus." The former should be taken as the holotype, as Browne's herbarium was not acquired by Linnaeus until 1758 (Stern, 1957). Linnaeus also cited names from Sloane and Ray in his protologue, but the specimen at BM appears to be the only one actually studied by him. This specimen has not been seen.

Tribulus trijugatus Nutt., Gen. **1**:277. 1818. TYPE: Georgia, Chatham Co.: Savannah, *Thomas Nuttall s. n.* (holotype presumably at BM, not seen; PH, isotype).

Kallstroemia tribulus Meisn., Pl. Vasc. Gen. **2**:43. 1837. *nom. superfl.* Based on "*Tribulus maximus* Loefl.", cited as a synonym.

Tribulus decolor Macfad., Fl. Jamaica 186. 1837. *nom. superfl.* Based on *T. maximus* L., cited as a synonym.

Tribulus dimidiatus Raf., Autikon Bot. 176. 1840. *nom. superfl.* Based on *T. trijugatus* Nutt., cited as a synonym.

Tribulus trijugus Steud., Nom. Bot. Ed. 2. **2**:699. 1841. *nom. superfl.* Orthographic error for *T. trijugatus* Nutt.

Tribulus tuberculatus Ses. & Moc., Fl. Mex. Ed. 2. 109. 1894. TYPE: Cuba, near Havana, *Martín Sessé* (holotype presumably at MA, not seen).

Kallstroemia canescens Rydb. in Vail & Rydb., N. Amer. Fl. **25**:113. 1910. TYPE: Mexico, Sinaloa: Rosario, 7 July 1897. *J. N. Rose 1547* (US, holotype; GH, NY, isotypes).

Annual; *stems* prostrate to decumbent, to 1 m or more long, sericeous and sparingly hirsute with apically-directed white or yellow trichomes, becoming glabrate; *stipules* 3–5 mm long, ca. 1 mm wide; *leaves* obovate, 1–6 cm long, 1.5–5 cm wide; *leaflets* 3–4 (–6) pairs, broadly oblong to elliptical, appressed-hirsute to glabrate, margins and veins sericeous, 5–29 mm long, 3–14 mm wide, terminal pair usually largest; *peduncles* at first shorter than subtending leaves, equalling them or longer in fruit and straight or curved, little thickened distally, 1–5 cm long; *flowers* pentamerous, 7–25 mm in diameter; *sepals* ovate, 3–8 mm long, 2–3 mm wide, as long or little shorter than petals, hirsute, trichomes appressed to spreading, in flower ca. as long as style, in fruit clasping but not entirely covering mature mericarps and shorter than beak, only scarious margins becoming involute, persistent; *petals* white through yellow to pale orange, base white to yellow-green or green or rarely red, often brighter than distal portion, fading white to bright orange, obovate, 5–12 mm long, to 10 mm wide, marcescent; *stamens* as long as style; *anthers* ovoid or rarely linear, ca. 1 mm in diameter, they and pollen yellow or red-orange; *ovary* ovoid, ca. 1 mm in diameter, usually glabrous but occasionally strigose at base or rarely to base of style; *style* 2–3 mm long, cylindrical, base slightly conical; *stigma* capitate, ca. 1 mm long, obscurely 10-lobed, papillose; *fruit* ovoid, 5–6 mm in diameter, usually glabrous but occasionally strigose at base or rarely to base of beak; *beak* 3–7 mm long, usually ca. as long as fruit body, glabrous, cylindrical, base widely conical; *mericarps* 3–4 mm high, ca. 1 mm wide, abaxially tubercled cross-ridged and slightly keeled, sides pitted, adaxial edge angled. *Fig. 1a, 1b. Map 1.*

FLOWERING DATES. Flowers year around, whenever sufficient moisture is available for seed germination and plant growth.

DISTRIBUTION AND HABITAT. Disturbed areas from sea level to about 1350 m, usually at lower elevations, from northern South America north through the Caribbean to South Carolina and through western Central America to Sinaloa on the west and Tamaulipas on the east coast of Mexico, also introduced into Texas *(Map 1)*. Sympatric with *Kallstroemia curta, K. hintonii,* and *K. standleyi,* and over much of its range with *K. pubescens;* to the northwest overlapping slightly with *K. californica, K. grandiflora, K. hirsutissima,* and *K. parviflora,* and more so with *K. rosei.*

DISTINGUISHING CHARACTERISTICS. *Kallstroemia maxima* is easily recognized by its combination of obovate leaves, usually three to four pairs of leaflets, white to pale orange flowers (the petal bases are white to green or rarely red) 7–25 mm in diameter, hirsute sepals which clasp the mature mericarps, only the scarious margins of the sepals becoming involute, usually glabrous ovaries and fruits, and a capitate obscurely ten-lobed stigma. *Kallstroemia pubescens* and *K. rosei* are the only species from the same area with which it is likely to be confused. However, in the latter species, the sepals spread from the base of the mature fruit, and the sepal margins become sharply involute, thus the sepals appear to be linear or linear-lanceolate. The sepal pubescence in *K. pubescens* is hirsutulous, in *K. rosei* hirsute and strigose; and both have pubescent fruits. There is some overlap in flower diameter between these three species, but the flowers in *K. maxima* on the average are larger than in *K. pubescens* and smaller than in *K. rosei.* The same relationship holds for overall plant size, and *K. maxima* also tends to be less decumbent than *K. rosei.* In addition, in areas where *K. maxima* and *K. rosei* overlap in their distributions, and in localities where both *K. maxima* and *K. pubescens* are to be found, petal color is yellow to orange in *K. maxima* and white in the other two species.

REPRESENTATIVE SPECIMENS EXAMINED. UNITED STATES. TEXAS. Washington Co.: Brenham, *Lehmann,* 10 July 1934 (GH, TEX). SOUTH CAROLINA. Charleston Co.: Charleston, *Elliott s. n.* (PH). GEORGIA. Chatham Co.: Savannah, *Backman s. n.* (PH). McIntosh Co.: Doboy I., *H. H. Smith 2348* (F). Glynn Co.: streets, Brunswick, near sea level, *Harper 1529* (BM, F, GH, MO, NY, US). FLORIDA. Escambia Co.: waste places, Pensacola, *Mohr,* July 1874 (F). Duval Co.: Jacksonville, *Williamson,* Aug

1894 (PH). St. Johns Co.: St. Augustine, dooryards, etc., *Curtiss 6424* (GH, MO, NY, SMU, UC, US). Hillsborough Co.: Tampa, waste ground, *Barnhart 2235* (NY). Monroe Co.: Key West, low waste places, *Curtiss 416* (BM, F, MO, NY, PH, US).

MEXICO. SINALOA: Mazatlán, *González Ortega 7295* (CAS, F, MEXU, US); near Rosario, sand dunes, *Rose, Standley & Russell 14641* (GH, NY, US). NUEVO LEON: Monterrey, *Black 39–7458* (NY). TAMAULIPAS: near Tampico, ca. 15 m, *Palmer 116* (BM, CAS, F, GH, MO, NY, US). NAYARIT: near Acaponeta, cultivated fields, *Rose, Standley & Russell 14400* (F, GH, NY); near San Blas, *Ferris 5388* (DS, GH, MEXU, US). JALISCO: outskirts of Ameca, roadside, 1225 m, *McVaugh 18579* (MICH); Puerto Vallarta, *Howell 10352* (CAS, POM). COLIMA: Colima, *Palmer 98* (US); Manzanillo, edge of dusty street, *Porter 1481* (GH, MEXU). SAN LUIS POTOSI: El Pujal, 100 ft, *Chase 7510* (ARIZ, F, GH, MICH, MO, NY); 15 mi E of Valles, flat bushy area, *Waterfall & Wallis 14310* (F, SMU). MICHOACAN: Aguililla, llano, 900 m, *Hinton 15153* (DS, GH, MICH, NY, RSA, US); Apatzingán, dry waste ground, 1200 ft, *Leavenworth & Hoogstraal 1423* (F, GH, MICH, MO, NY). MEXICO: Vigas, hill, 1080 m, *Hinton 4763* (BM, GH). MORELOS: Puente de Ixtla, *Rose, Painter & Rose 9436* (US); near Yautepec, pedregal, *Rose, Painter & Russell 8598* (MEXU, NY, US). VERACRUZ: Cuitláhuac, *Matuda 1420* (DS, GH, MICH, MO, NY); Mocambo, in road to beach, *Porter 1461* (CAS, DS, GH, MEXU). GUERRERO: Atoyac, plain, *Hinton 14575* (ARIZ, LL, NY, PH, TEX, US); 1 mi E of Acapulco, sandy flat above Playa Hornos, *Barkley 14084* (CAS, DS, F, GH, MEXU, MO, PH, POM, RSA, SMU, TEX, UC). OAXACA: Hacienda de Guadalupe, 1650 m, *Conzatti 2190* (F, GH, MEXU); 2 km S of Niltepec, clay loam, *King 1777* (MICH, NY, TEX, UC). TABASCO: San Juan Bautista, cultivated areas, *Rovirosa 160* (PH, US); between San Juan Bautista and Paso del Tierra Colorado, *Rovirosa 567* (NY, PH, US). CHIAPAS: between Mazapa and Motozintla, 1200 m, *Matuda 4831* (GH, LL). CAMPECHE: Ciudad del Carmen, *Mell 2074* (NY, US); Tuxpeña, *Lundell 1217* (ARIZ, DS, F, GH, LL, MEXU, MICH, MO, NY, UC, US). YUCATAN: Chichen Itzá, *Steere 1022* (BM, MEXU, MICH, MO, NY); Izamal, *Gaumer 462* (BM, CAS, DS, F, GH, MICH, MO, NY, PH, SMU, UC, US, WIS). QUINTANA ROO: Chichankanab, *Gaumer 1780* (BM, CAS, DS, F, PH, UC, US).

GUATEMALA. PETEN: near La Libertad, *Aguilar H. 175* (F, MICH, MO). HUEHUETENANGO: near Cuilco, thickets along Río Cuilco, 1350 m, *Steyermark 50759* (F, US). QUICHE: without locality, *Aguilar G. 492* (F). IZABEL: near Puerto Barrios, open bank, sea level, *Standley 25147* (GH, US). SAN MARCOS: Ocós, sands, 1–2 m, *Steyermark 37853* (F). RETALHULEU: Champerico, *Kellerman 4978* (US). SUCHITEPEQUEZ: Tiquisate, 100 m, *Steyermark 47630* (F). SOLOLA: Guatalón, 190 m, *Steyermark 48080* (F, US). SACATEPEQUEZ: Villa Nueva, foot of adobe wall, *Porter 1308* (DS, GH). GUATEMALA: La Aurora, *Aguilar G. 502* (F). ZACAPA: Gualan, waste places and yards, 620 ft, *Deam 6288* (F, GH, MICH, MO, NY, US). AMATITLAN: Río Amatitlán, 3900 ft, *J. D. Smith 1936* (GH, US). ESCUINTLA: near San José, roadside, sea level, *Standley 64062* (F, NY). SANTA ROSA: Cerro Gordo, 3500 ft, *Heyde & Lux 3958* (F, PH, US). JUTIAPA: near Jutiapa, gravelly open slope, ca. 850 m, *Standley 74980* (F).

BRITISH HONDURAS. COROZAL: Santa Rita, occupied clearing, *Lundell 4773* (ARIZ, DS, F, GH, MEXU, MICH, MO, NY, TEX). CAYO: El Cayo and vicinity, *Chanek 159* (F, MICH).

EL SALVADOR. SANTA ANA: Santa Ana, *Porter 1280* (GH, ITIC). SONSONATE: near Armenia, dry field, *Standley 23538A* (DS, US). LA LIBERTAD: La Libertad, railroad track, *Porter 1260* (DS, GH, ITIC). SAN SALVADOR: San Salvador, *Calderón 349* (GH, MO, NY, US). LA PAZ: 0.5 mi N of Comalapa toward Santo Tomás, roadside, *Porter 1286* (GH, ITIC). SAN VICENTE: near San Vicente, old corn field, *Standley 21708* (GH, US). SAN MIGUEL: Laguna de Olomega, ca. 1.8 km W of Hacienda Potrero Santo, ca. 60 m, *Tucker 892* (F, UC, US). LA UNION: La Unión, sunny fields on edge of forest, *Grant 706* (F, GH).

HONDURAS. CORTES: Finca Zapote, near La Lima, 30 m, *Williams & Molina R. 12458* (F, GH). COMAYAGUA: near Comayagua, ca. 600 m, *Standley & Chacón P. 5614* (F). MORAZAN: near Zamorano, sand along Río de la Orilla, 850 m, *Molina R. 261* (F, GH, MO, UC, US). EL PARAISO: Yascarán, open bank, 930 m, *Standley 25790* (F). CHOLUTECA: near Pespire, 160–200 m, *Standley 27259* (F).

NICARAGUA. CHINANDEGA: Corinto, *Greenman & Greenman 5828* (GH, MO). MANAGUA: Managua, railroad track, *Porter 1190* (DS, GH). MASAYA: Masaya, *Baker 211* (DS, GH, MO, NY, UC). CARAZO: near Jinotepe, dry thicket, ca. 600 m, *Standley 8536* (F). CHONTALES: near Juigalpa, roadside, ca. 160 m, *Standley 9417* (F).

COSTA RICA. GUANACASTE: Nocoya, roadsides, *Tonduz 13919* (CR, GH, US). PUNTARENAS: Puntarenas, railroad track, *Porter 1136* (CR, GC, GH, IJ). ALAJUELA: El Coyolar, dry field, ca. 240 m, *Standley 40079* (US).

PANAMA: CANAL ZONE: between Panamá and Corozál, 20–30 m, *Pittier 4443* (F, GH, NY, US).

BAHAMA ISLANDS. FORTUNE: *Hitchcock,* Nov 1890 (MO). NEW PROVIDENCE: hill S of Lyford Cay, *Degener 18742* (GH, NY, PH).

CUBA. PINAR DEL RIO: near Mariel, sandy flat ground along coast, *Palmer & Riley 711* (NY, US). HAVANA: Havana, *Schott 97* (BM). MATANZAS: near Matanzas, *Gundlach 291* (CAS). LAS VILLAS: Las Auaras, banks of Río Arimao, *Gonzales 539* (A, BM, IJ, MICH, NY). ORIENTE: Hicotea Estate, banks of Río Cañas, *Bro. Clemente 5699* (GH, US).

CAYMAN ISLANDS. GRAND CAYMAN: Bosun Bay, near Hell, pasture, coral rock and soil, 10–20 ft, *Kings GC403* (BM, MO).

JAMAICA. HANOVER: Lucea, *Hitchcock,* 9 Jan 1891 (MO). WESTMORLAND: New Hope Estate, 1.5 mi W of Little London, garden, 175 ft, *Proctor 11202* (IJ). ST. JAMES: Montpelier, *Churchill,* 16 Mar 1897 (GH). ST. ELIZABETH: Giddy Hall, *Maxwell,* Apr 1926 (BM). CLARENDON: halfway between Amity Hall and Portland Cottage, roadside at edge of sugarcane plantings. *Porter 1039* (GH). ST. CATHERINE: Spanish Town Road, 100 ft, *Campbell 6298* (BM, UCWI). ST. ANDREW: Mona, weedy field, *Crosby, Hespenheide & Anderson 69* (F, GH, MSC, UC). ST. THOMAS: Albion, *Orcutt 1421* (UC).

HAITI. NORD: Bayeux, dry streambed, sea level, *Nash 92* (F, NY). ARTIBONITE: Montagnes de Terre Neuve, 400 m, *Buch 55* (IJ). SUD: Miragoâne, roadside, *Eyerdam 32* (GH, US). OUEST: Port au Prince, 350 m, *Holdridge 1039* (F, MICH, NY, US). GONAVE: near Pikmi, cultivated and waste places, *Leonard 5194* (GH, US).

DOMINICAN REPUBLIC. MONTE CRISTI: Santiago, margins of Río Yaque, *Jiménez 1844* (US). AZUA. Azua, *Rose, Fitch & Russell 4012* (NY, US). BARAHONA: near Barahona, 20 m, *Fr. Fuertes 1574* (BM, F, GH, NY, US). PACIFICADOR: Pimental, along railroad, near sea level, *Abbott*

643 (US). SANTO DOMINGO: Santo Domingo, seashore, *von Türckheim 2547* (BM, GH, MO, NY, US). MACORIS: 20 km W of San Pedro de Macoris, limestone outcrop, *Howard & Howard 9496* (GH, NY, US).

PUERTO RICO. AGUADILLA: Camuy, *Underwood & Griggs 197* (NY, US). MAYAGUEZ: near Yauco, *Heller 6296* (CAS, F, GH, MO, NY, PH, US). ARECIBO: near Manati, cultivated area, *Sintenis 6731* (BM, F, GH, MO, NY, US). PONCE: Cayo Muertos, waste grounds, *Britton, Cowell & Brown 4985* (F, MO, NY, US). SAN JUAN: Cataño, waste ground, *Heller & Heller 114* (F, NY, US). GUAYAMA: Guayama, *Kuntze 578* (NY). HUMACAO: Luquillo Beach, along sidewalk, *Howard & Nevling 15523* (A). VIEQUES ISLAND: Isabel Segunda to Cerra Encanta, roadside bank, *Shafer 2519* (NY, US). CULEBRA ISLAND: Culebra, waste places, *Britton & Wheeler 282* (F, NY, US).

VIRGIN ISLANDS. ST. THOMAS: *Eggers 8* (F, NY). TORTOLA: Experiment Station, waste places, *Fishlock 131* (NY, PH). ST. CROIX: roadside, *Ricksecker 138* (F, GH, MO, NY, UC, US).

LEEWARD ISLANDS. ANGUILLA: near Blowing Point, roadside, *Proctor 18685* (BM, IJ). ST. BARTHELEMY: Gustavia, 2 m, *Questel 193* (US). ST. EUSTATIUS: Orangestäd, along roads, *Stoffers 3905* (A). ST. KITTS: near Basseterre, roadside, *Britton & Cowell 137* (NY, US). ANTIGUA: Cedar Valley, cultivated lands in drier districts, *Box 871* (GH). GUADELOUPE: Basse-Terre, *Fr. Duss 2427* (US). DESERADE: Grand Anse, roadside, 1 m, *Proctor 21294* (IJ). DOMINICA: Grand Savannah, grassy coastal xerophytic shallow-soiled areas, *Hodge & Hodge 3762* (GH, US).

WINDWARD ISLANDS. MARTINIQUE: St. Pierre, *Hahn 987* (BM, PH). ST. VINCENT: sandy land or cultivated fields, *Smith & Smith 584* (GH). BARBADOS: near Combermere School, *Dash 224* (F, NY, US). GRENADA: St. George's, ditch, *Broadway*, 2 Apr 1905 (NY).

COLOMBIA. ATLANTICO: Cabica, island in Río Magdalena, *Bro. Elias 1218* (F). MAGDALENA: Santa Marta, 250 ft, *H. H. Smith 572* (MICH, TEX, UC, WIS). BOLIVAR: near Cartagena, ca. sea level, *Killip & Smith 14039* (COL, F, GH, NY, US). CORDOBA: Montería, riverbank, 20–50 m, *Pennell 4706* (F, GH, MO, NY, US).

VENEZUELA. ZULIA: Maracaibo, *s. coll.* (CAS). TRUJILLO: La Concepción, 2500 ft, *Reed 1005* (MICH). DISTRITO FEDERAL: Blandin, waste places, *Pittier 11618* (NY, US). ANZOATEGUI: Guanta, roadside, ca. sea level, *Potter 5149* (US). BOLIVAR: Ciudad Bolívar, near river, ca. 35 m, *Holt & Gehriger 33* (US).

A specimen of *Kallstroemia maxima* at CAS, purportedly collected in California and labeled "*Jesse D. Skoss*, 7 May 1948. Kern Co.: Kern River Canyon, 7 miles below Hobo Hot Springs.", actually seems to have been collected by A. S. Crafts in the Dominican Republic (Dr. John M. Tucker, personal communication). There is also a specimen of *Tribulus cistoides* at CAS bearing Skoss' name and the same locality data. I have indicated previously (Porter, 1963) that this latter collection was made in California, but it, too, apparently was collected in the Dominican Republic by Crafts.

COMMON NAMES. Many common names have been applied to *Kallstroemia maxima*. This is to be expected with a plant that is so frequent and widespread among peoples who often utilize their natural flora and its products. The names reported in the literature, or noted on herbarium labels, are Abrojo (Cuba, Nicaragua, Puerto Rico); Chax-chauxnuc (Quintana Roo, Mexico); Cresson Courant (Guadeloupe); Golondrina, Guía de Parra, Hierba de Parra (El Salvador); Hierba de Pasmo (Venezuela); Hierba de Pollo (Colombia, El Salvador, Panama); Maconcherie (Dominica); Mata (Costa Rica); Pale-flowered Turkey-blossom (Jamaica); Parsley (Grand Cayman); Patagon (Martinique); Police Macca (Jamaica); Pourpier Bâtard (Guadeloupe); Pourpier Courant, Pourpier Rampant (Martinique); Shanapmucui (British Honduras); Talcacao (Costa Rica); Taraya (El Salvador); Verdolaga (Costa Rica, El Salvador, Venezuela); Verdolaga Blanca, Verdolaga del Caballo, Verdolaga del Monte, Verdolaguita (El Salvador); Xichiak (Quintana Roo); Xichilak (Yucatan, Mexico); Yerba de Gallina (Honduras); and Yerba de Paloma (Guerrero, Mexico).

The prevalence of Verdolaga or its derivatives as a common name for this species throughout much of Latin America is explained by its resemblance to the Verdolaga Vera (true verdolaga), *Portulaca oleracea* L. *(Portulacaceae).* The latter is another weedy plant common to the same area as *Kallstroemia maxima,* superficially similar to it, and much used by the native populations as a potherb.

It should be noted that the name *Caltrop* is often given to various members of the genus in manuals and floras, but it is to be doubted that anyone but a botanist would apply this common name to a *Kallstroemia.* It is more aptly applied to the spiny-fruited species of *Tribulus,* which show a decided resemblance to their namesake, a medieval weapon used to impede charging cavalry.

TAXONOMY. The name *Kallstroemia canescens* has been applied to specimens of *K. maxima* from southwestern Mexico with strigose fruits. Whereas the fruits of *K. maxima* usually are glabrous, individuals with strigose fruits are found occasionally. They come from scattered places throughout the range of the species, and taxonomic recognition on the basis of this single character is not warranted.

VARIATION. In *Kallstroemia maxima* there is a noticeable amount of variation in stem color, in flower size and color, in anther and pollen color, and in peduncle length and the amount of peduncle curvature at fruiting time. Variation is particularly striking in this species because these morphological characters may vary within the local population. Other species of the genus may be equally variable with respect to the same characteristics, but the variation occurs between populations, apparently never within them.

This interpopulation variation is especially common in Central America. In Costa Rica, for instance, where *Kallstroemia maxima* was observed in the town of Puntarenas the populations consisted of two morphological types. One type had yellow-orange flowers 1–1½ cm in diameter with yellow anthers and pollen, the sepals were about two-thirds as long as the petals, and the peduncles were 2–2½ cm long, bent strongly at the base and straight above. The second type had pale yellowish-white flowers 7–8 mm in diameter with red anthers and pollen; the sepals were as long as the petals, and the peduncles were 6–14 mm long and curved through their entire length. An accurate count of the two types in the populations was not taken, but they were estimated to be present in approximately equal numbers. Intermediates were not seen. Progeny of collections of both types *(Porter 1135, 1136)* proved to be self-compatible when grown in the greenhouse.

The situation discussed above in *Kallstroemia maxima* is similar to that described by Lewis (1963) for *Gayophytum* "taxon *B*" *(Onagraceae).* Discontinuous phenotypic variation in populations of the latter autogamous taxon could have a simple genetic basis, and if so such differences do not warrant formal taxonomic recognition. The same conclusion is applicable in this instance to *K. maxima,* especially in light of the populations reviewed below, although data concerning cytology and breeding behavior (i.e., the extent of outcrossing) are lacking.

Populations of *Kallstroemia maxima* examined in Managua, Nicaragua, and Ilopango and San Salvador, El Salvador, displayed all combinations of flower size and color, as well as anther and pollen color found in the two Puntarenas types. Stem color here varied independently as well, being either yellow-green or reddish. In one Managua population, some plants were also prostrate with smaller leaves, and the others were decumbent with larger leaves, additional characters that appeared to vary independently. This same population yielded individuals with yellow anthers and pollen and with flowers which had a few red pollen grains on their stigmas. Others possessed flowers with red anthers and pollen, and with a few yellow grains on their stigmas. This information suggests that these characters are under simple genetic control. Further evidence in support of this conclusion, at least for anther and pollen color, is provided by greenhouse plantings of the progeny of *Porter 1489,* an individual of *K. maxima* from Mazatlán, Sinaloa, with red-orange anthers and pollen. Some of the progeny plants had red-orange anthers and pollen, as in the parent, others had yellow anthers and pollen.

Another variation in flower color in this species is found in some populations in Guerrero and Michoacán. Here, the petals are proximally cream with a red spot at the base. Specimens with this red spot also have red anthers and pollen.

As mentioned above, there is some variation in this species with respect to fruit pubescence. Classically, the presence of a glabrous fruit has been used as the key character for the recognition of *Kallstroemia maxima.* This is true for the majority of individuals, but there are exceptions. Specimens with a varying pattern of strigose fruit pubescence have been found at scattered localities throughout the range of the species, some fruits being strigose only at the base, but others across the abaxial surfaces of the mericarps to the base of the style. The only area where the fruit pubescence presents a more consistent pattern is in southwestern Mexico where *K. maxima* overlaps with *K. rosei.* The sepals of individuals of *K. maxima* in this region also vary toward those of *K. rosei.* They extend further beyond the mature mericarps and the margins are more involute than is true for specimens from other parts of the species range. This variation possibly is due to the introgression of genes from *K. rosei.*

Despite the great range of variation in certain morphological characters in *Kallstroemia maxima,* it appears best not to give formal taxonomic recognition to the variants. The evidence indicates that they have a simple genetic basis, and there are no established ecological or geographical correlations present. More information, particularly of a cytogenetical nature, may lead to a more precise interpretation of the variability present.

RELATIONSHIPS. This species is most closely related to *Kallstroemia pubescens* and *K. rosei.* A discussion of the three species will be found above.

Millspaugh (1916, p. 428), in a discussion of *Tribulus alacranensis,* a species supposedly endemic to the Alacran Shoals off the northern coast of Yucatán, Mexico, wrote of its "probable parent *T. maximus* [= *Kallstroemia maxima*]." This undoubtedly was a slip of the pen, as he earlier (Millspaugh, 1900) indicated *T. alacranensis* as being a close relative of *T. cistoides*. It is probably conspecific with the latter, although a recent survey of the flora of these small islands (Bonet & Rzedowski, 1962) recognized *T. alacranensis* as a distinct species. However, *T. alacranensis* has no closer affinities to *Kallstroemia* than does any other species of *Tribulus*.

Kallstroemia maxima × K. pubescens?

As has been indicated in the introductory material, under "Hybridization," there are a number of collections of the genus from Colombia and Venezuela which appear to be morphologically intermediate between *Kallstroemia maxima* and *K. pubescens (Map 2)*. Comparative morphology suggests that these specimens may be the result of hybridization between the species indicated above, but there is no genetical evidence that this is the case. Until this becomes available, either through further field studies or crossing experiments, it is thought best to consider these specimens only as putative hybrids.

SPECIMENS EXAMINED. COLOMBIA. LOCALITY UNKNOWN: Magdalena, 600 m, *Triana,* 1851–1857 (BM). ATLANTICO: Barranquilla, *Bro. Paul B35* (US); around Galapa and Baranoa, *Dugand & Jaramillo 3271* (COL, US); wet ground at edge of marsh, Malambo, *Porter 1118* (GH); corral, Ponedera, *Porter 1123* (GH). BOLIVAR: near Cartagena, *Bro. Heriberto 1* (US). CORDOBA: highway from Cerati to Sahagún, 120 m, *Garcia Barriga 13445* (COL, US); dry rich soil near Montería, ca. 20 m, *Araque Molina & Barkley 19B01168* (COL, US). ANTIOQUIA: scattered woods on outskirts of Dabeiba and right bank of Río Sucio, ca. 1350 m, *Gutierrez V. & Barkley 17C486* (CAS, COL, GH); humid forest below Santa Elena summit, Medillín-Río Negro road, ca. 2500 m, *Barva L., Araque M. & Saiz A. 448* (US). VALLE: moist field, Dagua, *Killip 5432* (GH, NY, PH, US); San Jerónimo, 980 m, *Cuatrecasas 22807* (F, US). CUNDINAMARCA: near Anapoima, 600 m, *Triana 3744* (NY, US); Girardot, *Pérez Arbeláez 426* (COL, US), *Toro 56* (COL, NY); Tocaima, *Pérez Arbeláez 2442* (COL, US). HUILA: talus at base of dry eroded river bluffs, Río Ambicá just above confluence with Río Cabrera, *Fosberg 19334* (COL, US).

VENEZUELA. TRUJILLO: La Concepción, 2500 ft, *Reed 1005* in part (US).

2. **Kallstroemia rosei** Rydb. in Vail & Rydb., N. Amer. Fl. **25**:113. 1910

TYPE: Mexico, Morelos: near Yautepec, 27 August 1903, *J. N. Rose & Jos. H. Painter 6562* (US, holotype; NY, isotype).

Annual (occasionally perennial?); *stems* prostrate to decumbent, to 1 m long, densely hirsute and sericeous with white or gray apically-directed trichomes; *stipules* 4–9 mm long, ca. 1.5 mm wide; *leaves* obovate, 2–5 cm long, 1.5–5 cm wide; *leaflets* (2–)3(–4) pairs, ovate or oblong, appressed-hirsute, veins and margins sericeous, 12–26 mm long, 6–17 mm wide, terminal pair largest; *peduncles* usually shorter than leaves, thickened distally, 2–5 cm long, more or less curved in fruit; *flowers* pentamerous, 2–3.5 cm in diameter; *sepals* narrowly ovate, 6–10 mm long, 2–3 mm wide, hirsute and strigose, longer than style in flower, in fruit shorter than beak and usually spreading from base of fruit and curving upward, margins becoming sharply involute, persistent; *petals* white to light orange, base green to white or yellow, drying white, obovate, 5–17 mm long, 5–20 mm wide, marcescent; *stamens* as long as style; *anthers* ovoid, rarely linear, ca. 1 mm in diameter, they and pollen red-orange, rarely yellow; *ovary* conical, 1–2 mm high, strigose; *style* 2–3 mm long, conical, base hirsute; *stigma* capitate, obscurely 10-lobed, ca. 1 mm long, papillose; *fruit* ovoid, 5–6 mm in diameter, strigose; *beak* 4–10 mm long, ca. twice as long as fruit body, cylindrical, base somewhat conical and hirsute; *mericarps* 4 mm high, abaxially tubercled and cross-ridged, sides slightly pitted, adaxial edge angled. *Fig. 2a, 2b. Map. 3.*

FLOWERING DATES. Mainly from June through September, following the summer rains, but occasionally flowering until March.

DISTRIBUTION AND HABITAT. Disturbed areas in the pine-oak forests of the mountains of northeastern, central, and southern Mexico, and occasionally spreading to lower elevations *(Map 3).* Found from 200 to 3150 m, mainly above about 1000 m. Sympatric with *Kallstroemia parviflora* to the north and *K. maxima* to the southwest, and slightly overlapping with *K. californica, K. grandiflora, K. hirsutissima,* and *K. pubescens* in parts of its range.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia rosei* may be recognized by the combination of its obovate leaves, usually three pairs of leaflets, flowers 2–3½ cm in diameter, hirsute and strigose sepals which spread from the base of the mature fruit and curve upward, sharply involute sepal margins making the sepals appear linear or linear-lanceolate, usually white petals, usually red-orange anthers and pollen, conical ovary, strigose fruit, ring of white hirsute pubescence at the base of the beak, the latter being about twice as long as the fruit body, and a capitate obscurely ten-lobed stigma. The only other species from the same area with which it is likely to be confused is *Kallstroemia maxima.* The latter is easily distinguished from *K. rosei* by its flowers of from 7–25 mm in diameter, hirsute sepals which clasp the base of the mature fruit, only their scarious margins becoming involute, and usually glabrous ovaries and fruits. In those rare individuals of *K. maxima* with pubescent ovaries and fruits, these organs are sparingly strigose. *Kallstroemia maxima* tends also to be smaller in overall plant size and less decumbent than *K. rosei.* In areas where the two overlap in distribution, petal color is white in *K. rosei* and yellow to orange in *K. maxima.*

REPRESENTATIVE SPECIMENS EXAMINED. MEXICO. DURANGO: Trancas Canyon, ca. 7 mi SW of Chocolate, among limestone boulders, 1350 m, *Correll & Johnston 20014* (LL). NUEVO LEON: Cerro del Obispado, along road, 1500 ft, *Lacás 36* (F); Monterrey, 1800 ft, *Fisher 41* in part (CAS, DS, F). TAMAULIPAS: 5 km S of Hoja Verde, up arroyo, *Stanford, Lauber & Taylor 2219* (DS, GH, MO, NY, RSA, US); 4 mi S Jaumave, ditch bank, *Stanford, Lauber & Taylor 2283* (GH, NY, US); mountain top 7 km SW of Miquihuana, forest floor of low vegetation in forest of large pines, 3150 m, *Stanford, Retherford & Northcraft 917* (ARIZ, DS, GH, MO, NY). SAN LUIS POTOSI: 10 km S of Cárdenas, trailside, 1100 m, *Rzedowski 4588* (TEX); Río Verde, *Palmer 3* (F, GH, MO, NY, US). AGUASCALIENTES: 43 km W of Aguascalientes, gentle S slope in xeric matorral, 2045 m, *Detling 8737* (MICH); 9 mi E of Aguascalientes toward Ojuelos, brush-covered hills, 2000 m, *McVaugh 16627* (MICH). JALISCO: Jaday, *Davis,* 6 July 1959 (TEX); La Palma, *M. E. Jones 109* (MO, MSC, POM, US). GUANAJUATO: Cortazar, *Knobloch 1081, 1082* (MICH, MSC); near Irapuato, barren land, *Kenoyer 1859* (GH). QUERETARO: near San Juan del Río, stony hillside, *Rose, Painter & Rose 9617* (US). HIDALGO: Jacala, wooded mountain ravine, 4500 ft, *Chase 7200* (F); Zimapán, *Coulter 780* in part (GH, NY, PH). MICHOACAN: ca. 7 mi N of Ciudad Altamirano, *Porter 1373* (DS, GH, MEXU); Coalcomán, llano, 1000 m, *Hinton 13981* (GH, LL, NY, PH, US); Zitácuaro to San José Purua, trailside, lush shrubbery, *Hinton 13050* (ARIZ, GH, LL, MICH, NY, TEX, US). MORELOS: Km 117 on Cuernavaca-Taxco highway, *Langman 2081* (MEXU, PH); 5 km NW of Zacatepec toward Cuautla, edge of highway in sugarcane plantation, *Porter 1443* (GH, MEXU). PUEBLA: 1 mi E of Puebla-Morelos border between Axochiapan and Atencingo, fine sandy fill at roadside, *Porter 1457* (DS, GH, MEXU); 5 mi NW of Tehuacán toward Puebla, edge of highway, *Porter 1447, 1449, 1450* (GH). GUERRERO: Cutzamala, dry hill, *Hinton 5789* (GH, LL, NY, PH, US); 10 mi W of Iguala toward Teloloapan, roadside, *Porter 1345* (DS, GH, MEXU); Río Balsas, *Orcutt 4169* (BM, F, GH, MO, US). OAXACA: Cuicatlán, 1900 ft, *L. C. Smith 494* (GH); near Oaxaca, 1550 m, *Conzatti 1832* (F, GH, MEXU). CHIAPAS: Tuxtla Gutiérrez, vacant lot, 1800 ft, *Breedlove 10619* (DS, GH).

VARIATION. Fruit pubescence in *Kallstroemia rosei* varies from dense to sparse. Lightly pubescent fruits appear most commonly in the area south of the volcanic cordillera of south-central Mexico where this species is sympatric with *K. maxima.* This variation in fruit pubescence may be due to the introgression of genes from *K. maxima.* There is also some evidence that older fruits tend to be less pubescent than younger ones because of the loss of trichomes.

RELATIONSHIPS. *Kallstroemia rosei* is most closely related to *K. maxima.* A discussion of their differences will be found above.

3. **Kallstroemia pubescens** (G. Don) Dandy in Keay, Kew Bull. **10**:138. 1955

Tribulus pubescens G. Don, Gen. Syst. 1:769. 1831. TYPE: Cape Coast [Accra, Ghana], *G. Don s. n.* (BM, holotype, not seen).

Kallstroemia minor Hook. f. in Hook., Niger Fl. 269. 1849. *nom. superfl.* Based on *Tribulus pubescens* G. Don, cited as a synonym.

Tribulus maximus var. *minor* Oliver, Fl. Trop. Afr. 1:284. 1868. TYPE: Cape Coast, *T. Vogel.*

Kallstroemia caribaea Rydb. in Vail & Rydb., N. Amer. Fl. **25**:111. 1910. TYPE: West Indies, Montserrat: Cocoanut Hill, creeping in cotton patch, fls. yellow; 5 February 1907, *J. A. Shafer 388* (NY, holotype; F, US, isotypes). The name "*Kallstroemia maxima* var. *caribaea* (Rydb. in Vail & Rydb.) Macbr." occasionally has been applied to this taxon. However, this combination was never validated. Macbride (1930) argued that the taxon merited only varietal recognition but did not make the relevant combination.

Kallstroemia glabrata Rydb. in Vail & Rydb., *op. cit.* 112. 1910. TYPE: Mexico, Guerrero: Acapulco and vicinity, October, 1894, to March, 1895 [November, 1894, according to McVaugh (1956)], *Edward Palmer 131* (US, holotype; GH, isotype).

Kallstroemia longipes Rydb. in Vail & Rydb., *op. cit.* 114. 1910. TYPE: Mexico, Sinaloa: Rosario; 22 July 1897, *J. N. Rose 1829* (NY, holotype; MEXU, MO, US, isotypes).

Annual; *stems* prostrate to decumbent, to 1 m or more long, sparsely to densely hirsute and sericeous with apically-directed or rarely retrorse fine white trichomes; *stipules* 2-6 mm long, 1–2 mm wide; *leaves* obovate, 1–6 cm long, 1.5-5 cm wide; *leaflets* (2–)3(–4) pairs, elliptical to obovate, appressed-hirsute to glabrate, veins and margins more or less sericeous, 3–26 mm long, 5–17 mm wide, terminal pair largest; *peduncles* shorter than or equaling subtending leaves, 1–3.5 cm long, length and amount of curvature in fruit variable; *flowers* pentamerous, 9–15 mm in diameter; *sepals* lanceolate, 4–8 mm long, 2–3 mm wide, hispidulous with fine white trichomes of two lengths, in flower ca. as long as style, spreading from base of mature fruit and appearing linear-lanceolate through margins becoming sharply involute, persistent; *petals* white through yellow to pale orange, base green, fading white or yellow, obovate, 6–11 mm long, 5–8 mm wide, marcescent; *stamens* as long as style; *anthers* globose, less than 1 mm in diameter, they and pollen yellow or red-orange; *ovary* pyramidal, 3–5 mm long including style, densely appressed short-pilose with fine white trichomes; *style* stout, conical, rarely cylindrical above; *stigma* capitate, obscurely 10-lobed, ca. 1 mm long, papillose; *fruit* ovoid, 5–6 mm in diameter, densely appressed short-pilose; *beak* 5–8 mm long, ca. as long as fruit body, short-pilose to glabrous, cylindrical, base conical; *mericarps* 3–4 mm high, ca. 1 mm wide, abaxially cross-ridged and tubercled to rugose, sides pitted, adaxial edge angled. *Fig. 3, 3b. Maps 4, 5.*

FLOWERING DATES. Apparently flowering throughout the year whenever sufficient moisture is available for seed germination and plant growth.

DISTRIBUTION AND HABITAT. The Lesser Antilles, Puerto Rico, and Jamaica; across northern South America and north through Central America to Yucatán on the east and Sinaloa on the west coast of Mexico; south through Colombia and Ecuador to northern Peru *(Maps 4 and 5).* Introduced into Florida, Ghana and Nigeria, Africa (Keay, 1955), and West Bengal, India (Bennet, 1965). Disturbed areas from sea level to 1400 m, most common at lower elevations. Sympatric with *Kallstroemia hintonii* and *K. standleyi,* and over most of its range with *K. maxima.* Extending into the ranges of *K. curta* in the Caribbean and *K. californica, K. grandiflora,* and *K. rosei* in western Mexico.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia pubescens* may be recognized by its combination of obovate leaves, usually three pairs of leaflets, usually white flowers 9–15 mm in diameter, hispidulous sepals spreading from the base of the mature fruit, the sepals appearing linear or linear-lanceolate through the sepal margins becoming sharply involute, usually red-orange anthers and pollen, pyramidal ovary, densely appressed short-pilose fruit, with the beak about as long as the fruit body, and a capitate obscurely ten-lobed stigma. *Kallstroemia maxima* is the only species from the same area with which *K. pubescens* is likely to be confused. The two are readily distinguishable to the naked eye because of fruit and sepal differences. In *K. maxima,* the sepals are hirsute, clasp the mature mericarps, and only their scarious margins become involute; the fruit is usually glabrous, rarely being strigose. In localities where the two species grow together, the herbage of *K. pubescens* tends to be lighter in color and less succulent than that of *K. maxima.* In such areas, the petals of *K. pubescens* invariably are white, while those of *K. maxima* are yellow to orange.

REPRESENTATIVE SPECIMENS EXAMINED. UNITED STATES. FLORIDA. Franklin Co.: Apalachicola, *Chapman s. n.* (MO), *4099* (NY).

MEXICO. SINALOA: Rosario, *Rose 1830* in part (NY). NAYARIT: near Jesús María, dry woodland, *Feddema 1329* (MICH). JALISCO: Bolaños, *Rose 3693* in part (NY). MICHOACAN: El Capire, 15 mi SSW of Apatzingán, moist open, often by standing water, *Leavenworth 439* (ARIZ, F, GH, MICH, MO, NY); Tepalcatepec, grassy hill, 350 m, *Hinton 12097* (DS, GH, MICH, NY, US). GUERRERO: Atoyac, shrubby plain, *Hinton 14543* (ARIZ, GH, LL, NY, PH, US); Placeres to Pinzon Morado, llano, 400 m, *Hinton 9119* (ARIZ, GH, LL, NY, US). OAXACA: Puerto Angel, *Orcutt 5017, 5029* (DS); 4 km NNE of Tehuantepec, gravelly roadside, flat grazed areas, *King 1315* (MICH, NY, SMU, TEX, UC, US). CHIAPAS: 8 mi E of Cintalapa on Highway 190, wooded slope, 2200 ft, *Breedlove 10315* (DS, GH). YUCATAN: Valladolid, *Steere 1693* (F, MEXU, MICH). QUINTANA ROO: Chichankanab, *Gaumer 1570* in part (BM, MO).

GUATEMALA. ZACAPA: near Zacapa, damp field, ca. 200 m, *Standley 73599* (F, US).

EL SALVADOR. LA PAZ: Bosque la Herradura, 100 m, *Lagos,* 28 Sept 1956 (ITIC).

HONDURAS. SANTA BARBARA: San Pedro Sula, 1000 ft, *Thieme 5170* (F, GH, US). COMAYAGUA: W of Comayagua near El Taladro, savannahs and roadside, 650 m, *Molina R. 14287* (F). VALLE: San Lorenzo, 20 m, *Valerio Rodriguez 3449* (F).

NICARAGUA. CHINANDEGA: E base of Volcán Cosegüina, *Howell 10269* (CAS). MATAGALPA: just N of Las Maduras, rocky roadside embankment, *Porter 1215* (GH). MANAGUA: E of Tipitapa toward Rama at Km 43, edge of highway, *Porter 1213* (DS, GH, IJ). MASAYA: Masaya, *Baker 211* (ARIZ, POM), *665* (US). CHONTALES: near Juigalpa, waste ground, ca. 160 m, *Standley 9316* (F).

COSTA RICA. GUANACASTE: Catalina, forest, *Stork 2769* (F, MICH). PUNTARENAS: Mata de Limón, along railroad track, 7 m, *Porter 1187* (CR, GH).

PANAMA. PANAMA: near beach at Nueva Gorgona, *Duke 4499* (MO).

JAMAICA. ST. ANDREW: St. Benedict's School, E of Harbour View, bank, ca. 25 ft, *Porter 1034* (GH, IJ, UCWI).

PUERTO RICO. GUAYAMA: near Salinas, sandy plain, *Britton, Britton & Brown 6045* (NY).

VIRGIN ISLANDS. ST. THOMAS: along road, *Eggers,* June 1887 (US). TORTOLA: Experiment Station, waste places, *Fishlock 131A* (NY).

LEEWARD ISLANDS. ST. BARTHELEMY: Gustavia. *Questel 164, 201* (NY). SABA: *Boldingh 1951B* (NY). ST. EUSTATIUS: Oranjestad to Ft. de Windt, along road, *Stoffers 3500* (IJ). ST. KITTS: *Walsh,* Sept 1889 (NY). ANTIGUA: Cedar Valley, cultivated lands in drier districts, *Box 871* (BM, US). MONTSERRAT: O'Garras estate, S of Plymouth, track to cove, *Proctor 19029* (BM, IJ). GUADELOUPE: Viux Habitants, 10 m, *Questel 2167* (US).

WINDWARD ISLANDS. MARTINIQUE: Morne Vert, dry thicket, 350 m, *Stehlé & Stehlé 4784* (US). ST. VINCENT: sandy soil near seashore, *Smith & Smith 388* (UCWI). BARBADOS: Hastings, neglected gardens, *Waby 2* (F, US). BEQUIA: open lands and clearings, *Joseph B241* (NY). CANOUAN: sandy beach trail, *Howard 11096* (BM, IJ, NY). GRENADA: St. George's, *Broadway,* 16 Aug 1905 (F, GH).

TOBAGO: Stoer Bay direction, open land, *Broadway 9065* (A, BM, MO).

CURAÇAO: Groot St. Martha, sea level, *Fr. Arnoldo 2116* (US).

COLOMBIA. BOLIVAR: near Cartagena, *Bro. Heriberto 1, 72, 301* (US). ATLANTICO: Salgar, roadside, *Porter 1111* (COL, DS, GH, IJ). MAGDALENA: Santa Marta, 250 ft, *H. H. Smith 572* (BM, COL, F, GH, MICH, MO, NY, PH, TEX, UC, US, WIS). GUAJIRA: *s. coll. 596* (US). BOYACA: Puerto Boyacá, *Romero Castañeda 3062* (COL). CUNDINAMARCA: Arbeláez, 1400 m, *Garcia Barriga 4878* (COL, US). TOLIMA: Armero, *Barreneche E. 9* (COL).

VENEZUELA. ANZOATEGUI: Guanta, roadside, ca. sea level, *Potter 5149* (GH, US). NUEVA ESPARTA: El Valle, Margarita I., *Miller & Johnston 7* (ARIZ, BM, F, GH, MO, NY, POM, US).

ECUADOR. MANABI: Bahía, *Mille 1140, 1994* (F). GUAYAS: Playas, sandy seashore, *Asplund 5063* (CAS, F, NY, US). LOJA: Río Guayabas 5 km NW of Catamayo, dry brushy thorn-forest flats, 1300 m, *Fosberg & Giler 22937* (COL, US).

PERU. PIURA: Pariñas Valley, *Haught F-51* (F), *147* (F, GH, NY, PH, US).

GHANA: Accra, near beach, *Enti,* 31 May 1964 (GH).

Two specimens of *Kallstroemia pubescens* have been seen that were supposedly collected in the southwestern United States. These are "*Walter H. Evans,* 23 June 1891, Ft. Hancock, Texas" (MO) and "*Dr. Woodhouse,* 29 Sept. 1851. N. M. Camp No. 6, Little Colorado" (PH), the latter from Apache County, Arizona. These collections are sufficiently removed from the known range of the species, which is essentially tropical, to cast doubt on the authenticity of the label data. The problem of the wrong label being applied to a specimen also has been encountered in *K. grandiflora* and *K. maxima.*

A mixed collection of *Kallstroemia pubescens* and *K. maxima* from Georgia, *Beyrich s. n.* (MO), probably is a product of a misapplied or lost label. A collection of this species from Florida, *Chapman s. n.* (MO), is labeled "Cult."

COMMON NAMES. Most of the common names applied to *Kallstroemia pubescens* are identical to those used in the same area to designate the superficially very similar *K. maxima.* Common names of which I am aware are Abrojo (Colombia); Angglo Boobo (Bonaire, Curaçao); Anglo Bobo (Aruba, Bonaire, Curaçao); Coclí (Colombia); Golondrina (Costa Rica); Huistolohuetzli (Guerrero, Mexico); Pourpier Bâtard (Guadeloupe, Martinique); Pourpier Jaune Courant (Martinique); Pourpier Marron (Guadeloupe); Verdolaga (Colombia, El Salvador); and Verdolaguilla (Nayarit, Mexico). In addition, Irvine (1930, p. 419) reports that in Ghana the plant is called Akwamfãnu, and that "the vernacular name comes from 'Okwan afãnu,' which means 'on both sides of the road,' probably because it is a common weed along bush paths."

TAXONOMY. The name *Kallstroemia longipes* has been given to somewhat larger than average specimens of *K. pubescens* from southwestern Mexico. However, specimens at this extreme in variation are found scattered throughout the range of *K. pubescens* and probably are due to optimum growth conditions.

As has been indicated above, this species was first described from Africa, 80 years before being recognized as distinct from *K. maxima* in the West Indies, where it is indigenous. It undoubtedly was introduced into West Africa very early, as is attested by its wide use in the native *materia medica* (cf., Irvine, 1930). Introduction probably came about through the activities of the slave trade between West Africa and the West Indies, which began in the first half of the sixteenth century (Penrose, 1952).

VARIATION. This species is rather constant in its morphological characters, especially for one of such a wide geographical range, except for the quantitative variation in size mentioned above. Almost all specimens seen had stem trichomes that were antrorse, but in *Haught F-161* (F) and *Haught 262* (NY) from Peru, these trichomes were retrorse, similar to those in *K. peninsularis.* The anther and pollen color in most populations is red, but populations in which it is yellow occasionally are found.

RELATIONSHIPS. *Kallstroemia pubescens* is most closely related on the one hand to *K. maxima,* and on the other to the southern South American *K. tucumanensis.* Morphological comparison of *K. maxima* and *K. pubescens* will be found above.

The initial recognition of the close relationship between *Kallstroemia pubescens* and *K. tucumanensis* was by Svenson (1946b), who considered that specimens of the former from Ecuador and Peru were conspecific with those of the latter from Argentina. However, *K. tucumanensis* may be easily distinguished from *K. pubescens* by its usually two to three pairs of leaflets, pale yellow to yellow-orange flowers 4–8 mm in diameter, yellow anthers and pollen, ovoid ovary, strigose fruit, and capitate ten-ridged stigma.

4. **Kallstroemia tucumanensis** Desc., O'Don. & Lourt., Lilloa 4:218. 1939

TYPE: Argentina, Tucumán: Tapia to Vipos, elev. 750 m; 4 February 1939, *C. A. O'Donell & A. Lourteig s. n.* (LIL, holotype, not seen; DS, F, GH, NY, UC, isotypes).

Annual; *stems* prostrate to decumbent, 1–6 dm long, hirsute and sericeous with apically-directed white trichomes; *stipules* 2.5–3 mm long, ca. 1 mm wide; *leaves* obovate, 3–5.5 cm long, 1.5–3 cm wide; *leaflets* 2–3(–4) pairs, oblong, appressed-hirsute, veins and margins sericeous, 7–19 mm long, 5–11 mm wide, ultimate pair usually largest; *peduncles* shorter than subtending leaves, scarcely thickened distally, 5–6 mm long in flower, 12–20 mm long and straight or curved in fruit; *flowers* pentamerous, 4–8 mm in diameter; *sepals* subulate, 4–5 mm long, 1–2 mm wide, ca. as long as petals, hispidulous with fine white trichomes of two lengths, longer than style in flower, spreading from base of mature fruit and little longer than mericarps, margins becoming sharply involute, persistent; *petals* pale yellow to yellow-orange, narrowly obovate, 3–5 mm long, 2–3 mm wide, marcescent; *stamens* as long or longer than style; *anthers* globose, less than 1 mm in diameter, they and pollen yellow; *ovary* ovoid, ca. 1.5 mm in diameter, pubescent; *style* 1 mm long, stout, conical, strigose; *stigma* capitate, 10-ridged, less than 1 mm long, papillose; *fruit* ovoid, 5 mm in diameter, strigose; *beak* 2–3.5 mm long, stout, conical, strigose to stigma base; *mericarps* ca. 4 mm high and 1 mm wide, abaxially more or less tubercled and laterally grooved, sides pitted, adaxial edge angled. *Fig. 4a, 4b. Map 6.*

FLOWERING DATES. November through April following summer rains.

DISTRIBUTION AND HABITAT. Semiarid southern Bolivia and northwestern Argentina *(Map 6)*. Disturbed areas, sandy riverbanks, railroad embankments, and roadsides from 420 to 1250 m. Sympatric over much of its range with *Kallstroemia tribuloides.*

DISTINGUISHING CHARACTERISTICS. *Kallstroemia tucumanensis* is easily recognized by its combination of obovate leaves, usually two to three pairs of leaflets, pale yellow to yellow-orange flowers 4–8 mm in diameter, hispidulous sepals spreading from the base of the mature fruit and appearing linear or linear-lanceolate through the margins becoming sharply involute, yellow anthers and pollen, ovoid ovary, capitate ten-ridged stigma, and strigose fruit with a stout conical beak shorter than the fruit body. *Kallstroemia tribuloides,* the only other species in the genus known from the same area as *K. tucumanensis,* is not likely to be confused with the latter. It differs in having elliptical leaves, three to six pairs of leaflets, orange flowers 1½–2½ cm in diameter, hirsute and strigose sepals clasping and almost entirely covering the mature mericarps, sepal margins not becoming involute, orange anthers and pollen, a conical ovary, an oblong ten-ridged stigma, and a glabrous fruit with a cylindrical beak as long or longer than the fruit body.

SPECIMENS EXAMINED. BOLIVIA. SANTA CRUZ: Cabezas, 420 m, *Peredo 250* (A). TARIJA: Villamontes, *Pflanz 4041* (US).

ARGENTINA. JUJUY: Perico, roadsides, *Parodi 9070* (GH). SALTA: La Viña *Spegazzini 10025* (NY); Tiro Federal *Correa 19* (GH, NY). CHACO: La Fidelidad, *Jorgensen 1989* (GH, MO, US). TUCUMAN: Cerro del Campo, dry hard clay soil, 900 m, *Venturi 7710* (BM, CAS, GH, MO, US); La Madrid, 430 m, *Bailetti 342* (F, GH); Tapia, 700 m, *Rodriguez 223* (F, GH), railroad embankments, 750 m, *Venturi 1077* in part (GH, US); Vipos, 786 m, *Schreiter,* 24 Jan 1926, in part (A, UC). CATAMARCA: Balcozna, sandy riverbank, 1250 m, *Venturi 7142* (CAS); Campo del Pilciao, *Schickendantz 168* in part (F, UC, US). SANTIAGO DEL ESTERO: La Banda, *Lillo 6175* (F, GH); La Dársena, *Meyer 12718* (MO); Las Termas, *Legname 5* (CAS). CORDOBA: Km 969, Dept. Ischilin, *Brizuela 897* (SMU). MENDOZA: Rancho de Tofora, 500 m, *Ruíz Leal 9021* (ARIZ).

This species also has been reported from the Argentinean states of La Rioja and Entre Rios (Descole, *et al.,* 1939) and *San Luis* (Ruíz Leal, 1947).

TAXONOMY. Svenson (1946b) considered *Kallstroemia tucumanensis* to be conspecific with *K. adscendens,* but the two are distinct. The latter is endemic to the Galápagos Islands, Ecuador.

RELATIONSHIPS. *Kallstroemia tucumanensis* is most closely related to the more northerly *K. pubescens.* The latter differs from *K. tucumanensis* in having mostly three pairs of leaflets, flowers 9–15 mm in diameter, obovate petals 6–11 mm long and 5–8 mm wide that are usually white, anthers and pollen only occasionally yellow, a pyramidal ovary, a densely appressed short-pilose fruit with a beak 5–8 mm long, and an obscurely ten-lobed stigma.

5. **Kallstroemia hirsutissima** Vail in Small, Fl. SE. U. S. 670. 1903

TYPE: New Mexico, Dona Ana Co.: plains S White Sands, elev. 4200 ft, 28 August 1897, *E. O. Wooton 564* (NY, holotype; MO, NY, US, isotypes).

Annual; *stems* prostrate, 1.5–7 dm long, copiously sericeous and hirsute with white or gray apically-directed trichomes, forming a dense carpet-like mat; *stipules* 3–6 mm long, ca. 1 mm wide; *leaves* obovate, 1–4 cm long, 2–4 cm wide, copiously and conspicuously pubescent; *leaflets* 3–4 pairs, broadly elliptical to oblong-ovate or broadly ovate, densely hirsute and conspicuously ciliate, veins and margins sericeous, 12–19 mm long, 5-11 mm wide, terminal pair largest; *peduncles* shorter than subtending leaves, thickened distally, 5–12 mm long, curved or straight in fruit; *flowers* pentamerous, less than 1 cm in diameter; *sepals* subulate, 2.5–4 mm long, ca. 1 mm wide, hirsute and sparingly strigose, in flower ca. as long as style, in fruit clasping mature mericarps and ca. 1/2 as long as them, only scarious margins becoming involute, persistent; *petals* yellow, fading white or orange, obovate, 2–4 mm long, ca. 1.5 mm wide, marcescent; *stamens* as long as style; *anthers* ovoid, less than 1 mm in diameter, they and pollen yellow; *ovary* globose, pubescent, ca. 1 mm in diameter; *style* very short, ca. 1/3–1/2 as long as ovary, stout, broadly conical, pubescent; *stigma* more or less clavate, appearing almost sessile on ovary, 10-ridged, papillose; *fruit* broadly ovoid, 4–5 mm high, 6–8 mm wide, strigillose; *beak* 1–4 mm long, shorter than fruit body, hirsute with short white trichomes to stigma base, conical above, base broadly conical; *mericarps* 4 mm high, ca. 1 mm wide, abaxially prominently tubercled, sides pitted, adaxial edge angled. *Fig. 5a, 5b. Map 7.*

FLOWERING DATES. Following the summer rains from June to October, but mainly from July to September.

DISTRIBUTION AND HABITAT. Chihuahuan Desert and adjacent areas of semiarid grassland from southeastern Arizona to Tamaulipas and southern Texas *(Map 7).* Found from sea level to about 1700 m, mainly at higher elevations. Sympatric with *Kallstroemia californica, K. grandiflora, K. parviflora,* and *K. perannans,* and slightly overlapping with *K. maxima* and *K. rosei* in Nuevo Leon and Tamaulipas.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia hirsutissima* has copiously pubescent stems which form a dense carpet-like mat, obovate leaves, three to four pairs of conspicuously ciliate leaflets, yellow flowers less than 1 cm in diameter, hirsute and sparingly strigose sepals which clasp the mature mericarps, only their scarious margins becoming involute, a stout broadly conical very short style that is ⅛–½ as long as the ovary, the more or less clavate ten-ridged stigma appearing almost sessile on the ovary, a broadly ovoid strigillose fruit 4–5 mm high and 6–8 wide, and a conical beak 1–4 mm long, hirsute with a ring of short white trichomes. *K. hirsutissima* is unlikely to be confused with any other species of the genus growing in the same area.

SPECIMENS EXAMINED. UNITED STATES. ARIZONA. Pima Co.: Tucson, *Lemmon,* Oct 1880 (MO). Santa Cruz Co.: near Elgin, *Peebles, Harrison & Kearney 3349* (ARIZ, US). Cochise Co.: Benson, *Harrison 8227* (ARIZ, US); Douglas, *W. W. Jones,* 12 Sept 1948 (RSA); San Bernardino Ranch, *Mearns 597* (US). NEW MEXICO. Locality unknown: east side Rio Grande, *Wright 912* (BM, GH, US). Chaves Co.: 20 mi. S of Roswell, *Earle & Earle 307* in part (POM). TEXAS. Locality unknown: Pecos Valley, *Havard,* Sept 1881 (F, US); Lander, *Knicker,* 24 June 1916 (GH, TEX); Ft. Stockton to Alpine, *Tharp,* 18 Aug 1935 (GH, MO, UC). Jeff Davis Co.: Ft. Davis, *M. S. Young,* 5 Sept 1918 (TEX). Brewster Co.: Alpine, *Tharp 3512* (TEX, US). Dimmit Co.: without locality, *Tharp,* 24 June 1941 (GH, MO, TEX). Kerr Co.: Kerrville, *Cook 17, 19* (LL). Kinney Co.: creek bottom 6 mi. E of Bracketville, gray-brown calcareous silt, *Shinners 30833* (SMU). Bexar Co.: San Antonio, *Ball 908* (US), *Cook,* 1906 (LL), *Havard 1704* (MO), *Schulz 783* (US). Duval Co.: San Diego, *Croft 198* (NY). Cameron Co.: Brownsville, open grounds and dry fields, clay soil, 10 m, *Runyon 1857* (US); Santa Ana National Wildlife Refuge, gravel pile, *Fleetwood 3839* (TEX).

MEXICO. LOCALITY UNKNOWN: Limpia Valley, *Edwards 78* in part (MICH). CHIHUAHUA: 10 km. E of Barreal, dry sandy hillsides, *Stewart 662* (GH); 25 mi. SE of Camargo, 4500 ft, *Shreve 8874* (ARIZ, GH); between Casas Grandes and Sabinal, 5000–5500 ft, *Nelson 6376* (MICH, NY, US); Chihuahua, *LeSeuer 253* (GH, SMU); hills and plains near Chihuahua, *Pringle 679* (BM, CAS, F, MICH, NY, PH, RSA, US); 5 mi. E of Ciudad Jiménez, ca. 4500 ft, *S. S. White 2143* (GH, MICH); Cuauhtémoc, *LeSeuer 253* (F, TEX); broad valley 25 km. NW of Jaco toward Victoria, silty flat, *Stewart 678* (GH); 5.5 mi. S of Ojinaga toward Alamos Chapo, outwash from saline shales, *Johnston 8004* (GH). COAHUILA: arroyo between Grutas Villa Garcias SW of Saltillo, ca. 5500 ft, *Bell & Duke 16578* (MO); NE margin of Laguna de Leche, flooded soil, *Johnston 8595* (GH); Llano de Guaje, margins of playa between Lomas del Aparejo and Tanque La India, *Johnston & Muller 788* (GH); 2 km. E of Tanque La India, flats in bottom of bolson, *Stewart 1166* (GH); 12 mi. N of Monclova toward Piedras Negras, silty mesquite thicket, *Johnston 7190* (GH, US); valley floor E of Puerto del Caballo toward Tanque Jerico, barreal, *Johnston 8335D* (GH); valley between low hills 15 mi. S of Sabinas, *Waterfall 16656* (SMU, UC); dry valley floor 10–15 km. E of San Antonio toward Buenavista, savanetta, *Johnston,* 21 Aug 1941 (GH); 5 mi. NW of Zenzontle toward

San José, sabaneta, *Johnston & Muller 971* (GH). NUEVO LEON: Monterrey, *Edwards s. n.* (NY); near Monterrey, *Edwards 140* in part (MICH); desert 21 mi. W of Monterrey, along arroyo, *Waterfall & Wallis 13182* (SMU); along highway 40 mi. S of Monterrey, *Drushel 9327* (NY). TAMAULIPAS: 0.5 mi. S of Huisachal, *Stanford, Lauber & Taylor 2172* (GH, NY, US); near Victoria, ca. 320 m, *Palmer 218* in part (MO). SAN LUIS POTOSI: Las Palmas, *Rose & Hough 4877* (US).

COMMON NAME. Carpetweed.

RELATIONSHIPS. *Kallstroemia hirsutissima* is most closely related to *K. curta,* a species of Hispaniola and the southern islands of the Netherlands Antilles. The latter differs in having usually three pairs of leaflets, the sepals spreading from the base of the mature fruit, and their margins becoming sharply involute, white to yellow-orange petals, a style about as long as the ovary, and the ovoid fruit 4–5 mm in diameter with the strigose beak 1½–2 mm long.

6. **Kallstroemia curta** Rydb. in Boldingh, Fl. Nederland. West-Ind. Eilanden 230. 1913

TYPE: West Indies, Curaçao: rocky coastal hill, St. Joris Bay, prostrate branches 8 dm long; 20–27 March 1913, *N. L. Britton & J. A. Shafer 3096* (NY, lectotype; F, PH, US, isotypes). This name usually is attributed to "Rydb. in Boldingh, Fl. Dutch West Ind. Islands 2:45. 1914.", but the above citation is its first valid publication. No specimens were cited in the 1913 publication, but three were listed in 1914. Of these three, *Britton & Shafer 3096* at NY bears the word "Type" in Rydberg's handwriting. Therefore, it is confirmed to be the lectotype.

Kallstroemia incana Rydb. in Britt., Bull. Torr. Bot. Club **51**:3. 1924. TYPE: West Indies, Dominican Republic: Barahona, sea level, flower yellow, July 1910, *Fr. Miguel Fuertes 418* (NY, holotype; GH, IJ, MO, US, isotypes).

Annual; *stems* prostrate, 2–3 dm (rarely to 1 m) long, hirsute and sericeous with white apically-directed trichomes, usually forming a dense carpet-like mat; *stipules* 2–4 mm long, ca. 1 mm wide; *leaves* obovate, 1–4 cm long, 2–3 cm wide, usually appearing grayish because of dense pubescence; *leaflets* 3(–4) pairs, ovate, densely appressed-hirsute, veins and margins sericeous, becoming glabrate, 9–15 mm long, 5–10 mm wide, terminal pair largest; *peduncles* shorter than leaves, 2–3 mm long in flower, in fruit 2–13 mm long and curved or straight; *flowers* pentamerous, less than 1 cm in diameter; *sepals* subulate, 2.5–4 mm long, 1–2 mm wide, hirsute and strigose, longer than style in flower, shorter than beak and spreading from base of mature fruit, margins becoming sharply involute, persistent; *petals* white to yellow-orange, elliptical to obovate, 3–4 mm long, marcescent; *stamens* as long as style; *anthers* globose, much less than 1 mm in diameter, they and pollen yellow; *ovary* ovoid, ca. 1 mm in diameter, pubescent; *style* ca. as long as ovary, stout, conical, strigose; *stigma* clavate, 10-ridged, less than 1 mm long, papillose; *fruit* ovoid, 4–5 mm in diameter, strigillose; *beak* 1.5–2 mm long, stout, conical above, base widely conical, strigose; *mericarps*

3 mm high, ca. 1 mm wide, abaxially tubercled, sides pitted, adaxial edge angled. *Fig. 6a, 6b. Map 8.*

FLOWERING DATES. Known to flower in March in Curaçao and in July in Cuba, but flowering from January through October in Hispaniola. As in the other Caribbean species, seed germination, plant growth, and flowering probably take place at any time of the year following sufficient rainfall and appropriate temperatures.

DISTRIBUTION AND HABITAT. Disturbed areas from sea level to 1300 m, mainly at lower elevations. Apparently native to Hispaniola and introduced into Cuba and the Netherlands Antilles *(Map 8)*. Sympatric with *Kallstroemia maxima* in Hispaniola and Cuba, and with *K. pubescens* in the Netherlands Antilles.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia curta* may be recognized by its stems forming a dense carpet-like mat, which appears grayish because of the dense pubescence, obovate leaves, usually three pairs of densely pubescent leaflets, white to yellow-orange flowers less than 1 cm in diameter, hirsute and strigose sepals which spread from the base of the mature fruit and have sharply involute margins, clavate ten-ridged stigma, and ovoid strigillose fruit with a conical beak 1½–2 mm long. This species is apt to be confused with *Kallstroemia pubescens* in the southernmost part of its range. The latter may be distinguished by its more upright open habit, peduncles 1–3½ cm long in fruit, usually white flowers 9–15 mm in diameter, hispidulous sepals, pyramidal ovary, capitate obscurely ten-lobed stigma, and densely appressed short-pilose fruit with a beak 5–8 mm long.

SPECIMENS EXAMINED. CUBA. ORIENTE: Estación Naval de Caimanera, *Bro. Hioram 3958* (US).

HAITI. NORD-OUEST: near Bassin Bleu, road to Port de Paix, roadbed, *Leonard & Leonard 14729* (US); near Le Mole St. Nicolas, Mole gorge, rock crevices, *Leonard & Leonard 13322* (US); Presquîle du Nord-Ouest, *Ekman H4038* (US). ARTIBONITE: Cap St. Marc, railroad track near lighthouse, *Ekman H6652* (A); road SE of Gros Morne, ca. 235 m, *Leonard 9972* (GH, NY, UC, US); near Ennery, Puilboreare road, *Leonard 8813* (GH, NY, UC); Hinche, Savane-Papaye, 225 m, *Ekman H6011* (IJ, US). OUEST: Port-au-Prince, Plaine de Léogane, *Buch 1173* (IJ).

DOMINICAN REPUBLIC. SANTIAGO: Hato del Yaque, fields, *Ekman H15981* (US); Valverde, *Uniola* savannah, ca. 100 m, *Ekman H13107* (US). AZUA: San Juan, fields, *Ekman H13395* (A, US). BARAHONA: Rincon, 25 m, *Fr. Fuertes 1352* (NY, US); near Rincon, 1300 m, *Fr. Fuertes 1353* (GH); La Salina, decomposed salt rock, *Howard & Howard 8410* (GH, NY, US).

CURAÇAO. Without locality, *Read s.n.* (PH).

Boldingh (1914) reports *Kallstroemia curta* from the island of Aruba, and Arnoldo (1964) records it from this island and also from Bonaire, but the only specimens I have seen from the southern Caribbean are those from Curaçao cited above.

COMMON NAMES. No common names have been recorded for this species in Cuba or Hispaniola. However, in Aruba, Bonaire, and Curaçao it is known by the same names as is *Kallstroemia pubescens:* Angglo Boobo or Anglo Bobo.

TAXONOMY. In publishing *Kallstroemia incana,* Rydberg indicated its affinities with *K. curta,* but stated that it differed in being "more canescent, more branched, with shorter internodes and smaller leaves, and the beak different, not at all swollen." Except for the beak, these differences all are of vegetative characters that prove to be very plastic in all species of the genus where environmental conditions vary. Upon examination of the specimens cited above, all differences given by Rydberg and others, both of a vegetative and floral nature, overlap between the populations in Hispaniola and Cuba and those from Curaçao. The more northerly collections tend to be more pubescent than those from Curaçao, but this single difference hardly makes them worthy of taxonomic recognition, even at the subspecific level.

RELATIONSHIPS. *Kallstroemia curta* is most closely related to *K. hirsutissima,* a species of northern Mexico and the southwestern United States. *Kallstroemia hirsutissima* differs in having three to four pairs of leaflets, hirsute and sparingly strigose sepals which clasp the mature mericarps, with only their scarious margins becoming involute, yellow petals, a very short stout broadly conical style that is ⅓–½ as long as the ovary, the stigma appearing to be almost sessile on the ovary, and a broadly ovoid strigillose fruit that is 4–5 mm high and 6–8 wide, with a 1–4 mm long beak which is hirsute with a ring of short white trichomes.

7. **Kallstroemia adscendens** (Anderss.) Robins., Proc. Amer. Acad. 38:156. 1902

Tribulus adscendens Anderss., Svensk. Vet-akad. Handl. **1853**:245. 1854. TYPE: Ecuador, Galápagos Islands: "Hab. locis graminosis, siccis regionis inferioris insularum Chatham et Charles (Ipse)," *N. J. Andersson s. n.* (holotype presumably at S, not seen; GH, isotype).

Tribulus maximus var. *adscendens* (Anderss.) Anderss., *op. cit.* **1857**:107. 1861. I follow Rose (1892) and Robinson (1902) in assuming that Andersson intended to make this combination, although his citation might lead one to the conclusion that he considered *T. adscendens* to be a synonym of *T.*

maximus. This is a valid assumption, as Andersson later (1861b) referred to this taxon as "*T. maximus* var. A.", A. indicating "of Andersson."

Annual; *stems* prostrate to decumbent, to several dm long, sericeous and hirsute with apically-directed white trichomes; *stipules* 3–4 mm long, ca. 1 mm wide; *leaves* elliptical, to ca. 2 cm long and 1 cm wide; *leaflets* 2–3 pairs, oblong to subfalcate, appressed-hirsute, veins and margins sericeous, to almost glabrate, 9–18 mm long, 3.5–7 mm wide, penultimate pair largest; *peduncles* in fruit longer than subtending leaves and sharply bent at base and straight above, slightly thickened distally, 5–21 mm long; *flowers* pentamerous, less than 1 cm in diameter; *sepals* subulate, 3–3.5 mm long, ca. 1 mm wide, little shorter than petals, hirsute and strigose, longer than style in flower but not extending beyond tops of mature maricarps in fruit, spreading from base of mature fruit and margins becoming sharply involute, persistent; *petals* yellow, obovate, ca. 4 mm long, 2–3 mm wide, marcescent; *stamens* as long as style; *anthers* globose, much less than 1 mm in diameter, they and pollen yellow; *ovary* ovoid, ca. 1.5 mm in diameter, strigose; *style* ca. 1 mm long, stout, conical, strigose; *stigma* clavate, 10-ridged, less than 1 mm long, papillose; *fruit* ovoid, 3–4 mm in diameter, strigose; *beak* ca. 2 mm long, ca. 1/2 as long as fruit body, conical, strigose; *mericarps* ca. 3 mm high and 1 mm wide, abaxially cross-ridged and tubercled, sides pitted, adaxial edge angled. *Fig. 7a, 7b. Map 9.*

FLOWERING DATES. Known to flower from April through June, during the last half of the rainy season.

DISTRIBUTION AND HABITAT. Endemic to the Galápagos Islands, Ecuador *(Map 9)*. Found on the beaches and lower slopes of the arid coastal zone of the islands.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia adscendens* may be recognized by its elliptical leaves, two to three pairs of leaflets, fruiting peduncles longer than the subtending leaves, yellow flowers less than 1 cm in diameter, hirsute and strigose sepals spreading from the base of the mature fruit, with the margins becoming sharply involute, and tubercled strigose fruit with the beak about ½ as long as the fruit body.

SPECIMENS EXAMINED. LOCALITY UNKNOWN. *Andersson s. n.* (NY), 1852 (MO).

BARRINGTON ISLAND. Bahía de Barrington, NE part of island, in stony ground, ca. 325 ft, *Snow 113* (DS). Along intermittent water course 1/4 mi inland to SW from NE corner of island, *Wiggins & Porter 587* (CAS).

CHAMPION ISLAND. Without locality, *Wiggins & Porter 513* (CAS).

CHARLES ISLAND. Post Office Bay, beach and environs at E end, *Wiggins & Porter 558* (CAS).

CHATHAM ISLAND. Punta Pitt, *Snow 244* (DS). Along road from Wreck Bay to El Progreso, *Wiggins & Porter 368* (CAS).

DUNCAN ISLAND. Without locality, Agassiz, 2 Apr 1891 (GH, US). Lower slopes, middle eastern part of island, *Howell 9819* (CAS, GH).

GARDNER ISLAND. Without locality, *Snodgrass & Heller 615* (DS, GH). Common over much of island, *Wiggins & Porter 473* (CAS).

HOOD ISLAND. Without locality, *Snodgrass & Heller 756* (GH). On beach, Gardner Bay, *Howell 8653* (CAS). Along S side of Punta Suárez, *Wiggins & Porter 489* (CAS). W end inland from Punta Suárez, *Wiggins & Porter 457* (CAS).

VARIATION. Although Andersson described *Kallstroemia adscendens* as having a five-carpellate fruit with two single-seeded locules per carpel, examination of available material shows this species to be a typical *Kallstroemia* with ten one-seeded mericarps.

RELATIONSHIPS. Robinson (1902) was the first to suggest the close relationship of *Kallstroemia adscendens* and the North American *K. californica* (as *K. brachystylis*). The latter may be distinguished from *K. adscendens* by its hirsute and strigose stems, three to seven pairs of leaflets, fruiting peduncles shorter than the subtending leaves, usually deciduous sepals, strigillose fruit with prominent tubercles that may reach 1½ mm in length, and cylindrical beak that is little shorter than the fruit.

8. **Kallstroemia californica** (S. Wats.) Vail, Bull. Torr. Bot. Club 22:230. 1895

Tribulus californicus S. Wats., Proc. Amer. Acad. **11**:125. 1876. TYPE: Mexico, Baja California: eastern side of the peninsula, 1870, *Palmer s. n.* (GH, holotype). As indicated elsewhere (Porter, 1963), the type probably was collected in January or February, 1870, in southern Baja California.

Kallstroemia brachystylis Vail, Bull. Torr. Bot. Club **24**:206. 1897. TYPE: New Mexico, Dona Ana Co.: mesa near Las Cruces, alt. 3900, 12 August 1895, *E. O. Wooton s. n.* (NY, holotype; GH, isotype).

Tribulus brachystylis (Vail) Robins. in Gray, Syn. Fl. N. Amer. **1**:354. 1897.

Kallstroemia californica var. *brachystylis* (Vail) Kearn. & Peeb., Jour. Wash. Acad. Sci. **29**:485. 1939.

Annual; *stems* prostrate to decumbent, 1–6.5 dm long, hirsute and strigose with apically-directed white trichomes, becoming glabrate; *stipules* 1.5–5 mm long, ca. 1 mm wide; *leaves* elliptical to occasionally obovate, 1.5–6 cm long, 1–3 cm wide; *leaflets* 3–6(–7) pairs, elliptical to oval, appressed-hirsute, veins and margins sericeous, becoming glabrate, 4–17 mm long, 1.5–9 mm wide, middle pairs largest; *peduncles* shorter than subtending leaves, thickened distally, to 15 mm long in flower, in fruit 8–33 mm long and bent sharply at base and straight above; *flowers* pentamerous, to 1 cm in diameter; *sepals* lanceolate, 2–4 mm long, 1–1.5 mm wide, strigose or hirsutulous and strigillose, margins become involute, usually deciduous, if persistent spreading from base of mature fruit and not reaching tops of mature mericarps; *petals* yellow, drying white or orange, obovate, 4–6 mm long, 2.5–3 mm wide, marcescent; *stamens* as long as style; *anthers* ovoid, less than 1 mm in diameter, they and pollen yellow; *ovary* ovoid, ca. 1 mm in diameter, pubescent; *style* shorter than ovary, stout, conical, strigillose; *stigma* clavate, 10–ridged, less than 1 mm long, papillose; *fruit* ovoid, 3–5 mm wide including tubercles, to 4 mm high, strigillose; *beak* 2–4 mm long, shorter than fruit body, cylindrical, base conical, glabrous or base sparingly strigillose; *mericarps* ca. 3 mm high and 1 mm wide, abaxially with 4–5 blunt oblong tubercles that may reach 1.5 mm long, tubercles becoming more prominent as fruits mature, sides pitted or smooth, adaxial edge angled. *Fig. 8a, 8b. Map 10.*

FLOWERING DATES. Following summer rains (mainly July through October) through most of the range, but occasionally beginning in March in Texas, and August through March (following both fall and winter rains) in Baja California.

DISTRIBUTION AND HABITAT. Flat sandy and disturbed areas of the Sonoran Desert across the northern Chihuahuan Desert to the semiarid grasslands of Tamaulipas and southern Texas; also along the west coast of Mexico to southern Sinaloa and the Tres Marias Islands, and extending into northern Arizona and southern Baja California *(Map 10).* Found from sea level to about 1600 m, mainly at lower elevations. Sympatric with *Kallstroemia grandiflora, K. hirsutissima, K. parviflora, K. peninsularis,* and *K. perennans,* and slightly overlapping in the southwest with *K. maxima* and *K. pubescens* and in the southeast with *K. maxima* and *K. rosei.*

DISTINGUISHING CHARACTERISTICS. *Kallstroemia californica* is easily recognized by the combination of its hirsute and strigose stems, usually elliptical leaves, three to seven pairs of leaflets, fruiting peduncles shorter than the subtending leaves, yellow flowers less than one centimeter in diameter, usually deciduous sepals, strigillose fruit with prominent tubercles that may reach 1½ mm in length, and a cylindrical beak that is little shorter than the fruit body. Although there may be some overlap in these characteristics with other species in the same geographical area, in combination they readily distinguish *Kallstroemia californica* from its congeners.

REPRESENTATIVE SPECIMENS EXAMINED. UNITED STATES. CALIFORNIA. San Bernardino Co.: Conrise Valley, sands, *Jaeger,* 15 Sept 1925 (POM); 8 mi W of Ludlow, *Ferris 1326* (DS). Riverside Co.: hay fields, *M. E. Jones 24963* (CAS, GH, MO, NY, POM, UC); Palm Springs, *M. E. Jones,* 7 Sept 1925 (DS). San Diego Co.: SW part of Colorado Desert, *Orcutt,* 8 Oct 1890 (US). Imperial Co.: Heber, *Abrams 4002* (DS, F, GH, MO, NY, POM); sand dunes N of Picture Rocks, *Reed 6697* (POM). ARIZONA. Mohave Co.: Ash Creek, near Sandy River, *Braem 563* (DS).

Coconino Co.: Havasupai Canyon, fields and waste places, *Clover 7065* (ARIZ, MICH), *7138* (MICH); W bank of Colorado River 1.5 mi below Lee's Ferry, 3800 ft, *Cutler 3149* (DS, GH, MO, NY). Yavapai Co.: Verde, *W. W. Jones,* 23 July 1920 (UC, US). Gila Co.: San Carlos, *Hoyt,* Aug 1892 (NY). Yuma Co.: near Mohawk, *Peebles, Harrison & Kearney 4924* (ARIZ, US); Yuma, mesas and depressions, *Thornber,* 24 Sept 1912 (ARIZ, UC). Maricopa Co.: Litchfield, *Peebles, Harrison & Kearney 4525* (ARIZ). Pinal Co.: near Phoenix, roadsides, *Kearney 123* (US); Sacaton, *Peebles 10597* (ARIZ, POM, US). Pima Co.: 4 mi W of Mission San Xavier, near shallow arroyo, *Wiggins & Rollins 57* (ARIZ, DS, GH, MICH, MO, NY, US); Tucson, 2400 ft, *Thornber 234* (ARIZ, DS, MO, NY, POM, UC). Graham Co.: Clifton, *Davidson 17* (DS). Santa Cruz Co.: hills near Nogales, *Peebles, Harrison & Kearney 5568* (ARIZ, US). Cochise Co.: Dos Cabezas, *Orcutt 2229* (MO); San Simon, *Thornber 5682* (ARIZ). NEW MEXICO. Grant Co.: Red Rock, *Goldman 1539* (US). Luna Co.: Nutt, 1420 m, *Eggleston 16262A* (US). Dona Ana Co.: Mesilla Valley, ca. 3850 ft, *Wooton & Standley 3189* (ARIZ, DS, F), *27249* (WIS); Organ Mts., *Wooton 422* (DS, MO, NY, POM, UC, US). Eddy Co.: sandhills near Loving, *Standley 40357* (US). TEXAS. El Paso Co.: desert near El Paso, *Knobloch 199* (MSC). Hudspeth Co.: between Nulo and Harris Siding, *Ferris & Duncan 2449* in part (MO). Presidio Co.: Presidio, *Trelease 311* (MO). Brewster Co.: near San Vicente, muddy bank of Rio Grande, *Young,* 26 Aug 1915 (TEX). Kerr Co.: Kerrville, *Cook 20* (LL), *20A* (LL, NY). Kinney Co.: 17 mi E of Del Rio, *Shreve 8387* (ARIZ). Bexar Co.: San Antonio, *Berlandier 2541* in part (WIS). Lavaca Co.: Hallettsville, *Fisher 109* (US). Atascosa Co.: 13.6 mi S of Jordanton, silty clay roadside, *Shinners 16953* (SMU). La Salle Co.: US Highway 81, 13 mi N of Encinal, orange-brown sand, *Solis 56* (SMU). Live Oak Co.: George West, sandy loam, *Schiller 950* (US). San Patricio Co.: 7.5 mi S of Taft, sandy loam, *F. B. Jones 491* (SMU). Aransas Co.: Aransas Refuge, *Blakey 43* (GH). Webb Co.: Laredo, *Palmer 131* in part (F, MICH, NY). Duval Co.: Colmena Creek, saline soil, *Correll & Johnston 19737* (LL). Kleberg Co.: Kingsville, dry neglected soil in disturbed areas, *Bogush 11845* (ARIZ, US). Zapata Co.: San Ygnacio, *Tharp 3517* (TEX, US). Jim Hogg Co.: State Highway 359, 5 mi W of Hebronville, loose pale orange sand, *Ramirez, Alva & McCart 8717* (SMU, TEX). Starr Co.: US Highway 83 below Falcon Dam, fine sandy silt, *Garza Gongora, de Anda & McCart 8465* (LL, SMU, TEX). Hidalgo Co.: Rio Grande Valley, *Walker 67* (GH, LL, TEX, UC). Willacy Co.: Sauz Ranch, sandy loam, *Johnston & Davis,* 23 Nov 1953 (TEX). Cameron Co.: Brownsville, open ground, *Runyon 2021* (F), *5804* (LL); Rio Hondo, *Chandler 7067* (GH, MO, NY, UC, US).

MEXICO. BAJA CALIFORNIA NORTE: 15 mi N of Bahía de San Luis Gonzaga, granitic sand, *Wiggins 16037* (DS, MICH, TEX); open sandy area near S end of Laguna Chapala, ca. 2200 ft, *Thomas 8201* (CAS, DS). BAJA CALIFORNIA SUR: ca. 6 mi N of Cuarenta, sandy coastal plain, *Thomas 8362* (ARIZ, CAS, DS, GH, UC, US); 8.5 mi N of La Paz toward Bahía Pichilingue, rocky red volcanic soil at roadside, *Porter 384* (ARIZ, CAS, DS, MEXU, UC); San José del Cabo, *Brandegee,* Sept 1891 (DS, GH, NY, US). SONORA: Agiabampo, *Palmer 786* (GH, MICH, NY, US); Guaymas, waste places, *Palmer 107* (BM, GH, MICH, NY, US); 27 mi W of Hermasillo toward Bahía Kino, *Wiggins & Rollins 130* (ARIZ, DS, GH, MICH, MO, NY, UC, US). CHIHUAHUA: Colonia Juarez, *M. E. Jones,* 11 Sept 1903 (POM); Ramos, open grassland, 4800 ft, *Leopold 257* (UC). COAHUILA: Monclova, *Palmer 131A* (US); Sabinas, *Kenoyer 32* (F).

TAMAULIPAS: Papalote de Mirandena, prairie on sandy loam shallowly overlying caliche, *Crutchfield & Johnston 5552* (MEXU, MICH, TEX); near Victoria, ca. 320 m, *Palmer 218* in part (F, GH, NY, UC, US). SINALOA: rocky areas 12–15 km SE of Mazatlán, wet soil along road, 25 m, *Worth & Morrison 8812* (GH, MO, UC, US); Porvenir and Norote, 10 m, *Gonzalez Ortega 5889* (DS, GH, PH, US). DURANGO: ca. 3 mi W of Durango, *Hevly, Martin & Arms,* 1 Aug 1960 (ARIZ). NAYARIT: Isla María Madre, edge of beach near penal colony, *Ferris 5624* (DS, US). SAN LUIS POTOSI: locality unknown, *Schaffner,* 1876 (NY).

COMMON NAME. Golondrina (Nayarit, Sinaloa, and Sonora, Mexico).

TAXONOMY. The name *Kallstroemia brachystylis* has been applied to those specimens with fewer leaflets and less pronounced tubercles on the fruits than is usual for this species. However, Kearney and Peebles treating *K. brachystylis* as a variety of *K. californica,* pointed out that there was much intergradation in these characters. An examination of a number of collections made throughout the range of *K. californica* shows that variation in these characters is continuous, and there is no real justification for the recognition of two taxa.

In the past, confusion has led to the recognition of two taxa. This confusion arose largely from the determination of a number of collections (usually immature or depauperate specimens) of *Kallstroemia parviflora* as *K. brachystylis.* Such determinations include at least two specimens (at NY and US) with the same locality and date as the type specimen of *K. brachystylis.*

VARIATION. As indicated above, there may be considerable variation in leaflet number (three to seven pairs) and fruit tubercles (blunt, oblong, and 1½ mm long to less prominent), but this variation is of a continuous nature. Another character which occasionally shows marked variation is leaf shape. Although the overwhelming number of specimens have elliptical leaves, with the middle leaflets largest, some individuals have obovate leaves, with the terminal leaflets largest, and still others may have leaves of both shapes.

Watson (1876); Brewer *et al.* (1876); and Gray (1887) have stated that *Kallstroemia californica* has five two-loculed and two-seeded carpels and a deeply five-lobed fruit. These statements undoubtedly are due to the only fruit on the holotype specimen (at least the only one now present) having the alternate carpels abortive and superficially appearing five-lobed. Close inspection shows it to be ten-lobed, typical for the genus. All the mature mericarps of this species examined proved to be one-seeded, also typical for the genus.

RELATIONSHIPS. *Kallstroemia californica* appears to be closely related to *K. adscendens* from the Galápagos Islands, Ecuador, and perhaps to *K. standleyi* from Oaxaca, Mexico. *Kallstroemia adscendens* differs in having hirsute and sericeous stems, two to three pairs of leaflets, fruiting peduncles longer than the subtending leaves, persistent sepals, a strigose fruit with much less prominent tubercles, and a conical beak about ½ as long as the fruit body. *Kallstroemia standleyi* may be distinguished by its densely sericeous and sparingly hirsute stems, fruiting peduncles longer than the subtending leaves, persistent sepals, yellow-orange petals 10–12 mm long, linear-oblong anthers, style longer than the ovary, oblong stigma, and broadly ovoid strigose fruit 5–6 mm high and 7–10 wide, including the elongate blunt or slightly fungoid tubercles, which may be to 2 mm long.

9. **Kallstroemia standleyi** D. M. Porter, *sp. nov.*

TYPE: Mexico, Oaxaca: sand dunes along beach, 0.5 mi E of Salina Cruz, petals yellow-orange, 10–12 mm long; 16 July 1946, *Thomas Morley 681* (GH, holotype; F, MO, UC, US, isotypes). This species is named in honor of Paul Carpenter Standley (1884-1963), prolific writer on the flora of the Americas and student of the *Zygophyllaceae*.

Annua; caules prostrati, 1.5–2 dm longi, dense sericei, sparse hirsuti, trichomata alba, antrorsa; stipulae 3–4 mm longae, 1–1.5 mm latae; folia elliptica, 2–3 cm longa, 1–1.5 cm lata; foliolorum pares 4–6, elliptica vel anguste ovata, sericea, 8–11 mm longa, 3–4.5 mm lata, pares in medio laminae maxima; pedunculi quam folia subtendentia longiores, ad apicem incrassati, ad anthesin 2.5–3 cm longi, in fructu 2.5–3 cm longi et curvati; sepala anguste ovata, 5–8 mm longa, 2–3 mm lata, in fructu quam mericarpia longiora, quam rostrum breviora, in fructu e basi patentia, margines deinde involuti, persistentia; petala luteo-aurantiaca, 10–12 mm longa, late obovata; stamina et stylus aequilongus; antherae lineari-oblongae, 4 mm longae, antherae et pollen luteum; ovarium ovoideum, 1.5–2.5 mm in diametro, pubescens; stylus 3–3.5 mm longus, cylindricus, ad basin strigosus; stigma oblongum, 1 mm longum, 10-porcatum, papillosum; fructus late ovoideus, 5–6 mm altus, 7–10 mm latus (tuberculis inclusis), strigosus; rostrum 4–5 mm longum, quam fructificatio 1/2 brevius, cylindricum, ad basin conicum strigosumque; mericarpia 5 mm alta, ca. 1 mm lata, abaxialiter plurituberculata, tubercula ad 2 mm longa, obtusa ad fungoidea, elongata, in maturitate prominentiora, latera foveolata, adaxialiter recta.

Annual; *stems* prostrate, 1.5–2 dm long, densely sericeous and sparingly hirsute with white apically-directed trichomes; *stipules* 3–4 mm long, 1–1.5 mm wide; *leaves* elliptical, 2–3 cm long, 1–1.5 cm wide; *leaflets* 4–6 pairs, elliptical to narrowly ovate, sericeous, 8–11 mm long, 3–4.5 mm wide, middle pairs largest; *peduncles* longer than subtending leaves, thickened distally, 2–2.5 cm long in flower, 2.5–3 cm long and curved in fruit; *sepals* narrowly ovate, 5–8 mm long, 2–3 mm wide, sericeous, spreading from base of mature fruit and longer than mericarps but shorter than beak, margins becoming involute, persistent; *petals* yellow-orange, 10–12 mm long, broadly obovate; *stamens* as long as style; *anthers* linear-oblong, 4 mm long, they and pollen yellow; *ovary* ovoid, 1.5–2.5 mm in diameter, pubescent; *style* 3–3.5 mm long, cylindrical, base strigose; *stigma* oblong, 1 mm long, 10-ridged, papillose; *fruit* broadly ovoid, 5–6 mm high, 7–10 mm wide including tubercles, strigillose; *beak* 4–5 mm long, ca. 1/2 to as long as fruit body, cylindrical, base conical and strigose; *mericarps* 5 mm high, ca. 1 mm wide, abaxially with several elongate blunt to slightly fungoid tubercles to 2 mm long, becoming more pronounced as fruit matures, sides pitted, adaxial edge straight. *Fig. 9a, 9b. Map 11.*

FLOWERING DATES. Known to flower in July.

DISTRIBUTION AND HABITAT. Known only from the type locality *(Map 11).* Both *Kallstroemia maxima* and *K. pubescens* are known from the same general area.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia standleyi* may be distinguished by its elliptical leaves, four to six pairs of leaflets, fruiting peduncles longer than the subtending leaves, sericeous sepals which spread from the base of the mature fruit, their margins becoming involute, yellow-orange petals 10–12 mm long, linear-oblong anthers 4 mm long, cylindrical style longer than the ovary, oblong ten-ridged stigma, broadly ovoid strigose fruit 5–6 mm high and 7–10 wide, including the prominent elongate blunt to slightly fungoid tubercles, which may become 2 mm long, and beak ½ to as long as the fruit body.

RELATIONSHIPS. *Kallstroemia standleyi* appears to be most closely related to the more northerly *K. californica.* The latter differs in having hirsute and strigose stems, fruiting peduncles shorter than the subtending leaves, yellow flowers to 1 cm in diameter, usually deciduous sepals, conical style shorter than the ovary, ovoid strigillose fruit up to 4 mm high and 3–5 wide, including the prominent elongate blunt tubercles, which become 1½ mm long, and the beak shorter than the fruit body.

10. **Kallstroemia boliviana** Standl., Field. Mus. Nat. Hist. Publ. Bot. 11:161. 1936

TYPE: Bolivia, Cochabamba: Cerro San Pedro, Cochabamba, elev. 2600 m, 25 December 1928, *José Steinbach 8784* (F, holotype; BM, GH, MO, NY, US, isotypes).

Tribulus maximus var. *roseus* O. Ktze., Rev. Gen. Pl. 3(2):30. 1898. TYPE: Bolivia, Cochabamba: Parotani, elev. 2400 m, 20 March 1892, *Otto Kuntze s. n.* (NY, holotype; NY, isotype).

Perennial; *stems* prostrate to decumbent, to 5–8 dm long and several dm high, hirsute and sericeous with white apically-directed trichomes; *stipules* 3–6 mm long, 2–3 mm wide; *leaves* obovate, 2.5–3 cm long, to ca. 2 cm wide; *leaflets* 2–3(–4) pairs, broadly ovate, sericeous, 12–23 mm long, 7–14 mm wide, terminal pair largest; *peduncles* longer than subtending leaves, thickened distally, 7–35 mm long in flower, 8–41 mm long and curved in fruit; *flowers* pentamerous, 2–3 cm in diameter; *sepals* ovate, 6–9 mm long, ca. 2 mm wide, ca. 1/2 as long as petals, hirsute and strigose, longer than style in flower, in fruit clasping and almost entirely covering mature mericarps but shorter than beak, scarious margins may or may not become involute, persistent; *petals* yellow to orange, base darker, fading orange, obovate, 12–19 mm long, 8–18 mm wide, marcescent; *stamens* as long as style; *anthers* globose, ca. 1 mm in diameter, they and pollen red; *ovary* conical, 3–4 mm high, strigose; *style* ca. as long as ovary, narrowly conical, strigose; *stigma* oblong, 10-ridged, 1–2 mm long, papillose; *fruit* ovoid, 5–6 mm in diameter, strigose; *beak* 5–7 mm long, cylindrical, base conical, strigose to stigma base; *mericarps* 4–5 mm high, ca. 1 mm wide, abaxially rugose and margins flattened, sides pitted, adaxial edge angled. *Fig. 10a, 10b. Map 12.*

FLOWERING DATES. October through April, following summer rains.

DISTRIBUTION AND HABITAT. Disturbed areas in the semiarid valleys on the eastern face of the Cordillera Oriental of Bolivia, and known from a single similar locality in Peru *(Map 12)*. Occurring from about 1100 to 2800 m.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia boliviana* may be distinguished by the combination of its perennial habit, obovate leaves, usually two or three pairs of sericeous leaflets, yellow to orange flowers (bases darker) 2–3 cm in diameter, hirsute and strigose sepals that clasp and almost entirely cover the mature mericarps, the scarious margins may or may not become involute, red anthers and pollen, conical ovary, oblong ten-ridged stigma, strigose fruit, with the beak longer than the fruit body, and the mericarps abaxially rugose with flattened margins.

SPECIMENS EXAMINED. PERU. HUANCAVALICA: Río Mantaro Valley, NE of Pampas, 1300–1400 m, *Weberbauer 6516* (US).

BOLIVIA. WITHOUT LOCALITY: *Mandon s. n.* (F). LA PAZ: Cotaña am Illimani, 2500 m, *Buchtein 97* (GH), 2400 m, *671* (BM, F, MO, NY), *3198* (GH, NY, US); San Pedro, near Sorata, 2600–2700 m, *Mandon 857* (GH), *899* (BM, NY). COCHABAMBA: Cerro San Pedro, near Cochabamba, sandy place, 2550 m, *Cárdenas 2260* (GH), hard-packed soils, 2600 m, *Cutler & Cárdenas 10014* (GH); near Cochabamba, *Bang 927* (BM, F, GH, MICH, MO, NY, PH, US); ca. 3 km E of Cochabamba, hillside, 2800 m, *Eyerdam 24902* (GH, UC); ca. 5 km SE of Cochabamba, dried mudflat, 2800 m, *Eyerdam 24901* (F); Coronilla, near cemetery S of Cochabamba, waste soil, 2566 m, *Cutler 7460* (US); Mizque, 2040 m, *Cárdenas 3860* (GH); Panduro, sandy slopes near Río Caine, 1800 m, *Cárdenas 2426* (US); Quioma silver mines, dry red clay soil, slopes, *Eyerdam 25343* (F, UC);

beyond Rosario, dry bank, 8400 ft, *Brooke 5228* (F, NY); Samaipata, sandy soil, 1120 m, *Cárdenas 3130* (US); Tako Tako, farm near Mizque, edge of cultivated land, 2035 m, *Brooke 5889* (F, NY); Las Yungas, 6000 ft, *Rusby 739* (MICH, NY). SANTA CRUZ: Puente Pilato (Morochata), sandy soil, 2600 m, *Cárdenas 4446* (US). TARIJA: Padcaya, 2100 m, *Fiebrig 2511* (GH); outskirts of Tarija, semiarid plain, 1900 m, *West 8290* (GH, MO, UC, US); near Tarija, waste ground, 6600 ft, *Balls B6089* (F, UC, US).

The Peruvian collection, *Weberbauer 6516,* has the same collector's number as specimens of *Kallstroemia parviflora* at F and GH. However, the latter collection was made "below Pampas," while that of *K. boliviana* was made "northeast of Pampas."

RELATIONSHIPS. *Kallstroemia boliviana* is most closely related to the more southerly *K. tribuloides* and perhaps to the more northerly *K. pennellii. Kallstroemia tribuloides* differs in its annual habit, sericeous stems, elliptical leaves, three to six pairs of leaflets, occasionally hexamerous orange flowers 1½–2½ mm in diameter, broadly ovate sepals, with the margins not becoming involute, linear-oblong anthers, and glabrous fruits. *Kallstroemia pennellii* has an annual habit, strigose stems, elliptical leaves, three to four pairs of leaflets, fruiting peduncles about 8 cm long, sericeous sepals 15 mm long, with the margins not becoming involute, and longer than the beak in fruit, yellow petals 3 cm long, the fruit strigillose, with a glabrous beak, and the mericarps abaxially cross-ridged and slightly keeled.

11. **Kallstroemia tribuloides** (Mart.) Steud., Nomencl. Bot. ed. 2. 1:844. 1840

The name "*Kallstroemia tribuloides* (Mart.) Wight & Arn., Prodr. 1:145. 1834." commonly is used for this taxon, but as discussed under *K. maxima* and pointed out by Foster (1958) the combination was never made by Wight and Arnott. Steudal was the first to validly publish the combination, incorrectly attributing it to Wight and Arnott.

Ehrenbergia tribuloides Mart., Nov. Gen. Sp. Brasil. 2:73. 1827. TYPE: Brazil, "Crescit in herbosis sabulosis, ad fluvium S. Francisci, prope Joazeiro et alibi in mediterraneis Provinciae Bahiensis," *K. F. P. von Martius* (holotype presumably at BR or M, not seen). There can be no doubt as to the application of this name, due to von Martius' excellent colored illustration of the holotype (his pl. 163).

Tribulus brasiliensis Spreng., Syst. Veg. ed. 16. 4(2):343. 1827. *nom. superfl.* Based on *Ehrenbergia tribuloides,* cited as a synonym.

Annual; *stems* prostrate to decumbent, to 6 dm long, densely sericeous with apically-directed white trichomes, becoming glabrate; *stipules* 4–8 mm long, 1–2 mm wide; *leaves* elliptical, 3–7 cm long, 2–3 cm wide; *leaflets* 3–6 pairs, oval or oblong, appressed-hirsute and sericeous, becoming glabrate, 10–20 mm long, 3–13 mm wide, middle pairs largest; *peduncles* usually longer than subtending leaves and curved in fruit, becoming thickened distally, 1–3.5 cm long; *flowers* pentamerous, rarely hexamerous, 1.5–2.5 cm in diameter; *sepals* broadly ovate, 6–7 mm long, 2–4 mm wide, ca. 1/3–1/2 as long as petals, hirsute and strigose, in flower as long or longer than style, in fruit clasping and almost entirely covering mature mericarps but shorter than beak, margins not becoming involute, persistent; *petals* orange, basally sometimes darker, obovate, 7–12 mm long, 5–6 mm wide, marcescent; *stamens* as long as style; *anthers* linear-oblong, rarely linear, 1 mm long, they and pollen orange; *ovary* conical, 2–3 mm high, glabrous; *style* 3 mm long, cylindrical, base conical; *stigma* oblong, 10(–12)-ridged, ca. 1 mm long, papillose; *fruit* ovoid, 5–6 mm in diameter, glabrous; *beak* 3–10 mm long, glabrous, cylindrical, base conical; *mericarps* 4–5 mm high, ca. 1 mm wide, abaxially rugose and margins flattened and slightly keeled, sides pitted, adaxial edge curved. *Fig. 11a, 11b. Map 13.*

FLOWERING DATES. November through May following summer rains.

DISTRIBUTION AND HABITAT. Semiarid northeastern Brazil, southern Bolivia, and northwestern Argentina *(Map 13).* Apparently native to Argentina and Bolivia and introduced into Brazil. Open sandy places, riverbanks, railroad embankments, and roadsides from 300 to 1800 m. Sympatric over much of its range with *Kallstroemia tucumanensis.*

DISTINGUISHING CHARACTERISTICS. *Kallstroemia tribuloides* is easily recognized by its combination of densely sericeous stems, elliptical leaves, three to six pairs of leaflets, rarely hexamerous orange flowers 1½–2½ cm in diameter, broadly ovate hirsute and strigose sepals which clasp and almost entirely cover the mature mericarps, the margins not becoming involute, linear-oblong anthers, conical ovary, oblong ten-ridged stigma, glabrous fruit, with the beak usually longer than the fruit body, and the mericarps abaxially rugose with flattened and slightly keeled margins. *Kallstroemia tribuloides* is commonly found growing with (but is not likely to be confused with) the obovate-leaved, small, yellow-flowered, and strigose-fruited *K. tucumanensis.*

SPECIMENS EXAMINED. BRAZIL. PIAUI: Boa Esperança, *Gardner 2084* (BM, GH, NY). BAHIA: Joazeiro, *Curran 252* (GH, US). ALAGOAS: Ilha São Pedro, Rio do São Francisco, open sandy places, *Gardner 1264* (BM, GH, NY).

BOLIVIA. TARIJA: Villamontes, *Pflanz 2001* (US).

ARGENTINA. SALTA: Burela, *Luna 979* (CAS); Metán, *O'Donell 2488* (A); Pasaje del Río Juramento, *Lorentz & Hieronymus 325* (F); El Quebrachal, *Luna 701* (CAS, DS). TUCUMAN: El Cajón, sandy banks of Río Nio, 700 m, *Venturi 8524* (DS, MO); road S of Jarami, *Lillo 2494* (F, GH); Tapia, *Lillo,* Feb 1903 (GH), 750 m, *Venturi 1031,* railroad embankments, 750 m, *1077* in part (US); roadside near Tapia, 820 m, *Mexia 04344* (GH, MO, UC); Tapia to Cadellal, 500 m, *Schreiter 1028* (DS, F, GH, NY, UC); Tapia to Vipos, 750 m, *O'Donell & Lourteig,* 4 Feb 1939 (DS, F, GH, NY, UC); Vipos, fields, *Lillo 7896* (F, GH), 786 m, *Schreiter 1910* (F), 24 Jan 1926 in part (DS, F, GH, NY, UC). CATAMARCA: Campo del Pilciao, *Schickendantz 168* in part (UC, US); La Florida to Puerta del Corral Quemado, 1800 m, *Schreiter,* 19 Mar 1934 (F, GH); San Isidro to Río del Valle, *Rojas Paz 32* (GH); Sierra de Belén, 1500 m, *Schreiter,* Mar 1939 (F, GH). SANTIAGO DEL ESTERO: El Charco, hard dry soil, 300 m, *Venturi 10395* (BM, MO, NY). LA RIOJA: Río Hondo at road to Cantadero, *Hunziker 5020* (US).

In addition, collections which have not been seen have been reported from the states of Rio Grande do Norte, Brazil (von Luetzelburg, 1923), and Jujuy (Descole, *et al.,* 1940) and Mendoza (Ruíz Leal, 1947), Argentina.

COMMON NAME. Rosa do Campo (Brazil).

VARIATION. Ruíz Leal (1947) reports that specimens of *Kallstroemia tribuloides* from Mendoza, Argentina, had flowers half the size (ca. 1 cm in diameter) and were more reduced in height than those from farther north. These differences probably were due to environmental factors. The collections which he cited have not been seen.

RELATIONSHIPS. *Kallstroemia tribuloides* is most closely related to the more northerly *K. boliviana* and perhaps to *K. pennellii. Kallstroemia boliviana* differs in its perennial habit, hirsute and sericeous stems, obovate leaflets, usually two to three pairs of sericeous leaflets, yellow to orange flowers 2–3 cm in diameter, globose anthers, and strigose fruits. *Kallstroemia pennellii* has strigose stems, three to four pairs of leaflets, fruiting peduncles about 8 cm long, sericeous sepals 15 mm long, longer than the beak in fruit, yellow petals 3 cm long, strigillose fruits, and the mericarps abaxially cross-ridged and slightly keeled.

12. **Kallstroemia pennellii** D. M. Porter, *sp. nov.*

TYPE: Peru, Cajamarca: along Río Marañon, above Balsas, Amazonas, river bank, west shore, elev. 700–900 m; herb, petals yellow (lemon-chrome), 15 April 1948, *Francis W. Pennell 15185* (PH, holotype). This species is named for Francis Whittier Pennell (1886–1952), longtime Curator of Plants at the Academy of National Sciences of Philadelphia and collector of the type specimen.

Annua; caules ad 3 dm longi vel longiores, strigosi, trichomata antrorsa, alba, deinde glabrati; stipulae 4–5 mm longae, ca. 1 mm latae; folia elliptica, 2–4 cm longa, ca. 2 cm lata; foliolorum pares 3–4, late elliptica vel ovata, sericea, 9–14 mm longa, 3–6 mm lata, pares in medio laminae maxima; pedunculi quam folia subtendentia longiores, ad apicuem incrassati, in fructu recti et ca. 8 cm longi; sepala ovata, 15 mm longa, 3–4 mm lata, quam petala 1/2 breviora, sericea, marginea scarosi non involuti, ad anthesin quam stylus longiora, persistentia; petala lutea, 3 cm longa, ad apicem irregulariter erosa, marcescentia; stamina et stylus aequilongus; stylus ca. 10 mm longus; stigma oblongum, 2 mm longum; fructus ovoideus, 5 mm altus, 6 mm latus, strigillosus; rostrum 8 mm longum, cylindricum, ad basin conicum, glabrum; mericarpia 5 mm alta, abaxialiter rugosa et subcarinata.

Annual; *stems* to 3 dm long or longer, strigose with white apically-directed trichomes, becoming glabrate; *stipules* 4–5 mm long, ca. 1 mm wide; *leaves* elliptical, 2–4 cm long, to ca. 2 cm wide; *leaflets* 3–4 pairs, broadly elliptical to ovate, sericeous, 9–14 mm long, 3–6 mm wide, middle pairs largest; *peduncles* longer than subtending leaves, thickened distally, straight and ca. 8 cm long in fruit; *sepals* ovate, 15 mm long, 3–4 mm wide, 1/2 as long as petals, sericeous, scarious margins not becoming involute, longer than style in flower, persistent; *petals* yellow, 3 cm long, apex irregularly notched, marcescent; *stamens* as long as style; *style* ca. 10 mm long; *stigma* oblong, 2 mm long; *fruit* ovoid, 5 mm high, 6 mm wide, strigillose; *beak* 8 mm long, cylindrical, base conical, glabrous; *mericarps* 5 mm high, abaxially cross-ridged and slightly keeled. *Fig. 12a, 12b. Map 5.*

FLOWERING DATES. Known to flower in April.

DISTRIBUTION AND HABITAT. Know only from the type locality *(Map 5).*

DISTINGUISHING CHARACTERISTICS. *Kallstroemia pennellii* is characterized by its strigose stems, elliptical leaves, three to four pairs of sericeous leaflets, fruiting peduncles about 8 cm long, sericeous sepals 15 mm long, longer than the beak in fruit, the scarious margins not becoming involute, yellow petals 3 cm long, strigillose fruit, the beak glabrous and longer than the fruit body, and the cross-ridged and slightly keeled mericarps.

RELATIONSHIPS. *Kallstroemia pennellii* perhaps is most closely related to the more southerly *K. boliviana* and *K. tribuloides. Kallstroemia boliviana* differs by its hirsute and sericeous stems, obovate leaves, usually two to three pairs of leaflets, fruiting peduncles to about 4 cm long, hirsute and strigose sepals 6–9 mm long and shorter than the beak in fruit, yellow petals 12–19 mm long, strigose fruit, and abaxially rugose mericarps with flattened margins. *Kallstroemia tribuloides* has densely sericeous stems, three to six pairs of appressed-hirsute and sericeous leaflets, occasionally hexamerous orange flowers 1½–2½ cm in diameter, broadly ovate hirsute and strigose sepals shorter than the beak in fruit, glabrous fruit, and abaxially rugose mericarps with flattened and slightly keeled margins.

13. **Kallstroemia grandiflora** Torr. ex Gray, Pl. Wright. 1:28. 1852

TYPE: Arizona, Graham Co.: "Borders of the Gila," 28 October 1846, *Major Emory s. n.* (NY, lectotype). The label on Emory's specimen lists only the date, giving no locality data. Gray cited two collections following his description of *K. grandiflora,* "Borders of the Gila, *Col. Emory.*" and "Sonora Alta, Mexico, *Coulter,* No. 783." According to Emory's journal (Emory, 1848), on this date he was in what is now Graham County, Arizona, and collected along and near the Gila River. This specimen undoubtedly is the syntype cited by Gray. It was indirectly selected as the lectotype by Rydberg (in Vail & Rydberg, 1910, p. 114), who wrote "Type locality: Borders of the Gila River, Arizona." Notwithstanding Gray's citation of the authorship of this species (cf., Gray, 1853) as "Kallstroemia grandiflora, *Torr. in Pl. Wright.*", the correct citation undoubtedly is "Torr. ex Gray" rather than "Torr. in Gray," although Torrey himself used the latter (cf., Torrey, 1859). The original publication reads "Kallstroemia grandiflora *(Torr. in herb. Hook.),*" which leads one to conclude that this was a name taken by Gray from an annotation by Torrey on a specimen in W. J. Hooker's herbarium, rather than a name and description provided by Torrey. Further evidence is provided by Gray's original comment that, "Orders or genera elaborated by Dr. Engelmann, Dr. Torrey, Mr. Bentham, or others have the name of the author prefixed." In no other case that I can discover is a species published by another author in those sections of the publication authored by Gray. Gray probably came upon this name on his visit to Scotland in 1838–1839; Torrey had previously visited Hooker's Glasgow herbarium in 1833 (Rogers, 1942; Dupree, 1959).

Kallstroemia grandiflora var. *detonsa* Gray, *op. cit.* 1852. TYPE: Texas, "Near El Paso?" Sept. 1849, *Charles Wright* 75 (GH, holotype; NY, holotype photograph; GH, isotype).

Tribulus grandiflorus (Torr. ex Gray) Brew. & Wats. in Brew., Wats. & Gray, Bot. Calif. **1**:91. 1876. Brewer and Watson erroneously attributed this combination to Bentham and Hooker (1862). The latter authors never actually published it; they simply indicated that they considered *Kallstroemia* to be a subgenus of *Tribulus*.

Tribulus fisheri Kell., Proc. Calif. Acad. **7**:162. 1877. TYPE: Mexico, Sonora: Agiabampo, 15 Sept. 1876, *Wm. J. Fisher s. n.* (UC, holotype).

Kallstroemia grandiflora var. *arizonica* Cockll., Bull. Torr. Bot. Club **27**:87. 1900. TYPE: Arizona, Maricopa Co.: Phoenix, 9 Oct. 1899, *T. D. A. Cockerell s. n.* (Holotype presumably at COL, not seen; NY, US, isotypes).

Annual; *stems* decumbent to ascending, to over 1 m long and ca. 1 m high, densely sericeous with white and hispid with white or yellow apically-directed trichomes, rarely becoming glabrate; *stipules* 4–10 mm long, 1–2 mm wide; *leaves* elliptical, 1.5–7 cm long, 2–3 cm wide; *leaflets* 4–8(–10) pairs, elliptical to slightly obovate, appressed-hirsute, veins and margins sericeous, becoming glabrate, 8–25 mm long, 2–5 mm wide, middle pairs largest; *peduncles* longer than subtending leaves, extending flowers well above herbage, slightly thickened distally, 3–10.5 cm long, sharply bent at base and straight above in fruit; *flowers* pentamerous, 2–6 cm in diameter; *sepals* lanceolate, 6–16 mm long, 1.5–2.5 mm wide, ca. 1/2 as long as petals, hispid with much larger yellow or white and strigose with smaller white trichomes, in flower longer than style, in fruit much surpassing mature mericarps but shorter than beak, also shriveling and turning brown and margins becoming strongly involute making them appear linear, persistent; *petals* white through yellow to bright orange, base green to red and usually much brighter than distal portion, fading white to orange, broadly obovate, 10–34 mm long, 7–22 mm wide, marcescent; *stamens* as long as style; *anthers* ovoid or oblong, rarely linear, 2–3 mm long, they and pollen red, orange, or rarely yellow, same color as petal base; *ovary* ovoid, 2–3 mm in diameter, pubescent; *style* 6–8 mm long, cylindrical, base slightly conical, strigose at base or to stigma base; *stigma* clavate, 2–3 mm long, 10-ridged, papillose; *fruit* ovoid, 4–5 mm in diameter, strigose; *beak* 6–18 mm long, ca. 3 times length of fruit body, cylindrical, base conical, strigose at base or to stigma base; *mericarps* ca. 3.5 mm high and 1 mm wide, abaxially turbercled, sides slightly pitted, adaxial edge angled. *Fig. 13a, 13b. Map 14.*

FLOWERING DATES. In the north flowering mainly from June through October after the summer rains, and in the southwest (Jalisco to Guerrero) from August to March.

DISTRIBUTION AND HABITAT. Common in flat sandy areas throughout the Sonoran (except for Baja California) and Chihuahuan deserts from sea level to about 2000 meters; continuing southward through the semiarid lowland formations from Sinaloa to northern Guerrero and sparingly northward in Arizona *(Map 14).* In the north sympatric over much of its range with *Kallstroemia californica, K. hirsutissima, K. parviflora,* and *K. perennans,* and in the southwest overlapping with *K. hintonii, K. maxima, K. pubescens,* and *K. rosei.*

DISTINGUISHING CHARACTERISTICS. *Kallstroemia grandiflora* is easily recognized by its combination of decumbent to ascending stems, elliptical leaves, four to ten pairs of leaflets, fruiting peduncles longer than the subtending leaves and extending the flowers well above the herbage, white to bright orange flowers (the petal bases from green to red) 2–6 cm in diameter, lanceolate hispid and strigose sepals that much surpass the mature mericarps but are shorter than the beak, shriveling and turning brown and the margins becoming strongly involute making them appear linear, cylindrical style about three times as long as the ovary, clavate ten-ridged stigma, and strigose fruit with the beak about three times as long as the fruit body. *Kallstroemia parviflora* and *K. perennans* are the only species from the same area with which *K. grandiflora* is likely to be confused. *Kallstroemia parviflora* differs in its having three to six pairs of leaflets, fruiting peduncles 1–4 cm long, orange flowers 1–2½ cm in diameter, the anthers less than 1 mm in diameter, always yellow anthers and pollen, and oblong ten-ridged stigma; only depauperate individuals of *K. grandiflora* will be confused with this species. *Kallstroemia perennans* differs in having a perennial habit, densely hispid and strigose stems 1–2 cm long, four to five pairs of densely pubescent leaflets, fruiting peduncles shorter than the subtending leaves, fugaceous but not marcescent orange petals, the stamens only two-thirds as long as the style, oblong ten-ridged coarsely canescent stigma extending along the upper one-third of the style, broadly ovoid hispid and strigose fruits 5–6 mm high and 8–10 wide, the beak hirsute at the base, and the mericarps abaxially cross-ridged and more or less keeled and 2½ mm wide.

REPRESENTATIVE SPECIMENS EXAMINED. UNITED STATES. CALIFORNIA. Riverside Co.: Chuckawalla Valley near Desert Center, open ground near roadside, sandy soil, 900 ft, *Clary 2736* (POM). ARIZONA. Coconino Co.: Bill Williams Mt., *Anderson,* July 1864 (MO). Navajo Co.: McNary-Globe road near White River, *Gunning 3183* (ARIZ). Yavapai Co.: Beaver Creek, *Rusby,* Aug 1883 (F, MICH, NY, PH, US); 20 mi above Camp Verde, 4100 ft, *Wolf 2431* (CAS, DS, GH, RSA); Verde Valley, *W. W. Jones 80* (GH, UC), 25 July 1920 (POM, UC, US). Yuma Co.: dry arid hills around Ft. Yuma, *Schott,* 1 Dec 1854 (F); Mohawk, *M. E. Jones 24965* (POM). Maricopa Co.: 10 mi W of Aguila on US Highway 70, roadside, *J. D. Porter,* 30 Aug 1962 (GH); Sentinal, *M. E. Jones 24962* (CAS, GH, MO, NY, POM, UC). Gila Co.: near Globe, *Peebles, Harrison & Kearney 4391* (ARIZ, US); mesa near Rock & Rye Creeks, 990–1050 m, *Collom 187* (GH, MICH, MO, NY, US); San Carlos, 2500 ft, *Rothrock 777* (F, GH, RSA, US). Pinal Co.: desert mesa near Apache Junction, *Gillespie 8442* (DS, GH, UC, US); Oracle, 4500 ft, *Thornber,* 9–13 Sept 1905 (ARIZ, UC); Sacaton, *Gilman s. n.* (MO), *271* (DS, MO), *283* (CAS). Graham Co.: Camp Grant, 4753 ft, *Rothrock 442* (CAS, DS, F, NY); Galluro Mts., *Toumey,* 29 July 1894 (ARIZ, GH), *275* (UC). Greenlee Co.: Clifton, *Davidson 14* (UC), *758* (DS). Pima Co.: flats below Baboquivari Canyon, *Gilman 22* (DS, F, MO, NY); Continental, *Shreve 6600* (ARIZ, DS, MICH); Tucson, 2400 ft, *Thornber 263* (ARIZ, DS, MO, NY, POM, UC). Santa Cruz Co.: Nogales, *M. E. Jones 22312* (F, MO, POM); near Ruby, ca. 1375 m, *Morton 10* (POM). Cochise Co.: Apache Pass, *Lemmon,* Sept 1881 in part (BM, F, UC); Cave Creek Canyon, *Kusche,* 24–26 Aug 1927 (CAS, F, POM); San Bernardino Ranch, *Mearns 612* (DS, US). NEW MEXICO. Bernalillo Co.: Albuquerque, *M. E. Jones 4121* (POM). Grant Co.: Mangas Springs, 4770 ft, *Metcalfe 624* (ARIZ, BM, GH, MO, NY, UC, US); valley below Ojo de Gavilán, *Wright 911* (BM, GH, MO, NY, PH, US). Chaves Co.: Bottomless Lakes, sandy soil, *Stiteler,* 20 June 1949 (PH). Hidalgo Co.: Separ, sandy soil, 4300 ft, *Benson 7384* (POM). Luna Co.: near Akela, *Schallert 21174* (SMU); Florida Mts., *Mulford 1073* (MO, NY). Dona Ana Co.: along Rio Grande near Ft. Selden, *Rusby 56* (F, MICH, MO, NY, PH); Rio Grande Valley below Dona Ana, *Parry, et al. 139* (NY, PH, US). TEXAS. El Paso Co.: El Paso, alluvial hills, 1000 m, *Fosberg S3898* (GH, LL, NY, SMU); Franklin Mts., limestone soil, 4300 ft, *Warnock 8226* (LL, MICH, SMU, TEX). Hudspeth Co.: between Nulo and Harris Siding, *Ferris & Duncan 2447* (DS); 5 mi W of Van Horn, gravelly soil along highway, *Warnock 13619* (LL, TEX). Loving Co.: ca. 3 mi W of Mentone, limestone soil along highway, 2700 ft, *Warnock 10629* (LL, SMU). Jeff Davis Co.: 13.5 mi SW of Chispa, calcareous gravel, *Waterfall 5301* (GH, MO); Mt. Livermore, *Hinckley 8* (F, NY). Presidio Co.: dry creek beds near Chinati Mts., *Hinckley 818* (ARIZ, F, GH, NY, SMU, TEX); alluvial hills between Redford and Presidio, 3200 ft, *Warnock 10611* (LL, SMU). Brewster Co.: Big Bend Natl. Park, 6 mi N of Rio Grande, dry arroyo walls, 3000 ft, *Rollins & Chambers 2768* (DS, GH, UC, US); Boquillas, *Marsh 53* (GH, SMU, TEX); arroyos near Hot Springs, *Warnock,* 17 July 1937 (ARIZ, GH, TEX).

MEXICO. SONORA: Guaymas, hills and valleys, *Palmer 177* (BM, DS, GH, NY, PH, UC, US), stony slopes, *225* (BM, GH, MICH, NY, US); llano 27 mi W of Hermosillo toward Kino Bay, *Wiggins & Rollins 129* (ARIZ, DS, GH, MICH, MO, NY); San Bernardo, mesas and milpas, *Gentry 1667* (ARIZ, F, GH, MEXU, MO, NY, UC, US). CHIHUAHUA: Bachimba, roadside, *Knobloch 294* (BM, LL, MSC); El Carmen, *LeSueur 381* (F, GH, MO, SMU, TEX, UC); Hacienda San Miguel, near Batopilas, *Palmer 108* (BM, CAS, GH, MICH, NY, PH, US). COAHUILA: 2 km NE of Las Delicias, caliche slopes, *Stewart 2958* (GH); dry valley between La Vibora and Matrimonio Viejo, gypsum beds, *Johnston 9338* (GH). SINALOA: Imala, *Palmer 1440* (F, GH, NY, US); low hills 8 mi N of Mazatlán, *Waterfall 12751* (ARIZ, GH, MICH, RSA, TEX, UC); Rosario, *Lamb 471* (DS, GH, MICH, MO, MSC, NY, US). DURANGO: base of hills 2 mi W of Bermejillo toward Palmito Dam, silty soil, *Johnston 7749* (GH); 27 mi NE of Cuencame toward Torreón, desert scrub, among rocks, 6300 ft, *Straw & Forman 1520* (MICH, RSA). NAYARIT: Acaponeta, *Lamb 530* (GH, MO, MSC, NY, US), *534* (DS, GH, MSC, NY, US); Cañon de Jesús María, bottom lands along Río Jesús María, 1000 ft, *Goldsmith 141* (F, GH, MO, UC, US). JALISCO: between La Venta and Ixtlán, 1100 m, *Reko 4491* (US). COLIMA: Colima, *Palmer 83* (ARIZ, MICH, UC, US), *1110* (BM, GH, MICH, NY, US); Manzanillo, *Xantus,* 1863 (F, GH, NY, US); 5 km W of Tecomán, fine silt at roadside, *Porter 1482* (GH, MEXU). MICHOACAN: Tacupa, bank of Río Balsas, on sand, *Hinton 5487* (BM, GH, MO, NY, US), *7116* (ARIZ, BM, F, GH, LL, NY, PH, RSA, TEX, US). GUERRERO: Pungarabato, bank of Río Cutzamala, *Hinton 6480* (F, GH, MICH, NY, US).

A specimen at PH labeled "Moore's Flat, Sierra Nevada, Nevada Co., Cal. July 1867." could not have been collected in this locality, far from the range of any species of *Kallstroemia.* It is a mixed collection of *K. grandiflora* and *Tribulus cistoides* and possibly may be from western Mexico, where both of these species do occur. *Schott 1* from F, labeled "Cartejena [Colombia], beach.", was undoubtedly switched with a specimen of *T. cistoides,* which occurs in that locality. This collection of *K. grandiflora* probably is from Arizona, where Schott also collected.

COMMON NAMES. Like many other plants with conspicuous flowers, *Kallstroemia grandiflora* is graced with a number of common names. However, surprisingly, it is not known by nearly as many names as is the much less conspicuously flowered *K. maxima.* This undoubtedly is due to the latter's wide use in the native *materia medica,* while the former is utilized, if at all, only as an ornamental. Common names that have been reported for *K. grandiflora* are Abrojo de Flor Amarillo (Chihuahua, Durango); Arizona Poppy (Arizona); Baiburín (Sinaloa, Sonora); Desert Poppy (Texas); Mal de Ojos (Sonora); Manrubio (Colima); Mexican Poppy, Ojo Mal, Poppy (Arizona); San Miguelito (Sonora); and Summer Poppy (Arizona). Prevalence of the word "poppy" as part of the common name in much of the southwestern United States reflects the superficial resemblance of the flowers in size and color to the California Poppy, *Eschscholzia* *californica* Cham. *(Papaveraceae)*, commonly grown in the same area as an ornamental.

VARIATION. Variation in the color of trichomes on the vegetative parts of the plants is sometimes quite striking. If the larger, hispid trichomes are yellow, as is normally the case, individuals have a decided yellowish cast. If these trichomes are white, the plants appear gray. Specimens from the Sonoran Desert and its environs tend to be yellow, and those from the Chihuahuan Desert tend to be gray, but this criterion is too variable to be utilized in the recognition of subspecific entities.

Flower color in *Kallstroemia grandiflora* is rather variable, but that of individual populations appears to be remarkably stable. It ranges from yellow to distally orange with a dark orange basal spot, or dark orange with a red basal spot. Occasional populations are found in which the petals are white with a red basal spot. There appears to be genetic linkage between the color of the petal base and filament, anther, and pollen color. All are the same in an individual. This color variation is not such that subspecific taxa can be recognized, in that it appears to have no ecological or geographical correlation.

RELATIONSHIPS. *Kallstroemia grandiflora* appears to be the center of a group of interrelated species also involving *K. parviflora, K. peninsularis,* and *K. perennans.* The characters distinguishing *K. parviflora* and *K. perennans* from *K. grandiflora* are summarized above. *Kallstroemia peninsularis* differs in having hirsute and hirtellous stems with retrorse pubescence, two to five pairs of leaflets, yellow to orange flowers 1–3½ cm in diameter, hispid and hirtellous sepals, yellow anthers and pollen, and a clavate stigma that extends along the upper one-third to almost the entire length of the style.

14. **Kallstroemia peninsularis** D. M. Porter, *sp. nov.*

TYPE: Mexico, Baja California Sur: granitic hills 10 mi SE of La Paz on road to Los Planes, elev. 725 ft; petals golden yellow, 1 December 1959, *Ira L. Wiggins 15686* (GH, holotype; DS, GH, TEX, isotypes).

Annua; caules prostrati vel decumbentes, decimetra aliquot longi, albi- vel lutei-hirsuti et hirtelli, trichomata retrorsa; stipulae 2–4 mm longae, 1–2 mm latae; folia elliptica, 1.5–6.5 cm longa, 2–4 cm lata; foliolorum pares 2–5, foliola elliptica vel oblonga, appresse hirsuta, margines venaeque sericeae, 8–34 mm longa, 3–17 mm lata, pares in medio laminae maxima; pedunculi quam folia subtendentia longiores vel breviores, ad apicem incrassati, anthesin 10–52 mm longi, in fructu 19–64 mm longi, ad basin acute flexi et sursum recti; flores pentameri, 1–3.5 cm in diametro; sepala subulata, 5–8 mm longa, 1–2 mm lata, quam petala 1/2–1/3 breviora, lutei-hispida et albi-hirtella, ad anthesin quam stylus longiora, in fructu mericarpia matura multo excedentia sed quam rostrum breviora, margines deinde perinvoluti et quasi-linearia, persistentia; petala lutea vel aurantiaca, late obovata, ad apicem late rotundata vel irregulariter erosa, 11–20 mm longa, 7–15 mm lata, marcescentia; stamina et stylus aequilongus; antherae ovoideae, 1–2 mm in diametro, antherae et pollen luteum; ovarium ovoideum, 1–3 mm in diametro, pubescens; stylus 3–8 mm longus, anguste cylindricus, ad basin leviter conicus, ad basin stigmatis strigosus; stigma clavatum, stylum in longitudine subaequans vel 2/3 brevius, 10-porcatum, papillosum; fructus ovoideus, 3.5–5 mm in diametro, strigillosus; rostrum 7–10 mm longum, cylindricum, ad basin conicum, ad stigmatam strigosum; mericarpia 3–4 mm alta, ca. 1 mm lata, abaxialiter rotundato-tuberculata, latera foveolata, adaxialiter subangulata.

Annual; *stems* prostrate to decumbent, to several dm long, hirsute with white or yellow and hirtellous with white retrorse trichomes; *stipules* 2–4 mm long, 1–2 mm wide; *leaves* elliptical, 1.5–6.5 cm long, 2–4 cm wide; *leaflets* 2–5 pairs, elliptical to oblong, appressed-hirsute, veins and margins sericeous, 8–34 mm long, 3–17 mm wide, middle pairs largest; *peduncles* longer or shorter than subtending leaves, thickened distally, 10–52 mm long in flower, 19–64 mm long in fruit and bent sharply at base and straight above; *flowers* pentamerous, 1–3.5 cm in diameter; *sepals* subulate, 5–8 mm long, 1–2 mm wide, 1/3–1/2 as long as petals, hispid with yellow and hirtellous with white trichomes, longer than style in flower, in fruit much exceeding mature mericarps but shorter than beak, shriveling and margins becoming strongly involute making them appear almost linear, persistent; *petals* yellow to orange, broadly obovate, apex broadly rounded to irregularly notched, 11–20 mm long, 7–15 mm wide, marcescent; *stamens* as long as style; *anthers* ovoid, 1–2 mm in diameter, they and pollen yellow; *ovary* ovoid, 1–3 mm in diameter, pubescent; *style* 3–8 mm long, narrowly cylindrical, base slightly conical, strigose to stigma base; *stigma* clavate, extending along upper 1/3 to ca. entire length of style, 10-ridged, papillose; *fruit* ovoid, 3.5–5 mm in diameter, strigillose; *beak* 7–10 mm long, cylindrical, base conical, strigose to stigma base; *mericarps* 3–4 mm high, ca. 1 mm wide, abaxially with rounded tubercles, sides pitted, adaxial edge slightly angled. *Fig. 14a, 14b. Map 15.*

FLOWERING DATES. August through March, following both summer and winter rains.

DISTRIBUTION AND HABITAT. Endemic to the southern part of the territory of Baja California, Mexico *(Map 15).* Found mainly in low sandy areas and sand dunes near beaches from sea level to perhaps 1000 meters or higher. *Kallstroemia californica* also extends into this area.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia peninsularis* is easily recognized by its combination of hirsute and hirtellous stems with retrorse trichomes, elliptical leaves, two to five pairs of leaflets, yellow to orange flowers 1–3½ cm in diameter, hispid and hirtellous sepals which are longer than the mature mericarps but shorter than the beak, shriveling and the margins becoming strongly involute and making them appear almost linear, yellow anthers and pollen, narrowly cylindrical style about three times as long as the ovary, a clavate stigma extending along the upper one-third to almost the entire length of the style, and strigillose fruit with the beak about three times as long as the fruit body.

SPECIMENS EXAMINED. MEXICO. BAJA CALIFORNIA: Arroyo Salado, *Purpus 409* (UC); near Arroyo Salado, margin of ocean sand dunes, *Hammerly 189* (CAS, DS); Cabo San Lucas, *Xantus 14* (GH, NY, US); 3 km N of Cabo San Lucas, flat area, *Moran 7040* (DS); 14.4 km SW of Comondú, steep slope in canyon, *Carter, Alexander & Kellogg 2122* (DS, US); 0.5 mi W of SW base of Los Frailes, sandy dunes, *Porter 318* (CAS, DS); arroyo 95 km NW of La Paz, 75 m, *Wiggins 15413* (CAS, DS, UC); highway NW of La Paz near km 40, *Thomas 8439* (CAS, DS, GH, US); 24 mi W of La Paz, rocky sand at roadside, *Porter 438* (DS); ca. 15 mi W of La Paz, coarse granitic sand on bluff, *Hammerly 222* (CAS, DS, US); gulch in granitic hills 15.5 mi SE of La Paz toward Las Cruces, 570 ft, *Wiggins 15669A* (DS); near junction of roads to Punta Arenas and Bahía de los Muertos, rocky hillside, *Wiggins 14454* (CAS, DS, MICH); wash 1 mi S of San Antonio toward Santiago, *Chambers 860* (DS, UC); San José del Cabo, *Brandegee 78* (UC), 5 Sept 1891 (DS), 12 Sept 1891 (F), *M. E. Jones 27114* (POM); 3 mi NE of San Lucas, sandy red soil at roadside, *Porter 331* (CAS, DS); 14 mi N of San Lucas, sandy decomposed granite in road, *Porter 341* (DS); 12.8 km N of Santiago, granitic sand, *Carter, Alexander & Kellogg 2181* (DS, US).

COMMON NAME. Patagallina.

TAXONOMY. In a previous publication (Porter, 1963), this taxon was confused with *Kallstroemia grandiflora* and *K. pubescens*. However, a more adequate knowledge of the genus has revealed that it is a new species.

RELATIONSHIPS. *Kallstroemia peninsularis* is most closely related to *K. grandiflora*. The latter differs in having densely sericeous and hirsute decumbent to ascending stems, four to ten pairs of leaflets, fruiting peduncles 3–10½ cm long that extend the flowers well above the herbage, the flowers from 2–6 cm in diameter, hispid and strigose sepals, the petals basally darker in color than the distal portion, the anthers and pollen rarely yellow, a clavate ten-ridged stigma less than one-third as long as the style, and strigose fruits.

15. **Kallstroemia perennans** Turner, Field & Lab. **18**:155. 1950

TYPE: Texas, Val Verde Co.: Langtry, May 1913, *C. R. Orcutt 6126* (MO, holotype; GH, MO, holotype photographs). Based on *Kallstroemia hirsuta* L. Williams, Ann. Mo. Bot. Gard. **22**:49. 1935. Not *K. hirsuta* (Benth.) Engl.

in Engl. & Prantl, Nat. Pflanzenfam. 3(4):88. 1890 [=*Tribulus hirsutus* Benth., Fl. Austral. **1**:289. 1863].

Perennial; *stems* prostrate to ascending, 1–2 dm long, densely hispid with bulbous-based white or yellow and strigose with white apically-directed trichomes; *stipules* 3–5 mm long, 1–1.5 mm wide; *leaves* elliptical, 2–5.5 cm long, 2–3 cm wide, densely pubescent; *leaflets* 4–5 pairs, oblong to ovate, densely appressed-hirsute, veins and margins sericeous, 13–18 mm long, 6–10 mm wide, middle pairs largest; *peduncles* shorter than subtending leaves, little thickened distally, 15–20 mm long in flower, 25–36 mm long in fruit and bent sharply at base and straight above; *flowers* pentamerous, 3.5–4.5 cm in diameter; *sepals* lanceolate, 13–15 mm long, 1.5–2.5 mm wide, ca. 1/2 as long as petals, densely hispid and strigose, longer than style in flower, spreading from base of mature fruit and longer than mericarps but shorter than beak, margins becoming sharply involute, persistent; *petals* orange, obovate, 19–26 mm long, 10 mm wide, fugaceous but not marcescent; *stamens* 2/3 as long as style; *anthers* ovoid, 1.5 mm in diameter, they and pollen orange; *ovary* ovoid, 3 mm in diameter, pubescent; *style* 6 mm long, cylindrical; *stigma* oblong, 10-ridged, 2–3 mm long, coarsely canescent; *fruit* broadly ovoid, 5–6 mm high, 8–10 mm wide, hispid and strigose, hispid trichomes to 5 mm long; *beak* 6–10 mm long, cylindrical, base hirsute and slightly conical; *mericarps* 4 mm high, 2.5 mm wide, abaxially cross-ridged and more or less keeled, sides pitted, adaxial edge straight. *Fig. 15a, 15b. Map 15.*

FLOWERING DATES. May through August, following the spring and summer rains.

DISTRIBUTION AND HABITAT. The Chihuahuan Desert; known only from southern Presidio, Brewster, and Val Verde counties, Texas *(Map 15),* where apparently confined to limestone soils. Sympatric with *Kallstroemia californica, K. grandiflora, K. hirsutissima,* and *K. parviflora.*

DISTINGUISHING CHARACTERISTICS. *Kallstroemia perennans* may be easily recognized by its having a combination of perennial habit, short prostrate to ascending stems, elliptical leaves, four to five densely pubescent leaflets, fruiting peduncles shorter than the subtending leaves, densely hispid and strigose sepals that spread from the base of the mature fruit and curve upward surpassing the mature mericarps but shorter than the beak, margins becoming sharply involute, orange petals that are fugaceous but not marcescent, stamens two-thirds as long as the style, a cylindrical style about twice as long as the ovary, oblong ten-ridged coarsely canescent stigma that extends about one-third the length of the style, broadly ovoid hispid and strigose fruit from 5–6 mm high and 8–10 wide, cylindrical beak about twice as long as the fruit body, and abaxially cross-ridged and more or less keeled mericarps 2½ mm wide. The only species from the same area with which *Kallstroemia perennans* might be confused is *K. grandiflora.* The latter differs from *K. perennans* in its annual habit, decumbent to ascending stems reaching to over 1 m in length, four to ten pairs of leaflets, fruiting peduncles longer than the subtending leaves, sepals shriveling and turning brown, the margins becoming strongly involute and making them appear linear, fugaceous and marcescent yellow to bright orange petals with usually a darker base, the stamens as long as the style, clavate ten-ridged papillose stigma, ovoid strigose fruit, and abaxially tubercled mericarps about 1 mm wide.

SPECIMENS EXAMINED. UNITED STATES. TEXAS. Locality unknown: Rio Colorado, *V. Havard,* 1883 (F). Presidio Co.: limestone hills between Lajitas and Arroyo Segunda, 2215 ft, *Warnock & Turner 1350* (LL). Brewster Co.: Amarilla Mt., 7 mi W of Terlingua, 2640 ft, *Turner 1166* (GH); W of Lajitas toward Fresno Canyon, limestone soil, 3200 ft, *Turner & Parks 1350* (SMU). Val Verde Co.: rocky calcareous hillside 3.5 mi W of Langtry, *Turner 3779* (RSA, SMU, TEX); limestone hills 19 mi N of Langtry, *McVaugh 8226A* (GH, MICH).

RELATIONSHIPS. Williams *(loc. cit.)* was the first to indicate that *Kallstroemia perennans* is most closely allied to *K. grandiflora.* The differences between these two species are reviewed above.

16. **Kallstroemia parviflora** Norton, Ann. Rept. Mo. Bot. Gard. 9:153. 1898

TYPE: Texas, Bexar Co.: San Antonio, 1897, *E. H. Wilkinson 184* (MO, lectotype). Notwithstanding Rydberg's (in Vail & Rydberg, 1910) indirect citation of *Pollard 1295* as the type collection of this species by listing "Agricultural College, Mississippi" for the type locality, Wilkinson's specimen is the type. Both collections were cited by Norton in his description of the species, and the Wilkinson specimen at MO bears the word "Type," presumably in Norton's handwriting. It is confirmed as the lectotype.

Kallstroemia intermedia Rydb. in Vail & Rydb., N. Amer. Fl. **25**:113. 1910. TYPE: Texas, Bexar Co.: 1904. *Gust. Jermy s. n.* (NY, holotype; UC, holotype fragment).

Kallstroemia laetevirens Thornb. in Woot. & Standl., Contr. U. S. Nat. Herb. **16**:143. 1913: TYPE: New Mexico, Grant Co.: Hanover Mountain, 31 July 1911, *J. M. Holzinger s. n.* (US, holotype; MO, isotype?).

Annual; *stems* prostrate to decumbent or ascending, to 1 m or more long, more or less coarsely hirsute and sericeous with apically-directed white or gray trichomes, becoming glabrate; *stipules* 5–7 mm long, 1–3 mm wide; *leaves* elliptical, 1–6 cm long, to 3 cm wide; *leaflets* 3–5(–6) pairs, elliptical to oblong or oval, appressed-hirsute, veins and margins sericeous, 8–19 mm long, 3.5–9 mm wide, middle pairs largest; *peduncles* equalling or commonly longer than subtending leaves, thickened distally, 1–4 cm long in flower and fruit, in fruit straight or sharply bent at base and straight above; *flowers* pentamerous, 1–2.5 cm in diameter; *sepals* lanceolate, 4–7 mm long, 1–2 mm wide, hispid with white or rarely yellow and strigose with white trichomes, in flower longer than style, in fruit shriveling and turning brown, appressed to mericarps and reaching from top of mericarps to ca. as long as style, margins becoming sharply involute, persistent; *petals* orange, drying white to yellow, narrowly obovate, 5–11 mm long, 3.5–6 mm wide, marcescent; *stamens* as long as style; *anthers* ovoid, rarely linear, less than 1 mm in diameter, they and pollen yellow; *ovary* ovoid, pubescent, ca. 1 mm in diameter; *style* as long or longer than ovary, cylindrical, strigose to glabrous; *stigma* oblong, 10-ridged, ca. 1 mm long, papillose; *fruit* ovoid, 3–4 mm high, 4–6 mm wide, strigose; *beak* 3–9 mm long, as long as to 3 times fruit body, strigose to glabrous, trichomes appressed to spreading, cylindrical, base scarcely conical; *mericarps* 3–4 mm high, ca. 1 mm wide, abaxially rugose to tubercled, sides lightly to strongly pitted, adaxial edge angled. *Fig. 16a, 16b. Maps 5, 16.*

FLOWERING DATES. Seed germination, plant growth, and flowering take place mainly after summer rains. These phenomena usually occur from July through September in North America, and from November to April in Peru.

DISTRIBUTION AND HABITAT. Disturbed areas mainly in various grassland associations from Colorado and Kansas south to Guanajuato, Querétaro, and Hidalgo, Mexico, and west to Arizona, occurring sparingly in the Chihuahuan Desert, extending as a weed in all directions; introduced into western and central Peru *(Maps 5 and 16).* Found from about 100 to 2600 m in North America and 1300 to 2850 m in Peru. Sympatric with *Kallstroemia californica, K. grandiflora, K. hirsutissima,* and *K. perennans* in the north, *K. rosei* in the south, and barely overlapping with *K. maxima* in the southeast.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia parviflora* is distinguished by its combination of elliptical leaves, three to six pairs of leaflets, fruiting peduncles 1–4 cm long, orange flowers 1–2½ cm in diameter, hispid and strigose sepals longer than the mature mericarps but shorter than the beak, shriveling and turning brown and the margins becoming strongly involute, yellow anthers and pollen, cylindrical style as long or longer than the ovary, oblong ten-ridged stigma, cylindrical beak as long to three times as long as the strigose fruit body, and abaxially rugose to tubercled mericarps. Depauperate specimens of *K. parviflora* may be confused with *K. californica,* and more robust specimens with *K. grandiflora. Kallstroemia californica* differs in having hirsute and strigose stems, three to seven pairs of leaflets, fruiting peduncles shorter than the subtending leaves, yellow flowers 1 cm or less in diameter, usually deciduous sepals, a stout conical style shorter than the ovary, a clavate ten-ridged stigma, strigillose fruit with the beak shorter than the fruit body, and mericarps with four or five blunt oblong tubercles that may be 1½ mm long. *Kallstroemia grandiflora* has four to ten pairs of leaflets, fruiting peduncles 3–10½ cm long, white to bright orange flowers (petal bases darker than the distal portion) 2–6 cm in diameter, anthers 2–3 mm long, usually orange or red anthers and pollen, style about three times as long as the ovary, and clavate ten-ridged stigma.

REPRESENTATIVE SPECIMENS EXAMINED. UNITED STATES. CALIFORNIA. San Bernardino Co.: Coliseum Mine, Clark Mts., dry sandy exposed south slope, *Roos & Roos 4904* (CAS, DS, NY, RSA, UC). San Diego Co.: Warner Hot Springs, *Gander 2944* (POM). NEVADA. Clark Co.: Nelson, 3400 ft, *Low BL-8* (UC). UTAH. Without locality: *Bishop,* 1874 (POM). COLORADO. Boulder Co.: Boulder, *Pammel,* 25 Aug 1913 (TEX). Fremont Co.: Oil Creek, *Brandegee 705* (MO, NY, PH, UC). Pueblo Co.: Pueblo, along railroad track near depot, *Baker, Earle & Tracy 4* (BM, F, GH, MICH, MO, NY, POM, UC, US). Otero Co.: La Junta, 6000–7000 ft, *Beckwith 89* (NY). Bent Co.: Caddoa, Wooton, 13 Sept 1897 (US). Las Animas Co.: near Troy, *Rogers 5396* (MICH, TEX, US). Baca Co.: breaks of East Carrizo Creek 5 mi SW of Kirkwell, 4700 ft, *Weber 5102* (RSA, UC). KANSAS. Rooks Co.: Stockton, low prairie, *Runyon 231* (ARIZ). Wyandotte Co.: Wyandotte, railway yards, *Mackenzie,* 16 Aug 1896 (NY). Wallace Co.: Ft. Wallace, *Bell,* 1867 (PH). Logan Co.: without locality, cultivated soil, *Hitchcock 53* (GH, MO, NY, US). Russell Co.: bluff along Saline River 5 mi N of Russell, barren banks, *McGregor 12675* (US). Barton Co.: Chaflin, *Benke 2437* (F). Anderson Co.: Garnett, *Carlton 362* (ARIZ, US). Hamilton Co.: Coolidge, dry hills, *Smyth 216* (NY, US). Kearney Co.: Deerfield, along A.T.&S.F. railroad, *Blake 978* (LL, US). Ford Co.: without locality, *Eggert,* 24 Aug 1902 (MO). Sedgewick Co.: Wichita, along A.T.&S.F. railroad, *Bartley 1210* (NY, US). Meade Co.: Advance Flag Station, dry grassland, 2550 ft, *Horr 3436* (GH). MISSOURI. Jackson Co.: Kansas City, waste ground, *Bush 8168* (GH, MO, NY, US), *8168A* (CAS). St. Louis Co.: Allenton, *Letterman,* 1897 (MO). St. Louis City: St. Louis, railroad banks, *Eggert,* Aug 1883 (NY). ILLINOIS. Cook Co.: Chicago, *Moffatt 9507* (WIS). Macoupin Co.: along C.&A. railroad near Brighton, *Moffatt 498* (WIS). St. Clair Co.: East St. Louis, *Eggert,* 8 Aug 1897 (DS, F, MO, NY, TEX, UC, US). ARIZONA. Mohave Co.: Kingman, 3300 ft, *Kearney & Peebles 12594* (ARIZ, US). Coconino Co.: Havasupai Canyon, flat areas, *Clover 7007* (SMU). Navajo Co.: Holbrook, *Zuck,* 10 Aug 1896 (F, MO, NY, US). Apache Co.: Navajo Indian Reservation near N end of Carrizo Mts., dry hills, *Standley 7475* (US). Yavapai Co.: Prescott, *Peebles, Harrison & Kearney 8862* (ARIZ, F, POM). Gila Co.: mesa near Rock Creek, 1050 m, *Collom 322* (MICH, MO, US). Maricopa Co.: Agua Caliente, *Thornber 7286* (ARIZ, UC). Pinal Co.: San Tan Mts., *Peebles, Harrison & Kearney 145* (ARIZ). Greenlee Co.: Blue River, *Davidson 757* (DS, UC). Pima Co.: Stone Cabin Canyon, Santa Rita Mts., *Griffiths & Thornber 284* (ARIZ, NY, US). Santa Cruz Co.: 1 mi E of Canelo, desert grassland, *Benson 11494* (DS, POM). Cochise Co.: Paradise, under ditch, *Blumer 2272* (ARIZ, F, US). NEW MEXICO. San Juan Co.: desert draw S of Shiprock, sand, *Waterfall 11730* (RSA, TEX, UC, US). Rio Arriba Co.: Chama River, *Wooton 2897* (US). Taos Co.: Ojo Caliente, 6000 ft, *B. H. Smith,* 25 Aug 1893 (PH). Colfax Co.: Raton, *Cockerell,* 29 Aug 1900 (NY). Santa Fe Co.: Santa Fe, 7200 ft, *Heller & Heller 3746* (BM, DS, GH, MSC, NY, US). San Miguel Co.: Las Vegas, 1900 m, *Bro. Arsene 16203* (BM, F). Quay Co.: Nara Visa, sand soil, *Fisher 72* (US). Bernalillo Co.: Albuquerque, *M. E. Jones 4121* in part (BM, CAS, DS, F, MSC, NY, PH, POM, UC, US). Guadalupe Co.: 1.5 mi ENE of Santa Rosa, sandy soil, *Shinners 21039* (SMU). Catron Co.: S of Bat Cave, 14 mi SW of Horse Springs, gravelly soil on canyon floor, *C. E. Smith 213* (ARIZ, PH). Socorro Co.: Socorro, *Vasey 69* (BM, F), July 1881 (F, US). Lincoln Co.: Gray, ca. 6000 ft, *Skehan 52* (F, GH, MO, NY, POM, UC). Chaves Co.: 20 mi S of Roswell, ca. 3600 ft, *Earle & Earle 307* in part (BM, MO, NY, POM, US). Grant Co.: Mangas Springs, 4770 ft, *Metcalfe 644* (ARIZ, BM, GH, MO, NY, UC, US). Sierra Co.: Kingston, ca. 6600 ft, *Metcalfe 1197* (ARIZ, CAS, MO, US). Hidalgo Co.: near Steins, sandy soils, 4000 ft, *Hershey 3441* (GH). Luna Co.: 3 mi E of Deming, sand dunes, *Shreve 8227* (ARIZ). Dona Ana Co.: Organ Mts., 4500 ft, *Wooton 423* (DS, MO, NY, POM, UC, US). Otero Co.: White Sands, *Wooton,* 24 Aug 1899 (US). Eddy Co.: near US Highway 62 3 mi N of Texas state line, grassy gypsum flat between gypsum hills, *Waterfall 5739* (GH, MO, NY). OKLAHOMA. Cimarron Co.: John Regnier Ranch, Kenton, *Demaree 13384* (GH, NY, SMU). Kay Co.: without locality, *M. White,* 28 July 1898 (NY). Major Co.: bare old road near Cleo, *Stevens 1747* (GH, NY). Payne Co.: Stillwater, *Brillhart 123* (TEX). Oklahoma Co.: prairie 2 mi N of Bethany, clay soil, *Waterfall 1693* (NY). Harmon Co.: abandoned field near Hollis, *Stevens 1119* (GH, POM). Jackson Co.: 3 mi SW of Atlas, clay loam soil, *Prater 81* (TEX). Kiowa Co.: bare roadside near Mountain Park, *Stevens 1236* (DS, GH, MO, US). Comanche Co.: Ft. Sill, *Clemens 11652* (CAS, GH, MO). Murray Co.: 5 mi S of Sulphur, roadside, *Waterfall 12293* (RSA, TEX). Marshall Co.: 3.5 mi W of Kingston, gravel-clay bed of Buncombe Creek, *Goodman 6918* (RSA, SMU, UC). Bryan Co.: near Durant, *Blain 86* (US). TEXAS. Randall Co.: Palo Duro Canyon State Park, Permian redbeds, *Correll & Johnston 17130* (LL). Hardeman Co.: 8 mi NW of Quanah, spots denuded of grass in heavily grazed pasture, *Cory 50127* (NY, SMU). Foard Co.: 6.8 mi S of Crowell, brown-red sandy clay on road shoulder, *Shinners 30792* (SMU). Crosby Co.: near Walker Tank, SW of Spur, green edge of dried-up stream, *Erlanson 1143, 1155* (MICH). Knox Co.: 1 mi E of Benjamin, sandy clay roadside, *Shinners 20794* (SMU). Clay Co.: 11.8 mi NW of Henrietta, red-brown sandy silt and gravel between highway and railroad, *Shinners 15227* (SMU). Grayson Co.: Denison, 725 ft, *Letterman 70* (F, MO, NY). Jack Co.: 10.5 mi ENE of Jacksboro, sandy clay road margin, *Shinners 19012* (SMU). Denton Co.: Denton, sandy loam, *McCart 8913* (TEX). Collin Co.: along railroad near Plano, *Lundell & Lundell 9307* (LL, MICH). Shackelford Co.: 0.4 mi W of S entrance to Ft. Griffin State Park, road shoulder, *Cory 58436* (SMU). Stephens Co.: roadside just W of Caddo, *Thieret 16177* (SMU). Tarrant Co.: near airfield E of Euless, open grounds along highway, *Whitehouse 16438* (MICH, NY, SMU, UC, US). Dallas Co.: Dallas, outcropping limestone, *Lundell 11571* (LL, US, TEX). Martin Co.: Stanton, sandy ground, *Eggert,* 13 June 1900 (MO). Howard Co.: Big Spring, *Tracy 8298* (BM, F, GH, MO, MSC, NY, TEX, US). Mitchell Co.: Colorado, dry sandy open ground, *E. J. Palmer 13773* (MO, US, WIS). Nolan Co.: near Blackwell, sandy soil, open ground, *E. J. Palmer 34590* (MO, NY, PH).

Taylor Co.: Camp Berkeley, disturbed rocky soil, *Tolstead 7688* (GH, LL, NY, SMU, TEX, UC). Eastland Co.: Ranger, *Robinson 49* (GH, TEX). Hood Co.: Granbury, *E. J. Palmer 6517* (F, MO, POM). Ellis Co.: 1 mi W of Ennis, dry sandy soil, *Shackelford 24* (SMU). Gregg Co.: without locality, *C. L. York,* summer 1941 (GH, TEX). Loving Co.: along highway ca. 3 mi W of Mentone, limestone soil, *Warnock 10625* (LL, SMU). Brown Co.: Brownwood, open calcareous ground, *E. J. Palmer 29530* (MO). Comanche Co.: Highway 6 at Leon River 6.75 mi SE of DeLeon, highway shoulder, *Cory 58088* (SMU). Hamilton Co.: road margin E side of Hico, gray-brown silt and limestone gravel, *Shinners 15937* (SMU). McLennan Co.: Waco, roadside sand, *L. D. Smith 805* (TEX). Navarro Co.: Frost, *Mitchan 45* (TEX). El Paso Co.: El Paso, *Tharp 3541* (TEX, US). Hudspeth Co.: between Nulo and Harris Siding, *Ferris & Duncan 2449* in part (CAS, MO, NY). Culberson Co.: near creekside 6 mi NE of Pine Springs, limestone hills, *Waterfall 5768* (GH, MO). Reeves Co.: roadside 14 mi SSE of Orla, fine sandy silt, *Shinners 31060* (GH, SMU). Ward Co.: 2 mi W of Pyote Air Base, gypsum flats, *Waterfall 5492* (CAS, GH, MO, NY). Crane Co.: 13 mi N of Imperial, 2850 ft, *Warnock 15464* (LL). Tom Greene Co.: roadside 7 mi NE of San Angelo, sandy silt, *Shinners 26337* (SMU). McCulloch Co.: 5.5. mi NW of Fife, *Cory 43444* (GH). Bell Co.: Leon River bottom 2.1 mi NE of old Tennessee Valley Church site, *York & York 54565* (SMU, TEX). Pecos Co.: near Pecos River 3 mi from Sheffield, cultivated field, *Ferris & Duncan 2973* (CAS, DS, MO, NY). Schleicher Co.: Colcote Ranch, 11.5 mi N of Eldorado, *Cory 32555* (GH). Williamson Co.: road junction 0.5 mi N of Round Rock, open grassy field, *Gould 8412* (ARIZ, SMU, UC). Brazos Co.: College Station, *Reeves 709* (LL, SMU). Jeff Davis Co.: Geo. Jones Ranch, Davis Mts., flat, *Hinckley 1194* (ARIZ, F, NY, TEX). Presidio Co.: ca. 4–5 mi E of old Rawls ranch, 50 mi S of Marfa, alluvial soil near large dry creek, *Hinckley 2615* (GH, LL). Brewster Co.: Chisos Mts., *Muller 8058* (F, GH, MICH, MO, NY, TEX, US). Terrell Co.: Blackstone Ranch, 13 mi S of Sheffield, cedar-sotol mesa-top, 2750 ft, *Webster 400* (TEX). Crockett Co.: 15 mi N of Juno, limestone soil, 1500 ft, *Warnock & McBryde 15178* (LL, TEX). Sutton Co.: Roy Hudspeth, *Cory 1847* (GH). Blanco Co.: near Blowout Cave, dry sandy soil, *Johnson 290* (TEX). Travis Co.: near Waller Creek, dry calcareous soil, *Harpin, Waldorf & Barkley 13072* (CAS, MO, NY, PH, POM, TEX, UC). Val Verde Co.: Shumla, *Tharp,* 10 Oct 1936 (GH, MO, SMU, UC). Edwards Co.: Highway 55 NW of Rocksprings, *Hardy 43485* (GH). Kerr Co.: Kerrville, *Heller 1777* (ARIZ, BM, F, GH, MICH, MO, MSC, NY, PH, POM, UC, US). Hays Co.: San Marcos, *Fisher 96* (US). Caldwell Co.: Lockhart, *Mackensen 92* (F). Harris Co.: Houston, *Thurow 4* (F, UC, US). Uvalde Co.: Uvalde, *E. J. Palmer 11025* (DS, MO, US). Bexar Co.: San Antonio, clayey soil, *Lindheimer 342* (BM GH, MO, NY, PH, SMU, US). DeWitt Co.: without locality, *Reidel,* 27 Aug 1941 (TEX). Maverick Co.: Farm Road 1021 8 mi S of Eagle Pass, fine sandy silt, *de Anda, Salazar & McCart 8366* (ARIZ, LL, SMU, TEX). Atascosa Co.: dry roadside ditch 1 mi SSE of Pleasanton, black silty clay, *Shinners 24099* (SMU). Karnes Co.: Karnes City Cemetery, dry silty loam, *Johnson 1055* (SMU, TEX). Goliad Co.: Goliad, sandy prairies, *Williams 36* (PH). LaSalle Co.: State Highway 97, 2 mi W of Los Angeles, gray calcareous marl, *Gongora, Garza & McCart 8508* (SMU, TEX). McMullan Co.: 8 mi E of Tilden, gray silty clay and limestone gravel, *Shinners 16971* (SMU). Webb Co.: Laredo, *Palmer 131* in part (F, MICH, NY, US). Kleberg Co.: Kingsville, dry neglected soil, disturbed areas, *Bogusch 11845* (US). Zapata Co.: State Highway 496, 5 mi NE of Bustamante, sandy loam, *Garcia, Esquivel & McCart 55* (SMU). MISSISSIPPI. Oktibbeha Co.: Mississippi Agricultural College, *Pollard 1295* (GH, MO, NY, US).

MEXICO. SONORA: Río Bavispe, near Colonia Oaxaca, S. S. *White 666* in part (MICH). CHIHUAHUA: Carretas, 4800 ft, S. S. *White 2527* (GH, MEXU, MICH); Meoqui, *LeSueur 741* (F, MO, SMU, TEX, UC). COAHUILA: Monclova, *Palmer 131A* (GH, MICH, NY, PH); Saltillo, *Palmer 295* (BM, F, GH, MO, NY, UC, US). NUEVO LEON: Linares, *Frye & Frye 2532* (DS, GH, MO, NY, RSA, UC, US); Monterrey, 1800 ft, *Fisher 41* in part (CAS, DS, F). DURANGO: Durango and vicinity, *Palmer 477* (BM, F, GH, MEXU, MO, NY, UC, US). ZACATECAS: Hacienda de Cedros, flats, *Lloyd 178* (US). SAN LUIS POTOSI: Charcas, *Whiting 1024* (MICH). AGUASCALIENTES: Aguascalientes, *Hartweg 24* (BM). GUANAJUATO: roadside ditch 14 mi NW of Salamanca, sand, *Waterfall & Wallis 13898* (F, SMU). QUERETARO: near Querétaro, *Fr. Basile 118, 162* (US). HIDALGO: Zimapán, *Coulter 780* in part (GH). MEXICO: Penot de los Baños, *Berlandier 617* (BM).

PERU. HUANUCO: along trail near Huánuco, ca. 7000 ft, *Macbride & Featherstone 2335* (F). LIMA: near Lima-Oroya highway at km 70 E of Lima, heavy rocky soil, 1800 m, *Goodspeed & Weberbauer 33067* (GH, MO, UC, US). HUANCAVELICA: Río Mantaro valley below Pampas, 1300–1400 m, *Weberbauer 6516* in part (F, GH). ICA: between Cocharcas and Quilque, sandy soil, *Ferreyra 580* in part (US). CUZCO: Chuyani, right bank of Río Apurímac, sandy and rocky slopes, 2850 m, *Vargas C. 9725* (F, GH, MO, UC). APURIMAC: Río Pachachaca 20 km N of Abancay, sandy soil, 2000 m, *Stork, Horton & Vargas C. 10527* (UC).

COMMON NAMES. It is surprising that such a widespread plant has so few common names. Those that have been reported are Carpet Weed (Texas); Contrayerba (Arizona); Golondrina (Chihuahua); Guesillos (Texas); Jepo (Peru); and Ray Weed (Texas).

TAXONOMY. The name *Kalstroemia laetevirens* has been applied to somewhat larger than average and upright specimens from Arizona and New Mexico, but these individuals simply represent one extreme in the variation to be found in *K. parviflora.*

VARIATION. In addition to the variation in size alluded to above, there may be a considerable amount of variation in the species in terms of leaflet number (three to six pairs), sepal length in fruit (from extending only to the tops of the mature mericarps to the base of the stigma), beak length (from as long as to three times the length of the fruit body), and beak pubescence (trichomes appressed to spreading or absent). However, these characters appear to vary independently and show no ecological or geographical correlation and cannot be used in defining subspecific taxa in this somewhat variable species.

Specimens of *Kallstroemia parviflora* from Peru show a certain amount of variation in flower size and sepal and style length, but this variation is not nearly so wide as that found for the species in North America.

RELATIONSHIPS. The close relationship of *Kallstroemia parviflora* and *K. grandiflora* was first indicated by Norton. The differences between these two species are discussed above.

17. **Kallstroemia hintonii** D. M. Porter, *sp. nov.*

TYPE: Mexico, Michoacán: Apatzingán District, Tepalcatepec, elev. 400 m, woods, fl. light yellow, 25 Aug. 1938, *Geo. B. Hinton 12106* (ARIZ, holotype; CAS, LL, NY, PH, TEX, US, isotypes). This species is named for George Boole Hinton, Sr. (1883–1943), mining engineer and well-known collector of the flora of Mexico.

Annua (raro perennis?); caules prostrati, ad 4 dm longi vel longiores, hirsuti, trichomata lutea, et sericea, trichomata alba, antrorsa; stipulae 5–11 mm longae, 1–2 mm latae; folia elliptica, 2.5–8.5 cm longa, 1.5–4 cm lata, pares foliolorum 5–7, foliola elliptica vel ovata, appresse hirsuta, 9–19 mm longa, 3–8 mm lata, pares in medio laminae maxima; pedunculi quam folia subtendentia multo longiores, flores ergo folia excedentes, ad apicem vix incrassati, anthesin 3–10.5 cm longi, in fructu 5–10.5 cm longi, recti et patentes; flores pentameri in diametro 3–6 cm; sepala lanceolata, 8–12 mm longa, 1.5–3 mm lata, persistentia, quam petala 1/2 breviora, hirsuta, trichomata lutea, anthesin stylum excedentia, in fructu mericarpia amplectentia, quam basin stigmatis longa, margines scariosi, deinde involuti, persistentia; petala alba, deinde luteola, in siccis aurantiaca, ad basin luteo-viridia vel raro rubra, obovata, truncata, ad apicem irregulariter erosa, 15–30 mm longa, 9–20 mm lata, marcescentia; stamina et stylus aequilongus; filamenta ad basin alata; antherae ovoideae, in diametro 1.5–2 mm, rubro-aurantiacae sicut pollen; ovarium ovoideum, glabrum, 1–2 mm in diametro; stylus 6–9 mm longus, cylindricus, ad basin conicus, glaber; stigma clavatum, 10-porcatum, ca. 1 mm longum, papillosum; fructus late ovoideus, 4–5 mm altus, 6–8 mm latus, glaber; rostrum 8–11 mm longum, quam fructificatio duplo longius, cylindricum, ad basin conicum, glabrum; mericarpia 5 mm alta, 2 mm lata, abaxialiter rugosa, latera foveolata, adaxialiter subangulata.

Annual (occasionally perennial?); *stems* prostrate, to 4 dm long or longer, hirsute with yellow and sericeous with white apically-directed trichomes; *stipules* 5–11 mm long, 1–2 mm wide; *leaves* elliptical, 2.5–8.5 cm long, 1.5–4 cm wide; *leaflets* 5–7 pairs, elliptical to ovate, appressed-hirsute, 9–19 mm long, 3–8 mm wide, middle pairs largest; *peduncles* much longer than subtending leaves, extending flowers well above herbage, scarcely thickened distally, 3–10.5 cm long in flower, 5–10.5 cm long in fruit and straight and spreading; *flowers* pentamerous, 3–6 cm in diameter; *sepals* lanceolate, 8–12 mm long, 1.5–3 mm wide, ca. 1/2 as long as petals, hirsute with yellow trichomes, longer than style in flower, in fruit clasping but not entirely covering mature mericarps and reaching to stigma base, only scarious margins becoming involute, persistent; *petals* white, yellowing with age and drying orange, base yellow-green or rarely red, obovate, truncate, apex irregularly notched, 15–30 mm long, 9–20 mm wide, marcescent; *stamens* as long as style; *filaments* winged at base; *anthers* ovoid, 1.5–2 mm in diameter, they and pollen red-orange; *ovary* ovoid, glabrous, 1–2 mm in diameter; *style* 6–9 mm long, cylindrical, base conical, glabrous; *stigma* clavate, 10-ridged, ca. 1 mm long; *fruit* broadly ovoid, 4–5 mm high, 6–8 mm wide, glabrous; *beak* 8–11 mm long, ca. twice length of fruit body, cylindrical, base conical, glabrous; *mericarps* 5 mm high, 2 mm wide, abaxially cross-ridged and slightly keeled, sides pitted, adaxial edge slightly angled. *Fig. 17a, 17b. Map 11.*

FLOWERING DATES. Known to flower in August, September, and December.

DISTRIBUTION AND HABITAT. Found along roadsides at elevations from 300 to 400 m in the general vicinity of Apatzingán, Michoacán, Mexico *(Map 11). Kallstroemia maxima* and *K. pubescens* are known to occur in the same area.

DISTINGUISHING CHARACTERISTICS. *Kallstroemia hintonii* is easily recognized by its combination of prostrate stems, elliptical leaves, five to seven pairs of appressed-hirsute leaflets, fruiting peduncles 5–10½ cm long, extending the flowers well above the herbage, white flowers (petal bases yellow-green or red) 3–6 cm in diameter, hirsute sepals clasping the mature mericarps but not entirely covering them and reaching to the stigma base, the filaments winged at the base, red-orange anthers and pollen, cylindrical style three or four times as long as the ovary, clavate ten-ridged stigma, broadly ovoid glabrous fruit 4–5 mm high and 6–8 mm wide, beak about twice as long as the fruit body, and abaxially cross-ridged and slightly keeled mericarps about 2 mm wide. *Kallstroemia hintonii* is unlikely to be confused with any other species of the genus.

SPECIMENS EXAMINED. MEXICO. MICHOACAN: roadside near Apatzingán, 1000 ft, *Barr, Dennis & Hevly 62–654* (ARIZ); 1 mi S of Apatzingán, *Leavenworth 497* (MICH, MO); roadside 6 mi W of Apatzingán toward Aguililla, *Porter 1426* (DS, GC, GH, IJ, MEXU); cultivated valley 11 mi E of Cuatro Caminos toward La Huacana, edge of raised road, 310 m, *Porter 1414* (GH); dusty roadside 13 mi E of Cuatro Caminos, rocky valley alluvium, 310 m, *Porter 1413A* (GH).

VARIATION. Petal color in *Kallstroemia hintonii* varies from white aging to yellow to white with a red basal spot.

The collections *Porter 1413A* and *Porter 1414* are rather depauperate, but in all morphological respects they appear to be properly placed in this taxon.

RELATIONSHIPS. *Kallstroemia hintonii* shows no close morphological relationship to any other species in the genus.

EXCLUDED SPECIES

Kallstroemia angustifolia (R. Br. in Sturt) Engl. in Engl. & Prantl, Nat. Pflanzenfam. 3(4):88. 1890. = *Tribulopis angustifolia* R. Br. in Sturt, Appendix 70. 1849.

Kallstroemia bicolor (F. Muell.) Engl. in Engl. & Prantl, *loc. cit.* = *Tribulopis bicolor* F. Muell., Frag. Phyt. Austral. **1**:47. 1858.

Kallstroemia cistoides (L.) Endl., Ann. Naturg. Mus. Wein **1**:184. 1836. = *Tribulus cistoides* L., Sp. Pl. **1**:387. 1753.

Kallstroemia hirsuta (Benth.) Engl. in Engl. & Prantl, *loc. cit.* = *Tribulus hirsutus* Benth., Fl. Austral. **1**:289. 1863.

Kallstroemia hystrix (R. Br. in Sturt) Engl. in Engl. & Prantl, *loc. cit.* = *Tribulus hystrix* R. Br. in Sturt, *op. cit.* 69. 1849.

Kallstroemia macrocarpa (F. Muell. in Benth.) Engl. in Engl. & Prantl, *loc. cit.* = *Tribulus macrocarpus* F. Muell. in Benth., *loc. cit.*

Kallstroemia minuta (Leichh. ex Benth.) Engl. in Engl. & Prantl, *loc. cit.* = *Tribulus minutus* Leichh. ex Benth., *op. cit.* 291. 1863.

Kallstroemia pentandra (R. Br. in Sturt) Engl. in Engl. & Prantl, *loc. cit.* = *Tribulopis pentandra* R. Br. in Sturt, *op. cit.* 70. 1849.

Kallstroemia platyptera (Benth.) Engl. in Engl. & Prantl, *loc. cit.* = *Tribulus platypterus* Benth., *op. cit.* 289. 1863.

Kallstroemia ranunculiflora (F. Muell.) Engl. in Engl. & Prantl, *loc. cit.* = *Tribulus ranunculiflorus* F. Muell., *op. cit.* 48. 1858.

Kallstroemia solandri (R. Br. in Sturt) Engl. in Engl. & Prantl, *loc. cit.* = *Tribulopis solandri* R. Br. in Sturt, *op. cit.* 70. 1849.

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