SYSTEMATICS OF *FLAVERIA* (FLAVERIINAE–ASTERACEAE)[1]

A. Michael Powell[2]

Abstract

Twenty-one species are recognized for *Flaveria* in this first revision of the genus since 1915. Three new species are described. Morphological, cytological, chemical, and artificial hybridization approaches were used in the study. Interspecific crosses revealed both weak and strong reproductive barriers among various species of *Flaveria*, *Sartwellia*, and *Haploësthes*. *Flaveria* includes both self-compatible and self-incompatible species, some of which exhibit C_4 photosynthetic metabolism, and all of which produce sulfated flavonoids.

Most of the 21 species of *Flaveria* are native to North America where the taxa occur in Florida and adjacent states, in Kansas-Colorado, south through Texas, New Mexico, and Arizona in the United States, and throughout most of Mexico to Yucatán. Three species also occur in the West Indies, Greater Antilles, and South America, with two weedy taxa extending to Africa and India. One species is restricted to Australia.

The Flaverias have a strong preference for alkaline or gypseous soils, and frequently exist under disturbed conditions. The species in Florida occur only in alkaline soils at pH 7.2–8.2 (Long & Rhamstine, 1968). A few species, particularly the weedy *F. trinervia* and *F. bidentis*, may occur in various soil types. In the arid southwestern United States and northern Mexico the species are commonly found in moderate to strong saline or gypseous soils close to permanent or ephemeral water sources such as rivers, creeks, irrigation canals, fields, roadsides, ponds, and bolsons. The distribution of most species consists of colonies that are somewhat localized and spotty throughout the range. Seldom do Flaverias exist in continuous populations, except with coastal taxa where the habitats are continuous. Accordingly, most species are endemic, as though restricted by localized or regional edaphic and climatological features.

This is the first comprehensive study of *Flaveria* since Rydberg (1915) recognized 16 species of the genus in his treatment of Helenieae for the *North American Flora*. The account by Rydberg is strikingly different from the original mono-

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[2] Department of Biology, Sul Ross State University, Alpine, Texas 79830.

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graphic account of *Flaveria* in which Johnston (1903) recognized 15 species. Three species, one each from Mexico, Florida, and Arizona have been described since 1915, and three additional species, two from Mexico and one from Texas, are described in the present treatment.

Flaveria is related to *Sartwellia* (Turner, 1971) and *Haploësthes* (Turner, 1975). These three genera constitute the subtribe Flaveriinae which belongs in or near Senecioneae in the opinion of Powell & Turner (1974). Rydberg (1915) treated *Flaveria* and *Sartwellia* as the only members of Flaveriinae in the traditional tribe Helenieae. *Haploësthes* was positioned by Rydberg (1927) in the Senecioneae (subtribe Senecioninae). Turner & Johnston (1961) proposed that *Haploësthes* is allied with the Flaveriinae, and maintained that the three genera belong together in Senecioneae rather than in the unnatural tribe Helenieae. Ornduff et al. (1963) have suggested that the inclusion of *Flaveria* and *Sartwellia* in Heliantheae (or Helenieae) is less taxing morphologically and cytologically than would be their inclusion with Senecioneae. A more detailed discussion of Flaveriinae and its tribal relationships is presented by Turner & Powell (1977), Nordenstam (1977), and Baagøe (1977). The present study offers little information regarding the tribal redisposition of the Flaveriinae, but hybridization data (see below) document the relationship of *Haploësthes* as proposed originally by Turner & Johnston (1961).

MORPHOLOGY

In habit Flaverias vary from erect or spreading shrubs to robust or delicate annuals. In size some plants reach 4 m high (particularly *F. pringlei*), while the smallest individuals at ca. 6 cm may occur among populations of the desert annual taxa. Most of the species are rather stout herbaceous annuals or perennials which range from 0.5 to 2.5 m in height.

Branching stems and leaves are opposite and decussate in all species. The leaves are basally connate to weakly so in all taxa except *F. chloraefolia* where they are strikingly perfoliate. The plants typically are glabrous or microscopically pubescent except in *F. pubescens* where stems and leaves are covered rather densely with macroscopic hairs.

In capitulescence Flaverias are notable among the Asteraceae for their reduced and secondarily aggregated heads or synflorescences (Stuessy, 1976) in some species. The number of disc florets per head ranges from 1 to 15, with or without one ligulate ray floret. Synflorescences of maximum reduction are found in *F. trinervia* and *F. australasica* which have 1–2 floret heads clustered in axillary glomerules. Two major phyletic lineages are seemingly marked by number of phyllaries per head, one line with 5–6 phyllaries and the other with 3–4 phyllaries. Derived annuals may have fewer phyllaries per head.

The achenes of all Flaverias are black, ribbed, glabrous, and epappose except in *F. chloraefolia* and *F. mcdougallii* which have small pappus scales. In general *Flaveria* is characterized by reduced floral features which are similar in most species. In fact, most species differ by few morphological traits. Most dependable in delimiting taxa are differences in distribution, habit, foliage, capitulescence, and presence or absence of ray florets.

PHENOLOGICAL AND BREEDING CONSIDERATIONS

Within broad latitudinal ranges the flowering periods of different *Flaveria* species are generally overlapping. The Florida species seem to reach peak flowering in the fall and early winter, but may flower earlier or later, as is the case for *F. brownii* along the Texas coast, the species of southern Mexico, and other taxa. The xerophytic species of the southwestern United States and northern Mexico may flower from spring through fall depending upon moisture. Under controlled conditions in the greenhouse, annual species were noted to flower at vegetative maturity any time during the year, but they seemed to display most vigor from mid-summer into the fall. Perennials from Florida, Texas, and central Mexico also flowered from mid-summer through the fall. *Flaveria pringlei* of southern Mexico and *F. pubescens* from San Luis Potosí did not flower until late fall or winter, in the style of short-day plants.

Four of the annual species, *F. australasica*, *F. trinervia*, *F. bidentis*, and *F. campestris*, are self-compatible. The other annuals, *F. anomala*, *F. ramosissima*, *F. palmeri*, and probably *F. intermedia*, are basically self-incompatible as are all the perennial taxa so far as known. Self-fertilization occasionally may be stimulated by rubbing heads together as was done in attempts to secure artificial hybrids. The out-crossing species exhibit insect-pollinated florets in small heads that are secondarily aggregated into clusters that evidently attract pollinators. In some species the heads are discoid, while in others at least a few heads per cluster contain one ray floret each with the ligule being prominent to inconspicuous. In several species, most spectacularly in *F. anomala*, the uniligulate heads have peripheral arrangement in the clusters, and thus display the effect of a typical radiate composite head.

The four self-compatible annuals show reduced morphological features that are suggestive of the trend toward self-fertilization (Ornduff, 1966). The capitulescences of these species are reduced, inconspicuous, axillary glomerulate clusters, particularly in *F. trinervia* and *F. australasica*, and surely are not as attractive to insects as are the flower arrangements of other species. Furthermore, the self-fertilizing annuals have tiny, nearly microscopic ligules, and exhibit a low number of florets per head (1–8), smaller disc florets, and a smaller number of pollen grains per anther.

The self-compatible Flaverias characteristically produce only one or rarely two viable achenes per head when grown under insect free conditions. The viable achenes usually are produced by perfect disc florets which in most species exhibit shorter fruits than those of the pistillate ray florets. However, when intentionally crossed, or under field conditions, complete complements of mature fruits per head are often produced. Under natural conditions, therefore, it is assumed that a dual breeding system of self- and cross-pollination is operative in producing both uniform and variable genotypes.

The self-compatible species of *Flaveria* have widespread distributions as compared to the relatively localized self-incompatible taxa. This situation has been noted in other plant groups (Stebbins, 1957) where self-pollinators tend to be successful colonizers under ecologically variable conditions. The selfpollinating Flaverias are the only successful "weedy" species of the genus. I believe that the self-compatible species are derived, as suggested by specialized morphological features, annual habit, and breeding system (Stebbins, 1957; Ornduff, 1966).

CHROMOSOMAL CONSIDERATIONS

Chromosome numbers of $n = 18$ are known for 18 of the 21 species of *Flaveria* (Powell & Powell, 1977, 1978; Keil & Stuessy, 1977). The three taxa for which chromosome numbers are unknown are from Mexico: *F. angustifolia*, *F. intermedia*, and *F. vaginata*. *Flaveria* is consistently diploid, with two exceptions, and a base number of $x = 18$ seems certain for the genus. Anderson (1972) reported $n = 9$ for one collection of *F. campestris*, a species that otherwise is $n = 18$. Anderson concluded that the $n = 9$ was a case of polyhaploidy rather than a relict ancestral diploid, and I agree. Two collections of *F. pringlei* (*Dillon 681*; *Hartman et al. 3834*) were counted as $n = 36$, the only polyploids known for the genus or the subtribe; *F. pringlei* also is $n = 18$.

The related genera *Sartwellia*, with all four species counted, and *Haploësthes*, with five of six taxa counted, are uniformly $n = 18$ (Turner, 1971, 1975). Thus the base number of Flaveriinae seems well established as $x = 18$.

HYBRIDIZATIONS

All crosses were conducted in a greenhouse with plants grown from perennial bases, lower stem cuttings, or from seed. Crosses were attempted by rubbing heads together once or twice per day for two to four days until the styles had withered. Heads were bagged with thin plastic to prevent accidental pollination. Achenes usually matured in about two weeks, after which they were collected and stored at room temperature for one to several weeks before planting. Germination usually occurred in one or two weeks. Seedlings grew to flowering stages in one to several months.

Crossability estimates, pollen stainability (PS) percentages, and meiotic observations (Table 1) were obtained by procedures and techniques outlined in Powell (1972). In Table 1 absence in some cases of pollen stainability (PS) and meiotic observations signifies that no F_1 hybrids of the particular combination could be grown to maturity. Artificial crosses between self-sterile species, both closely and distantly related, were found in many instances to stimulate selfing. Crosses involving a self-compatible female parent (*F. australasica*, *F. bidentis*, *F. campestris*, or *F. trinervia*) often gave rise to a mixture of selfs and hybrids.

The recognition of hybrid as opposed to selfed progeny was sometimes difficult. Flaverias typically are reduced in vegetative and floral characters. While the species are easily recognized as distinct in their natural habitats, artificial hybrids between morphologically similar parents are often difficult to identify. Consequently, caution was always used in characterizing hybrid progeny. With certain combinations (e.g., *F. palmeri* × *F. anomala*) it was necessary to evaluate the low PS and asynaptic meiotic behavior (Table 1) before being sure the progeny were hybrids. In instances where PS and meiotic behavior failed to

TABLE 1. Artificial hybrids with crossability and indices of interfertility.

F_1 Hybrid combinations	Crossability	Pollen Stainability (%)	Meiotic Observations
	INTERSPECIFIC CROSSES (*Flaveria*)		
Flaveria anomala		97	
× *F. bidentis*	Zero[a]		
× *F. palmeri*	Low–medium	13	Highly asynaptic, 6–12 heteromorphic II, the remainder I
× *F. trinervia*	Zero[a]		
F. australasica		92	
× *F. bidentis*	Medium[b]		
× *F. linearis*	Low–high[c]	2	Highly asynaptic, 5–10 II or pseudoassociations, the remainder I
× *F. palmeri*	Medium	19	Seemingly regular, 18 II, but with slight II heteromorphism
× *F. trinervia*	High[c]		
F. bidentis		83	
× *F. anomala*	Medium[c]		
× *F. campestris*	Medium–high[c]	45	Mostly regular with 18 II; occasional cells with 17 II, 2 I
× *F. trinervia*	High[c]	62	
F. brownii		87	
× *F. anomala*	Very low		
× *F. floridana*	High	64	Seemingly regular, 18 II
× *F. oppositifolia*	High	36	Seemingly regular, 18 II; occasional pseudoassociations at diakinesis; occasional cells with 17 II, 2 I
F. campestris		87	
× *F. anomala*	Low		
× *F. bidentis*	Medium	49	Seemingly regular, 18 II, but with slight heteromorphic pairing; occasionally 17 II, 2 I; occasional laggards at anaphase I
× *F. palmeri*	Low–medium		
× *F. trinervia*	Medium		
F. chloraefolia		78	
× *F. linearis*	Medium		
× *F. mcdougallii*	Zero[a]		
× *F. pringlei* ($n = 36$)	Zero[a]		
× *F. trinervia*	Zero[a]		
F. floridana		61	
× *F. brownii*	High	47	Regular, 18 II; possibly with some slight II heteromorphism
× *F. linearis*	Medium–high	65	Regular, 18 II; occasionally 3–4 early separating II, or pseudoassociations
× *F. palmeri*	High	3	Irregular, 12–17 II, 12–2 I; occasionally appearing regular with 18 II; frequently pseudoassociations; frequent laggards at anaphase I
× *F. pringlei* ($n = 18$)	Zero[a]		
× *F. sonorensis*	Very low		
F. intermedia		96	

TABLE 1. (Continued)

F_1 Hybrid combinations	Crossability	Pollen Stainability (%)	Meiotic Observations
F. linearis		81	
× *F. australasica*	Very low	11	Irregular, 13–18 II, 10–0 I; frequent laggards at anaphase I; heteromorphic II
× *F. chloraefolia*	Very low	33	Regular, 18 II; rarely 17 II, 2 I
× *F. floridana*	Medium–high	65	Regular, 18 II; possible pseudoassociations
× *F. mcdougallii*	Zero[a]		
× *F. oppositifolia*	High	19	Mostly regular, 18 II; occasionally early separating II; some lagging at anaphase I
× *F. palmeri*	High	12	Irregular, 14–17 II, 8–2 I; obvious II heteromorphism and pseudoassociations; 1–4 laggards common
× *F. pubescens*	Medium		
F. mcdougallii		80	
× *F. chloraefolia*	Zero[a]		
× *F. linearis*	Zero[a]		
× *F. oppositifolia*	Zero[a]		
F. oppositifolia		84	
× *F. anomala*	Zero[a]		
× *F. brownii*	Low–medium	54	Mostly regular, 18 II, or with 2–4 I and heteromorphic II; occasionally 1–4 laggards
× *F. linearis*	High	8	Regular, 18 II; rarely 17 II, 2 I
× *F. mcdougallii*	Zero[a]		
× *F. pringlei* ($n = 18$)	Zero[a]		
× *F. pubescens*	Low–high	81	Mostly regular, 18 II, less often 13–17 II, 10–2 I
× *F. sonorensis*	Zero[a]		
F. palmeri		99	
× *F. anomala*	Zero–medium[a]	22	Highly asynaptic, 7–16 II, obviously heteromorphic, the remainder I
× *F. australasica*	Zero[a]		
× *F. campestris*	Zero–low[c]		Regular, 18 II
× *F. linearis*	Very low	11	Highly irregular, 13–18 II, 10–0 I; anaphase I lagging and unequal segregation; occasional anaphase I bridges
F. pringlei ($n = 18$)		96	
× *F. anomala*	Zero[a]		
× *F. chloraefolia*	Very low		
× *F. floridana*	Zero[a]		
× *F. oppositifolia*	Very low–zero		
F. pringlei ($n = 36$)		92	
× *F. pringlei* ($n = 18$)	Very low		
F. pubescens		95	
× *F. linearis*	Low		
× *F. oppositifolia*	Zero–medium	74	Mostly regular, 18 II; usually 2–3 slightly heteromorphic II

TABLE 1. (Continued)

F₁ Hybrid combinations	Crossability	Pollen Stainability (%)	Meiotic Observations
F. ramosissima		99	
× *F. anomala*	Zero–high	32	Seemingly regular, 18 II; slightly irregular, 16–17 II, 2–4 I; or irregular, 12–14 II, 12–8 I, pseudoassociations
× *F. palmeri*	Low	11	Mostly regular, 18 II; occasionally 2–4 I
F. sonorensis		74	
× *F. floridana*	Zero[a]		
× *F. oppositifolia*	Zero[a]		
F. trinervia		83	
× *F. anomala*	Medium[c]	35	Asynaptic, 12–13 II and the remainder I; pseudoassociations at diakinesis
× *F. bidentis*	High[c]	14	Seemingly regular, 18 II; occasional laggards
INTERSPECIFIC CROSSES (*Sartwellia*[d])			
Sartwellia flaveriae		87	
× *S. gypsophila*	Very high	52	Regular, 18 II; bivalents appear heteromorphic
S. gypsophila		99	
× *S. flaveriae*	Low–medium	40	Regular, 18 II
× *S. puberula*	Medium	76	Regular, 18 II
S. mexicana		88	
× *S. puberula*	Very high	92	Regular, 18 II
S. puberula			
× *S. mexicana*	Medium–very high	88	Regular, 18 II; rarely 1 early separating bivalent
INTERSPECIFIC AND INFRASPECIFIC CROSSES (*Haploësthes*[d])			
Haploësthes greggii var. *texana* (Ter.[e])		98	
× *H. greggii* var. *texana* (Grand.[e])	Very low		
H. greggii var. *texana* (Grand.[e])			
× *H. greggii* var. *texana* (Ter.[e])	Low–medium	64	Mostly regular, 18 II; in some cells 1–3 pseudoassociations or 2–6 unpaired chromosomes; slightly heteromorphic II present in some cells
H. greggii var. *texana* (Ter.[e])			
× *H. robusta*	Zero–medium		
H. robusta			
× *H. greggii* var. *texana* (N. Mex.[e])	Low–medium	22	Mostly regular, 18 II; heteromorphic II evident in some cells; occasionally 1–2 I
H. robusta			
× *H. greggii* var. *texana* (Grand.[e])	Medium	65	Seemingly regular, 18 II; in some cells 2–3 possible pseudoassociations

TABLE 1. (Continued)

F_1 Hybrid combinations	Crossability	Pollen Stainability (%)	Meiotic Observations
H. robusta			
× *H. greggii* var. *texana* (Ter.[e])	High	69	Mostly regular, 18 II; 2–4 unpaired chromosomes present in some cells; slightly heteromorphic II present in some cells
	INTERGENERIC CROSSES		
Haploësthes robusta			
× *Sartwellia puberula*	Very low	6[f]	Highly irregular, 9–12 II or pseudobivalents, 18–12 I; rarely 16–18 heteromorphic pairs
Haploësthes greggii var. *texana*			
× *Flaveria mcdougallii*	Very low		
Sartwellia puberula			
× *Flaveria chloraefolia*	Medium	0[g]	Highly asynaptic, 36 I or 1 II, 34 I; numerous laggards; unequal anaphase I segregation; laggards common; micronuclei common
× *Flaveria mcdougallii*	Very low (1 achene)		
Sartwellia mexicana			
× *Flaveria mcdougallii*	Zero		

[a] Crosses attempted, resulting in no seed-set.
[b] Seed germination poor, seedlings did not survive.
[c] Crossability estimated from seed-set; probably results from selfing in the self-compatible species.
[d] All species self-incompatible.
[e] Abbreviations of localities as follows: Ter. = Terlingua, Texas; Grand. = Grandfalls, Texas; N. Mex. = New Mexico.
[f] Pollen grains of several sizes; most obviously malformed.
[g] Three hybrid plants were grown to flowering stages; pollen was irregular in shape, obviously malformed.

indicate either selfing or hybridity, F_2 generation crosses often proved to be a convincing test in that F_2's could not be formed in most combinations (see below). Of course, hybrid progeny of crosses between species with clear morphological differences (e.g., rayed × discoid), and intergeneric crosses, were easily identified as such.

INTERSPECIFIC

Flaveria.—Artificial hybridizations were attempted with 16 species of *Flaveria* (Table 1). Interspecific F_1 hybrids were readily obtained from most combinations, even though the crossability of certain combinations did vary. Crossability was very low or zero (no viable seeds) in some combinations, but usually only zero crossability prevented the formation of experimental hybrids. Most F_1 hybrids were moderately to highly fertile as assessed from PS and meiotic behavior. Although PS (ranging from 2–99% in F_1 hybrids and parents; Table 1) must be viewed with caution (A. Jones, 1976), it may be useful in evaluating interfertility when compared with another criterion such as meiotic behavior.

Meiotic behavior in parental species is regular. In F_1 hybrids meiotic behavior varied from: regular, with seemingly normal bivalent formation; slightly irregular, with a few unpaired chromosomes, pseudoassociations, and/or heteromorphic bivalents; and highly irregular with numerous unpaired chromosomes in meiosis I configurations (Table 1). As expected, those combinations with grossly irregular meiosis were highly sterile. Multivalents were not observed in meiotic configurations of F_1 hybrids, suggesting an absence of translocations in the evolution of *Flaveria* species. The common observation of heteromorphic bivalents and pseudoassociations does suggest that small structural rearrangements and genic differences were involved with speciation. More drastic chromosomal and genic differences can be suspected where genomes of the interspecific hybrids are highly asynaptic.

Hybridizations were attempted between species that are relatively distantly related and between those that are presumably closely related, as judged from morphological and other characters. The experimental technique was not generally useful in assessing degrees of interspecific relationships in that the crossability and fertility data, themselves highly variable in F_1's, did not always correlate with seemingly obvious relationships. The F_1 hybrids of some distantly related species showed moderately high percentages of stainable pollen and quasi-regular meiosis, while the F_1's of more closely related species sometimes exhibited low PS and irregular meiosis. The interfertility measurements of some combinations corresponded with relationships which are suggested by morphology. Hybridization data with bearing on species relationships will be discussed in the taxonomic portions of this paper.

The ease with which wide-species crosses could be obtained was initially somewhat surprising. However, the same situation is true in *Perityle* (Powell, 1972), *Vernonia* (S. Jones, 1976), and other groups where the perennial taxa are exclusively allopatric and outcrossing, as they are in *Flaveria*. Perhaps reproductive barriers at the F_1 level are weak because they were not selected for in isolated populations. The strongest parental reproductive barriers in *Flaveria* are found to exist in the annual species. Several annual taxa occur sympatrically, even intermixed with other annual or perennial species, and yet I have not seen any evidence of natural hybridization. Perhaps this is because the annuals, which tend to have wider distributions, especially the weeds, are forced to develop reproductive barriers early in evolutionary divergence. Such evolutionary patterns have been noted among many other plant groups (Stebbins, 1950; Grant, 1971; Gadgil & Solbrig, 1972; Raven, 1976).

The true test of interspecific sterility in *Flaveria* is exhibited before or after the F_2 zygote level, at least under experimental conditions. Second or backcross generations were attempted with most of the F_1 combinations, but F_2's or backcrosses were obtained only with the following: *F. bidentis* × *F. campestris*; *F. bidentis* × *F. trinervia*; *F. brownii* × *F. floridana* (fertile); *F. campestris* × *F. bidentis*; *F. floridana* × *F. linearis*; *F. floridana* × *F. palmeri*; *F. linearis* × *F. chloraefolia*; *F. linearis* × *F. floridana* (fertile); *F. oppositifolia* × *F. brownii* (fertile); *F. oppositifolia* × *F. linearis*; *F. ramosissima* × *F. anomala*; *F. ramosissima* × *F. palmeri* (fertile); *F. trinervia* × *F. anomala*; *F. trinervia* × *F. bidentis*. All these crosses were sterile except for putative F_2's between the combinations indicated above as fertile. These exhibited moderate fertility based upon PS and meiotic behavior. However, the species are so similar morphologically (and theoretically related) that it was not possible to be certain that the plants tested were indeed second generation hybrids. The F_1's of the above crosses were at least moderately fertile (Table 1). Further comments on the possible significance of the F_2's can be found in discussions of the species (see Taxonomy).

Sartwellia and Haploësthes.—Interspecific crosses were attempted also between the species of *Sartwellia* and *Haploësthes* (Table 1). All of the F_1 *Sartwellia* combinations showed relatively high crossability and fertility, suggesting that speciation in the genus might have been recent. Also, the Sartwellias are more homogeneous morphologically and ecologically than are the Flaverias (Turner, 1971; Powell & Turner, 1976). The species are perennial except for the annual *S. flaveriae*. One F_2 combination, *S. flaveriae* × *S. gypsophila*, was sterile, but not many F_2 crosses were attempted with the Sartwellias.

Both interspecific and infraspecific crosses were obtained with two of the three species of *Haploësthes*; material of *H. fruticosa* was not available (Turner, 1975). As was the case in *Sartwellia*, the interspecific combinations exhibited good crossability and interfertility. All the species are perennial. One backcross combination, *H. robusta* × *H. greggii* × *H. robusta*, was moderately fertile. Interestingly, the infraspecific hybrids seemed to be slightly less interfertile than did the interspecific crosses (Table 1), but this stage of investigation is still in progress.

INTERGENERIC

Crosses have been attempted between various species of *Flaveria*, *Sartwellia*, and *Haploësthes*, involving over 30 different intergeneric combinations. Thus far only two intergeneric crosses have been successful (Table 1). The remarkable artificial intergeneric hybrids are intermediate in morphology between the grossly different species involved, and they are absolutely sterile by all indications (Table 1).

The results of experimental hybridizations strongly support the generic integrity of *Flaveria*, *Sartwellia*, and *Haploësthes*. Interspecific F_1 hybrids are easily synthesized within each of the three genera. Intergeneric crosses are difficult to synthesize and sterile, thus clearly delimiting the genera by this experimental criterion. The genera also are clearly delimited morphologically. The experimental data support a relationship of *Haploësthes* with the Flaveriinae as proposed originally by Turner & Johnston (1961), through formation of the hybrid combination *Haploësthes robusta* × *Sartwellia flaveriae* (Table 1). The artificial intergeneric hybrid *Sartwellia puberula* × *Flaveria chloraefolia* supports a generic relationship that has long been accepted (Rydberg, 1915; Turner, 1971).

Experimental data (Table 1) have been useful in assessing the relationship of *Flaveria mcdougallii*, a recently described species from the Grand Canyon of Arizona (Theroux et al., 1977). The authors questioned the generic relationship of *F. mcdougallii* in that the new entity exhibits at least some features which are intermediate between or characteristic of both *Flaveria* and *Sartwellia*, but they assigned *F. mcdougallii* to the former genus based upon the preponderance of data. Theroux et al. (1977) furthermore concluded that "If morphology alone were the deciding factor, the continued acceptance of *Flaveria* and *Sartwellia*, and possibly even *Haploësthes* as distinct genera might be questioned." Artificial crosses (Table 1) were attempted between *F. mcdougallii* and two species of *Sartwellia*, one species of *Haploësthes*, and three species of *Flaveria* in an effort to further evaluate the generic relationship of the new species. In all cases crossability was very low or zero, suggesting that *F. mcdougallii* is at least as isolated (or more so) from all three genera as they are from each other (Table 1). Although I agree with Theroux et al. (1977) that *F. mcdougallii* exhibits intermediate features, I do not believe that this obviously derived species bridges the morphological gap between three genera which are, in my opinion, both morphologically and biologically distinct. In fact, the experimental data thus far suggest that *F. mcdougallii* could be recognized as a monotypic genus (see Taxonomy).

NATURAL HYBRIDIZATION

Long & Rhamstine (1968) have reported evidence for the origin of *F.* × *latifolia* in Florida as a result of natural interspecific hybridization between *F. floridana* and *F. linearis*. They did not test the hypothesis experimentally because they were unable to grow the suspected parents in the greenhouse or garden. Both *F. floridana* and *F. linearis* have grown vigorously in the SRSU greenhouse, and F_1 interspecific hybrids are readily formed (Table 1). Furthermore, the *F. floridana* × *F. linearis* combination (and reciprocal) has given rise to seemingly fertile F_2 hybrids.

The interfertility of *F. linearis* × *F. floridana* supports the possibility of hybrid origin for *F.* × *latifolia* as concluded by Long & Rhamstine (1968). However, I have not been able to recognize *F.* × *latifolia* as a distinct taxon among collections from Florida. In fact, observations lead me to believe that *F. floridana* and *F. linearis* are spatially and ecologically isolated, or nearly so. If the two species do undergo natural hybridization, it is likely of sporadic occurrence, and the hybrids do not represent a populational entity in the sense of a species as proposed by Long and Rhamstine. At any rate, the morphological similarity of the two species causes difficulty in the positive recognition of experimental F_1 or F_2 hybrids.

Natural hybridization as a general phenomenon in *Flaveria* appears to be precluded by internal reproductive barriers and/or spatial isolation. Generally speaking any introgression would seem to be prevented by F_1 or F_2 sterility or by geographic isolation, except perhaps in *F. floridana* × *F. linearis*. The perennial species of *Flaveria* are all isolated geographically, with the possible exception of *F. floridana* and *F. linearis*, and some of the species in Puebla-Oaxaca, Mexico (see Taxonomy). The weedy annual species which may exist sympatrically exhibit the strongest internal reproductive isolation. I have not observed any indication of natural hybridization in *Flaveria* either from field investigations or from examination of exsiccatae, with the possible exception of *F. floridana* and *F. linearis*.

CHEMICAL CONSIDERATIONS

A preliminary flavonoid analysis of the Flaveriinae was published by Al-Khubaizi (1977) who found that ca. 85% of the total flavonoids in this group are sulfated. Eleven species were examined: *Flaveria anomala, F. brownii, F. campestris, F. chloraefolia, F. palmeri, F. pringlei,* and *F. trinervia*; *Sartwellia flaveriae* and *S. puberula*; *Haploësthes greggii* var. *texana* and *H. robusta*. Among all the taxa, 65 components (spots) were detected chromatographically, and structural determination was realized for 17 compounds; 13 sulfated and 4 non-sulfated. Thirteen of the identified flavonoids were previously unknown.

Al-Khubaizi found that the negatively charged sulfated flavonoids may be mono-, di-, or tri-sulfated, and based upon skeletons of kaempferol, quercetin, isorhamnetin, patuletin, or spinacetin. Also the sulfates may be attached directly to the flavonoid skeleton or to a sugar (in glycosides).

At the time Al-Khubaizi (1977) began her study, sulfated flavonoids were poorly known, difficult to isolate, and difficult to characterize for structure. Consequently, much of the preliminary work by Al-Khubaizi involved the elucidation of techniques for working with sulfated flavonoids. Her success in elaborating several new techniques, including separation by paper electrophoresis and structure identification by UV spectral methods (not previously applied successfully in the study of sulfated flavonoids), should provide a basis for further investigations.

Perhaps the major systematic value of the preliminary flavonoid data is that they support the subtribal relationship of *Flaveria*, *Sartwellia*, and *Haploësthes*. The three genera have in common many of the sulfated flavonoids and an array of the more common flavone and flavonol aglycones and glycosides. Interspecific relationships in *Flaveria* and the other genera can not yet be evaluated on the basis of flavonoid chemistry until more compounds are known for more species.

Sulfated flavonoids are now known to occur in a broad spectrum of both monocot and dicot taxa (Al-Khubaizi, 1977). Whether or not the ability to synthesize sulfated flavonoids is the result of environmental adaptation is still open to question. Plants inhabiting saline, gypseous, or marshy areas tend to produce sulfated flavonoids. The latter is certainly true in the Flaveriinae where many species occur in saline or gypseous substrates. But in a broader survey of plant species in various habitats, Molly Whalen (pers. comm.) has found that plants in a wide variety of habitats may produce sulfated flavonoids. Thus an adaptive role for sulfated flavonoids remains to be shown.

Future flavonoid investigations in *Flaveria* (and related genera) should involve an attempt to identify the major compounds of all the species so that interspecific and intergeneric comparisons can be made. Furthermore, any adaptive correlation between flavonoid complements and C_4 or C_3 metabolism can be investigated when more data are available.

KRANZ SYNDROME AND C_4 METABOLISM

Smith & Turner (1975) discovered the Kranz syndrome and C_4 photosynthetic metabolism in *Flaveria* during their survey of the Asteraceae for this physiological

TABLE 2. Species of *Flaveria* with C_3 and C_4 photosynthetic metabolism, as determined by C^{12}/C^{13} ratios (Walter Brown, pers. comm.).

C_3 Species	C_4 Species
1. *F. angustifolia*	1. *F. australasica*
2. *F. anomala*	2. *F. bidentis*
3. *F. chloraefolia*	3. *F. brownii*
4. *F. floridana*	4. *F. campestris*
5. *F. linearis*	5. *F. cronquistii*
6. *F. mcdougallii*	6. *F. intermedia*
7. *F. oppositifolia*	7. *F. palmeri*
8. *F. pringlei*	8. *F. trinervia*
9. *F. pubescens*	9. *F. vaginata*
10. *F. ramosissima*	
11. *F. robusta*	
12. *F. sonorensis*	

trait. In Asteraceae they found C_4 metabolism to occur in five small genera of subtribe Coreopsidinae (Heliantheae), in all members of the genus *Pectis* (Tageteae), and in four species of *Flaveria*. According to the above survey, *Flaveria* is unique in Asteraceae in that both C_3 and C_4 species occur in the same genus. Both *Sartwellia* and *Haploësthes* are characterized by C_3 species (W. V. Brown, pers. comm.).

Additional studies of the Kranz syndrome in *Flaveria* (W. V. Brown, pers. comm.) revealed five other C_4 species for a total of nine in the genus (Table 2). Furthermore, through leaf anatomical studies of most *Flaveria* species, Brown (pers. comm.) has concluded that certain species (e.g., *F. oppositifolia*, *F. linearis*, *F. floridana*) are intermediate between non-Kranz and Kranz anatomy. According to Brown, *Flaveria* is unique in having the intermediate species. Other genera that contain both non-Kranz and Kranz species do not have intermediates, except possibly the single species *Euphorbia acuta*. Thus some of the Flaverias seem to be in the process of evolution from non-Kranz to Kranz physiology.

In angiosperms C_4 metabolism is a fairly widespread, derived process, perhaps having several independent origins (Björkman & Berry, 1973; Smith & Brown, 1973; Kennedy & Laetsch, 1974; Brown, 1977). The Kranz syndrome also is derived in *Flaveria*, occurring mostly in the advanced annual species. If my phylogenetic speculation is correct (see below), C_4 metabolism has evolved twice in *Flaveria*.

Björkman & Berry (1973) emphasize the adaptive significance of C_4 metabolism in arid land plants. The annual C_4 species of *Flaveria* certainly thrive under arid conditions, although possibly under mesic conditions as well. *Flaveria brownii*, a weak perennial C_4 species, occupies mesic-saline habitats along the Texas Gulf Coast. The C_3 species of *Flaveria* also exist under both xeric and mesic conditions. Since both C_3 and C_4 species of *Flaveria* thrive in relatively arid and saline habitats, it does not seem likely that C_4 taxa evolved in selective response to these stringent environmental factors alone. Instead, I suspect that the adventitious annuals found C_4 metabolism to be advantageous in occupying a wide variety of habitats, including those dry and salty. *Flaveria brownii* also appears to be a derived and geographically dispersed species (see Taxonomy).

EVOLUTIONARY CONSIDERATIONS

The present distributional center for Flaveriinae is in the general Chihuahuan Desert region (Turner, 1971, 1975; present paper). All the species of both *Sartwellia* and *Haploësthes* are located within this region, as are many species of *Flaveria*, while several perennial species of *Flaveria* are distributed elsewhere in Mexico, Texas, and Florida.

Current distribution suggests that the Flaveriinae might have originated in the north central highlands of Mexico, and the centralization of Flaveriinae in the Chihuahuan Desert suggests that evolution of the group might have been correlated with formation of the desert in the Pliocene or Pleistocene (Axelrod, 1948; Sharp, 1953). The Flaveriinae could have evolved rapidly in response to Pleistocene climatic fluctuations, extending from mesic habitats into increasingly xeric and saline surroundings.

Of the three genera in Flaveriinae, *Haploësthes* (Turner, 1975) seems to possess the most ancestral traits, including larger heads, 5–8 ray florets, pappus of 25–40 setose bristles, and pubescent achenes (with scattered 2-celled hairs). *Sartwellia* (Turner, 1971) has smaller heads, five ray florets with reduced ligules, pappus of scales and bristles, and pubescent achenes. *Flaveria* is uniformly reduced in terms of these characters, having small heads with 1–15 florets, heads discoid or with one ray floret, pappus absent (except squamellate in two species), and glabrous achenes. *Flaveria* is by far the most successful genus in the Flaveriinae, with its 21 species, as compared with the 4 species of *Sartwellia* and 3 species of *Haploësthes*. *Flaveria* and *Sartwellia* clearly are closest in terms of intergeneric relationships, while *Haploësthes* does not seem as closely related to either of the former genera (although close enough to *Sartwellia* for rare artificial crosses). It is largely through *Haploësthes* that the Flaveriinae are related to Senecioneae (Turner & Powell, 1977) although the tribal relationships of Flaveriinae, like many Helenieae, are obfuscated by reduction and loss of characters.

The genus *Flaveria* with more, morphologically diverse species has a wider distribution (see Taxonomy) than the other two genera of the subtribe. However, only the derived annual species are widespread in South America, Africa, Australia, and the central United States. The perennial, supposedly more primitive taxa are located in Mexico. In my opinion the most primitive-looking Flaverias are to be found among the four species centered in the Tehuacán Valley of Puebla-Oaxaca, e.g., *F. angustifolia* and *F. vaginata*. These are somewhat woody shrubs or small trees to 3–4 m high, with large, thick leaves, and numerous, rather thick, radiate heads. *Flaveria chloraefolia* of the Chihuahuan Desert region also exhibits ancestral traits in its mesic-marshy habitat, large semisucculent habit, large perfoliate leaves, and large heads. Therefore, in terms of broader distribution and primitive habit, *Flaveria* could be considered ancestral in the Flaveriinae.

A phylogenetic scheme of *Flaveria* based upon morphological, experimental,

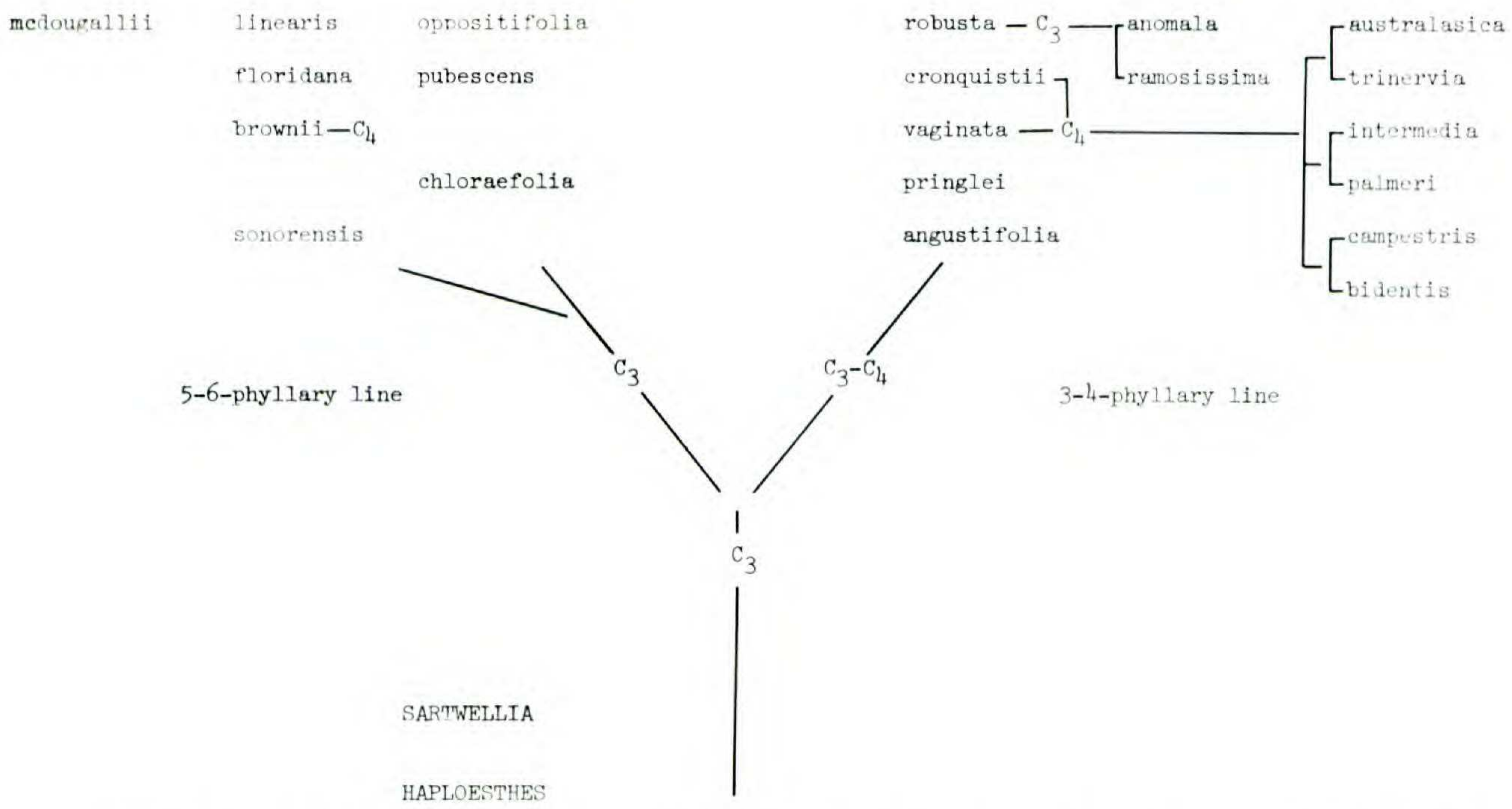

FIGURE 1. Phylogenetic arrangement of *Flaveria*, showing subgeneric groups informally designated as the 5–6-phyllary line and the 3–4-phyllary line. Groupings and brackets indicate suspected relationships; species and lineages with C_4 metabolism are indicated. *Sartwellia* and *Haploësthes* are the other two genera of Flaveriinae, both exhibiting more ancestral traits than *Flaveria*.

chemical, and eco-geographic considerations is presented in Fig. 1. There are two major lineages as indicated by the perennial group with 3–4 phyllaries and the group with 5–6 phyllaries, and the two phyletic lines occur in separate major centers of distribution. The species with 3–4 phyllaries are centered in Puebla-Oaxaca with one species, *F. robusta*, in Colima. The taxa with 5–6 phyllaries have a much wider distribution in central and northern Mexico. The large, shrubby species of the semiarid Tehuacán Valley and vicinity in Puebla-Oaxaca exhibit several ancestral traits, and it is tempting to hypothesize the origin of *Flaveria* from the Puebla-Oaxaca region with the northern species proliferating from this center. However, it is difficult to envision derivation of the line with 5–6 phyllaries directly from the Puebla-Oaxaca species. Both *Sartwellia* and *Haploësthes* have involucres with 5–6 phyllaries, thus supporting an ancestral position of the 5–6-phyllary line in *Flaveria*. *Flaveria oppositifolia* and *F. chloraefolia* have the widest distributions of the northern species. Populatons of *F. oppositifolia* from Zacatecas and San Luis Potosí and the localized *F. pubescens* of San Luis Potosí with wider, perfoliate leaves represent my idea of primitiveness in the 5–6-phyllary line, except that their rather large, numerous heads are discoid. Perhaps the two major lineages of *Flaveria* originated somewhere between the two present distributional centers, with conditions of increasing aridity enhancing the proliferation of each line. The Puebla-Oaxaca species have remained environmentally more restricted than the northern Chihuahuan Desert species.

The eight annual species seem obviously derived from one or more of the perennial groups as suggested in Fig. 1. All the annuals are radiate, and thus it appears that their origin is from one or more of the groups with radiate species. Although the annuals exhibit many reduced traits, they seem to be most like the *F. angustifolia* group in phyllary shape and number, and in capitulescence, but more like the *F. linearis* group in leaf shape and texture. The close relationship indicated for *F. anomala* and *F. ramosissima* in Fig. 1 requires additional study. All of the other annual species appear related morphologically, and all exhibit C_4 physiology (Fig. 1). All the C_4 annuals are self-compatible, except for *F. palmeri* and probably *F. intermedia.*

Speciation in *Flaveria* (and Flaveriinae), especially with the perennial species, would appear to have followed geographic isolation. Among annual species, both geographic speciation and that resulting from internal reproductive barriers seems to have occurred (Table 1).

Important evolutionary trends in the Flaveriinae include the formation of sulfated flavonoids, theoretically as an adaptation to gypseous and saline habitats, and the development of efficient C_4 metabolism in some annual and perennial taxa. The C_4 metabolism is best developed in the 3–4-phyllary line, but seems to have evolved at least twice in *Flaveria*, occurring also in one species (*F. brownii*) of the 5–6-phyllary line (Fig. 1). There is a trend toward more facultative genotypes such as those exhibiting annual habit, C_4 metabolism, and self-compatibility. The wide distribution of *F. linearis* also attests to its facultative nature even though it is C_3, self-incompatible, and perennial.

Additional discussions of species relationships, including evidence upon which such judgments are based, are included in Taxonomy.

TAXONOMY

Flaveria Juss., Gen. Pl. 186. 1789; J. F. Gmel., Syst. Nat. 2: 1269. 1791. LECTOTYPE: (Johnston, 1903).

Vermifuga R. & P., Prodr. Fl. Per. 114. 1794.
Brotera Spreng., J. Bot. (Schrader) 1800: 189, *pl.* 5. 1801, non *Brotera* Cass. 1799.
Nauenbergia Willd., Sp. Pl. 3: 2393. 1804.

Plants delicate or vigorous annuals or perennials, 5–200 cm high, in some species small trees to 4 m high, stems numerous or few, opposite and decussate, erect, lax, or decumbent, often purplish, glaucous, glabrous to densely short-pubescent, often merely tufted-pubescent in the axils. Leaves opposite and decussate, petiolate or sessile, often barely connate, less often connate or connate-perfoliate, 2–15 cm long, 0.2–5 cm wide, glabrous or short-pubescent, linear, lanceolate, oblong-ovate, ovate, elliptic, oblanceolate, the margins entire, serrate or weakly so, serrate-dentate, or spinulose-serrate; in many species, persistent sheathing bases of fallen leaves ringing the stems. Capitulescences of tightly or loosely aggregated heads on short peduncles in usually flat-topped corymbose panicles, or glomerulelike synflorescences in axils; heads radiate or discoid, if both are present then usually discoid heads central and radiate heads peripheral; receptacles small, convex, naked, or setose in 2 species; involucres 2.5–7 mm long, subcylindrical or angular, oblong or suburceolate, the phyllaries 2–5, concave or boat shaped, becoming swollen and corky in one species, ovate, lanceolate, or oblong, the apices rounded, acute, lacerate, or beaked; calyculate bracts linear-lanceolate. Ray florets 1 (rarely 2) when present, pistillate and fertile, the ligules yellow, cream yellow in *F. trinervia*, oblong, ovate or elliptic, usually rather small and inconspicuous; disc florets 1–15, the corollas yellow, 2–4 mm long, prominent tubes naked or minutely-pubescent, the throats gradually or abruptly expanded, narrowly funnelform to campanulate, usually with multicellular hairs, the lobes 5, short, acute, the styles less than 1 mm long, linear-oblong, flattened, obtuse and minutely pubescent at the apices, the anthers 1–2 mm long, with conic appendages. Achenes black, 10-ribbed, somewhat flattened, glabrous, 1–3.6 mm long, those of the ray florets usually larger and somewhat longer than those of the disc florets, narrowly oblanceolate or linear-oblong; pappus absent, or in one species of 2–4 unequal, hyaline, incurved squamellae, 0.5–1 mm long, or in another species a low crown of united scales. Base chromosome number, $x = 18$.

Type species: *Flaveria chilensis* J. F. Gmel. = *F. bidentis* (L.) Kuntze.

a. Pappus scales present.
b. Leaves perfoliate, to 4–5 cm wide; Chihuahuan Desert region ...... 1. *F. chloraefolia*
bb. Leaves weakly connate, to 0.7 cm wide; Arizona ...... 21. *F. mcdougallii*
aa. Pappus absent.
c. Receptacle of glomerule setose.
d. Achenes 2–2.6 mm long; plants widespread in North America and elsewhere. ...... 15. *F. trinervia*
dd. Achenes 2.3–4.5 mm long; plants of Australia ...... 16. *F. australasica*
cc. Receptacle naked.
e. Plants annual.
f. Heads tightly clustered in glomerules.
g. Ligules ca. 1 mm or less; South America to Florida, Africa, lower Europe ...... 13. *F. bidentis*
gg. Ligules 1.5–2.5 mm long; New Mexico and Texas north to Colorado to Kansas ...... 14. *F. campestris*
ff. Heads loosely clustered.
h. Ligules 2 mm long or less.
i. Throat of disc corolla narrowly funnelform; Coahuila ...... 17. *F. palmeri*
ii. Throat of disc corolla expanded to broadly funnelform or campanulate; Durango ...... 18. *F. intermedia*
hh. Ligules 3 mm or longer.
j. Disc florets 1–2(–3); achenes 1.3–2.2 mm long; Coahuila, Nuevo León, Tampico, Mexico ...... 19. *F. anomala*
jj. Disc florets 5–8(–10); achenes ca. 1 mm long; Oaxaca, Puebla ...... 20. *F. ramosissima*
ee. Plants perennial.
k. Phyllaries 3–4; southern Mexico, Puebla-Oaxaca to Colima.
l. Ligules absent.
m. Heads rather densely aggregated ...... 9. *F. pringlei*
mm. Heads rather loosely arranged in flat-topped panicles ...... 11. *F. cronquistii*
ll. Ligules present.
n. Upper herbage densely short pubescent ...... 10. *F. vaginata*
nn. Upper herbage glabrous or essentially so.
o. Florets 5–7; south-central Mexico ...... 8. *F. angustifolia*
oo. Florets 3; Colima, adjacent Michoacán ...... 12. *F. robusta*
kk. Phyllaries usually 5 or more.
p. Ligules absent.

q. Plants densely pubescent .... 2. *F. pubescens*
qq. Plants essentially glabrous, less often moderately pubescent .... 3. *F. oppositifolia*
pp. Ligules present.
r. Disc florets 10–15, sometimes as few as 5 in *F. brownii.*
s. Disc florets 5–10; plants of the Texas Gulf Coast .... 4. *F. brownii*
ss. Disc florets 9–14; plants of the Florida west coast, especially Tampa and vicinity south .... 5. *F. floridana*
rr. Disc florets usually 5–8.
t. Phyllaries 5(–6), linear or oblong; plants of Florida, Bahamas, Cuba, Yucatán, Quintana Roo .... 6. *F. linearis*
tt. Phyllaries (4–)5, linear; plants of the Río Mayo region, Sonora .... 7. *F. sonorensis*

In accounts of the following species, lists of Representative Specimens were selected from more extensive collections of the taxa concerned, while distribution maps were made from complete locality data. Label data are available at SRSU for all specimens of *Flaveria* examined during the study.

1. **Flaveria chloraefolia** A. Gray, Mem. Amer. Acad. Arts, n.s., 4: 88. 1849. TYPE: Mexico, Chihuahua (Durango?), Pelayo, NW of Mapimi, May, *Wislizenus 274*? (GH, holotype, not seen; MO, isotype).

Plants perennial, the stems erect to subdecumbent, 0.3–2 m long, glaucous, often purplish; leaves opposite, connate-perfoliate, 3–10 cm long, 1–4(–5) cm wide, glaucous, often purplish, oblong-ovate to lanceolate or hastate, the margins entire; capitulescence of numerous heads loosely to tightly aggregated into large, paniculate corymbs; heads discoid; involucres 6–7 mm long, oblong-urceolate, the phyllaries 5; calyculate bracts ca. 2 mm long; disc florets 9–13, the corollas ca. 4 mm long, the tube 1.2–1.4 mm long, the throat ca. 2 mm long, narrowly funnelform, the lobes ca. 0.5 mm long, acute; styles ca. 1 mm long, truncate-puberulent; anthers ca. 2 mm long; achenes 2.5–3 mm long, slightly dimorphic in length, narrowly oblanceolate to linear; pappus of 2(–4) unequal, hyaline scales, 0.5–1 mm long, usually on one shoulder, rarely absent; chromosome number, $n = 18$.

Widely distributed in the northern Chihuahuan Desert region, extending up the Pecos River drainage into central New Mexico, probably extending up the Rio Grande to north of Las Cruces, and south to central Coahuila, Mexico (Fig. 2); associated with permanent or ephemeral saline water sources such as marshes, springs, creeks, rivers, irrigation canals, or roadside ditches. Flowering usually in late summer or fall.

REPRESENTATIVE SPECIMENS: MEXICO. CHIHUAHUA: 2 mi NW of Meoqui, *Cronquist 10232* (CAS, GH, KSC, MICH, NY, TEX, US, WIS). COAHUILA: Hermanas, *Marsh 1635* (F, GH, SRSU, TEX). Near Parras and San Lorenzo, *Palmer 2083* (GH). 100 mi N of Monclova, Sabinas River, *Palmer 682* (GH, MO, NY, US). 6 mi SW of Cuatro Ciénegas, *Powell & Tomb 2622* (TEX, US). 12 mi E of Cuatro Ciénegas, *Powell & Turner 2278* (TEX).

UNITED STATES. NEW MEXICO: Chaves Co., 0.5 mi SW of Frazier, *Waterfall 6175* (GH, MO, NY). Guadalupe Co., Santa Rosa, *Crutchfield 2320* (LL). TEXAS: Culberson Co., 12 mi W of Orla, *Correll & Correll 24688* (LL). Pecos Co., Ft. Stockton, *Wooton s.n.* (US). Reeves Co., ca. 0.5 mi E of Toyahvale, *Powell 2799* (TEX, US). Terrell Co., Independence Creek, *Warnock & Johnston 17281* (SRSU).

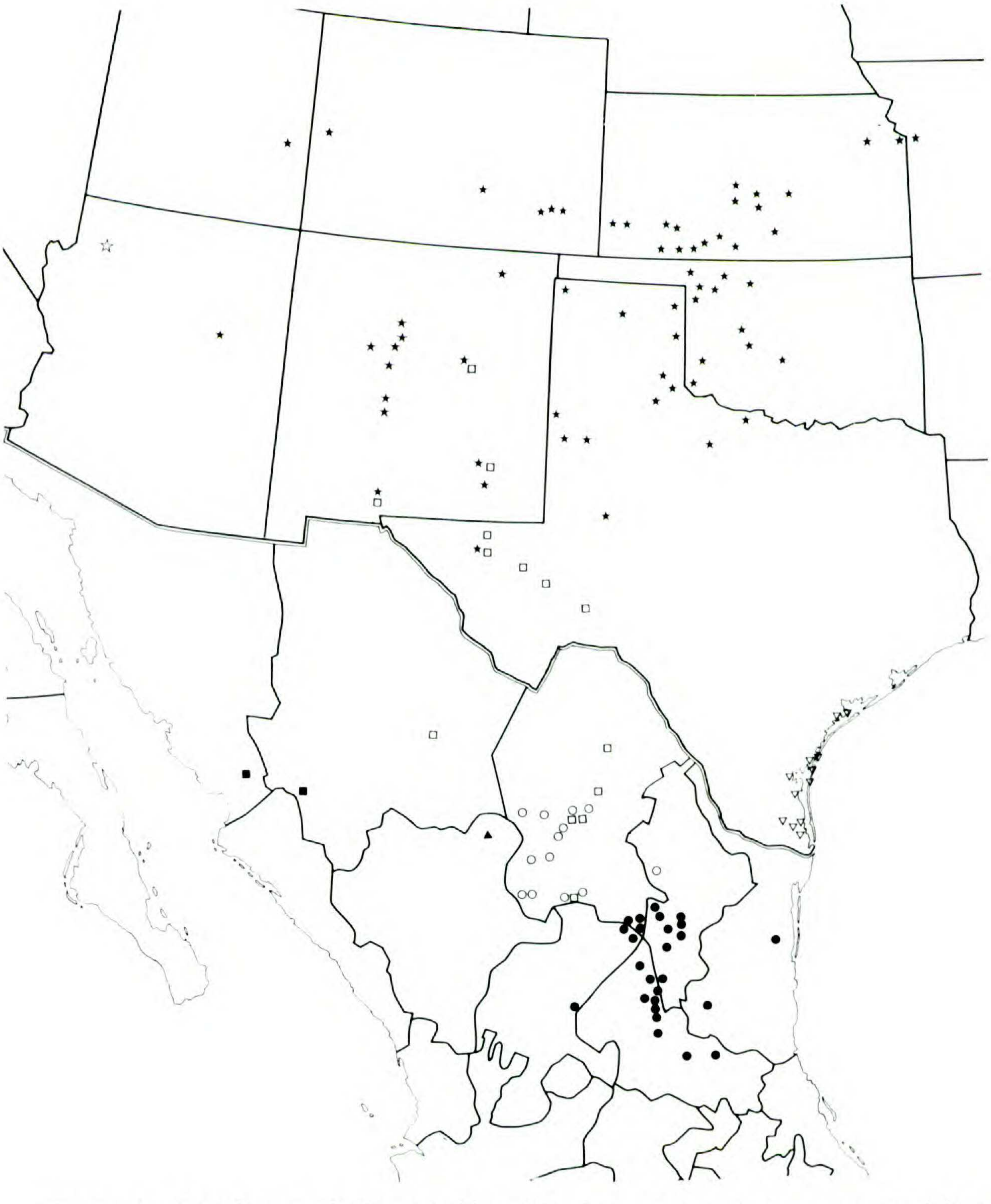

FIGURE 2. Distribution of *Flaveria chloraefolia* (open squares); *F. campestris* (closed stars); *F. palmeri* (open circles); *F. anomala* (closed circles); *F. sonorensis* (closed squares); *F. mcdougallii* (open star); *F. intermedia* (closed triangle); *F. brownii* (open triangles).

Flaveria chloraefolia is one of the most distinctive species of the genus with its rather succulent habit, perfoliate leaves, large flat-topped clusters of discoid heads, and 2–4 pappus scales. The taxon is not closely related to any other *Flaveria*, and could be considered primitive (Fig. 1) on the basis of its habit, leaves, and pappus scales. *Flaveria chloraefolia* does show some alliance with *F. oppositifolia* and *F. pubescens* with their large discoid heads and basally connate leaves in some populations. Interestingly the species did cross and form hybrids with *F. linearis* (Table 1), which would appear distantly related, and it did form an intergeneric hybrid with *Sartwellia puberula*, which has little in common morphologically except the pappus scales.

2. **Flaveria pubescens** Rydb., N. Amer. Fl. 34: 145. 1915. TYPE: Mexico, San Luis Potosí, Río Verde, 2–8 June 1904, *E. Palmer 26* (NY, holotype; F, GH, K, MO, NY, isotypes).

F. longifolia A. Gray var. *subtomentosa* Greenman & Thompson, Ann. Missouri Bot. Gard. 1: 413. 1915, pro parte. TYPE: Mexico, Río Verde, 17 Nov. 1910, *C. R. Orcutt 5421* (MO, holotype).

Plants stout perennials, 30–80 cm high, the stems erect, densely short-pubescent; leaves opposite, connate, 5–10 cm long, 0.4–1.2 cm wide, densly short-pubescent, linear, the margins entire; capitulescence of numerous heads rather tightly aggregated in flat-topped, rather loose, corymbose panicles; heads discoid; involucres ca. 4 mm long, the phyllaries 5, linear-oblong; disc florets 10–15, the corollas 2.8–3.3 mm long, the throats funnelform; achenes 1–1.7 mm long, oblanceolate or linear; pappus absent; chromosome number, $n = 18$.

Scattered localities, possibly in gypsum soils, San Luis Potosí and Tamaulipas, Mexico (Fig. 3).

REPRESENTATIVE SPECIMENS: MEXICO. SAN LUIS POTOSÍ: 1 mi SE of Río Verde, *Hartman et al. 3823* (LL). Minas de San Rafael, *Purpus 4776* (F, GH, UC, US). TAMAULIPAS: Jaumave Valley, *Nelson 4450* (F, GH, US).

Flaveria pubescens is closely related to *F. oppositifolia* which is perhaps of recent divergence. There is essentially no difference in floral characters of the two taxa, but *F. pubescens* is distinguished by the densely pubescent herbage and usually much broader, linear leaves which are connate-perfoliate. *Flaveria oppositifolia* is more widely distributed than is *F. pubescens* (Fig. 3), and the leaves are usually narrow, but in a few populations the leaves are wider and the plants are somewhat pubescent. It would be possible to regard *F. pubescens* and *F. oppositifolia* as varieties of one species. The crossability and interfertility of the two taxa are variable and fairly high (Table 1), but interfertility is not any greater than between some quite distinct species of the genus. I have maintained the two species primarily because they are morphologically distinguishable.

3. **Flaveria oppositifolia** (DC.) Rydb., N. Amer. Fl. 34: 146. 1915. TYPE: Mexico, Tamaulipas, between San Fernando and Santander, Oct. 1930, *Berlandier 2263* (=*843*), (GH, lectotype; K, MO, NY (2), isolectotypes).

Gymnosperma oppositifolium DC., Prodr. 5: 312. 1836.
Flaveria longifolia A. Gray, Mem. Amer. Acad. Arts, n.s., 4: 88. 1849. TYPE: Mexico, Coahuila, near Ciénega Grande, May, *Gregg s.n.* (GH, holotype; MO, isotype).

Plants stout perennials, 30–80 cm high, the stems erect, sometimes purplish, glabrous, essentially so, or short-pubescent; leaves opposite, sessile, rarely barely connate, 3.5–12 cm long, 0.2–0.9(–1.2) cm wide, glabrous, essentially so, or short-

FIGURE 3. Distribution of *Flaveria angustifolia* (closed triangles); *F. pringlei* (closed circles); *F. vaginata* (open squares); *F. cronquistii* (open triangles); *F. robusta* (closed squares); *F. oppositifolia* (open circles); *F. pubescens* (open stars); *F. ramosissima* (closed stars).

pubescent, linear, tapering from the sessile base, the margins entire or weakly spinulose-serrate; capitulescense of numerous heads rather tightly aggregated in flat-topped, rather loose, corymbose panicles; heads discoid; involucres 4–4.7 mm long, the phyllaries 5, linear-oblong, acute or rounded apically; calyculate bracts 1–2, linear, 1–2 mm long; disc florets 9–13(–15), the corollas 2.8–3 mm long, the tubes ca. 1.2 mm long, the throats 1.2–1.5 mm long, narrowly funnelform to broadly so, may be abruptly expanded in the distal half, the lobes ca.

1 mm long, acute; anthers ca. 1.5 mm long; achenes 1.5–1.8 mm long, oblanceolate or linear; pappus absent; chromosome number, $n = 18$.

Scattered populations, high gypsum plains or other areas with dilute gypsum, saline, or rarely loamy soil, usually in moist areas or in disturbed habitats at roadside, 1,450–2,340 m, northeast-central Mexico (Fig. 3).

REPRESENTATIVE SPECIMENS: MEXICO. AGUASCALIENTES: near Ciénega Grande, *McVaugh 23783* (DS, MICH). COAHUILA: Hermanas, *Marsh 1643* (GH, SRSU, TEX). Saltillo and vicinity, *Palmer 304* (ARIZ, F, GH, MO, NY, UC, US). 6 mi W of Nadadores, *Powell & Turner 2266* (TEX). 2 mi N of Parras, *Ward 5750* (MICH). 44 mi SW of Monterrey, *Warnock & Barkely 14765M* (F, TEX, US). DURANGO: 9 mi N of Dgo.-Zac. border, *Sikes et al. 831* (TEX, US). HIDALGO: near Tula, *Graham & Johnston 4024A* (MICH, TEX). NUEVO LEÓN: Galeana, *Chase 7636* (ARIZ, F, GH, MICH, NY). 45 mi SE of Saltillo, *Powell & Tomb 2561* (TEX, US). SAN LUIS POTOSÍ: 2 mi S of Cedral, *Johnston 7582* (GH, US). Hacienda de Angostura, *Pringle 3767* (CAS, G, GH, LL, MICH, MO, NY, TEX, UC, US). 6 km NE of Matehuala, *Rzedowski 4873* (TEX). TAMAULIPAS: Jaumave, *Berlandier 3173* (GH, K, MO, NY, US). ZACATECAS: 55 mi NE of Jnct. 49-54, *Powell & Tomb 2593* (TEX, US). Sierra Hermosa, *Shreve 8593* (ARIZ, CAS, US).

There are several species that occur within the same distributional range as *F. oppositifolia* (Figs. 2–3), but the latter taxon is readily distinguished by its perennial habit, linear, mostly glabrous leaves, capitulescene of numerous discoid heads rather loosely aggregated in flat-topped clusters, 5 phyllaries, and 9–15 florets per head. *Flaveria oppositifolia* is closely related to *F. pubescens* which has densely pubescent herbage.

Plants from separate populations of the wide-ranging *F. oppositifolia* do show notable variation in certain features, particularly in habit, leaf size, and pubescence, but this variation is without apparent taxonomic significance. Plants of the higher elevation gypsum plains are usually stiffly erect whereas those plants from near Monclova at lower elevations are usually lower and more reflexed in habit. Leaf width varies from more than 1 cm to about 0.2 cm. The plants of many populations are glabrous, but throughout the range it is common to find plants that are short and sparsely pilose on leaves and stems.

4. **Flaveria brownii** A. M. Powell, sp. nov. TYPE: United States, Texas, San Patricio Co., roadsides and saline marshes, Port Aransas, Mustang Island, 30 Dec. 1974, *A. M. Powell 2802* (TEX, holotype; US, K, FSU, SRSU, GH, NY, F, KSC, isotypes)—FIG. 4.

Herbae perennes vel annuae longaevae 15–70 cm altae erectae decumbentesve. Folia sessilia 5–12 cm longa 0.2–0.7 cm lata glabra linearia. Capitula radiata aut discoidea 5–7-flora; phyllaria 5–6; ligulae ca. 2 mm longae. Achaenia 1.5–2 mm longa. Chromosomatum numerus $n = 18$.

Plants herbaceous perennials or long-lived annuals, 15–70 cm high, the stems many from the base, erect or decumbent, often purplish at maturity; leaves sessile, barely connate, 5–12 cm long, 0.2–0.7 cm wide, glabrous or essentially so, linear, tending to persist and wither in spirals at senescence, the margins entire or weakly serrate; capitulescence of numerous heads rather tightly aggregated in flat-topped, rather open corymbose panicles; heads radiate and discoid; involucres 4–5 mm long, oblong-angular, the phyllaries 5–6, boat shaped, acute, the one enclosing a ray floret conspicuously keeled; calyculate bracts linear; ray

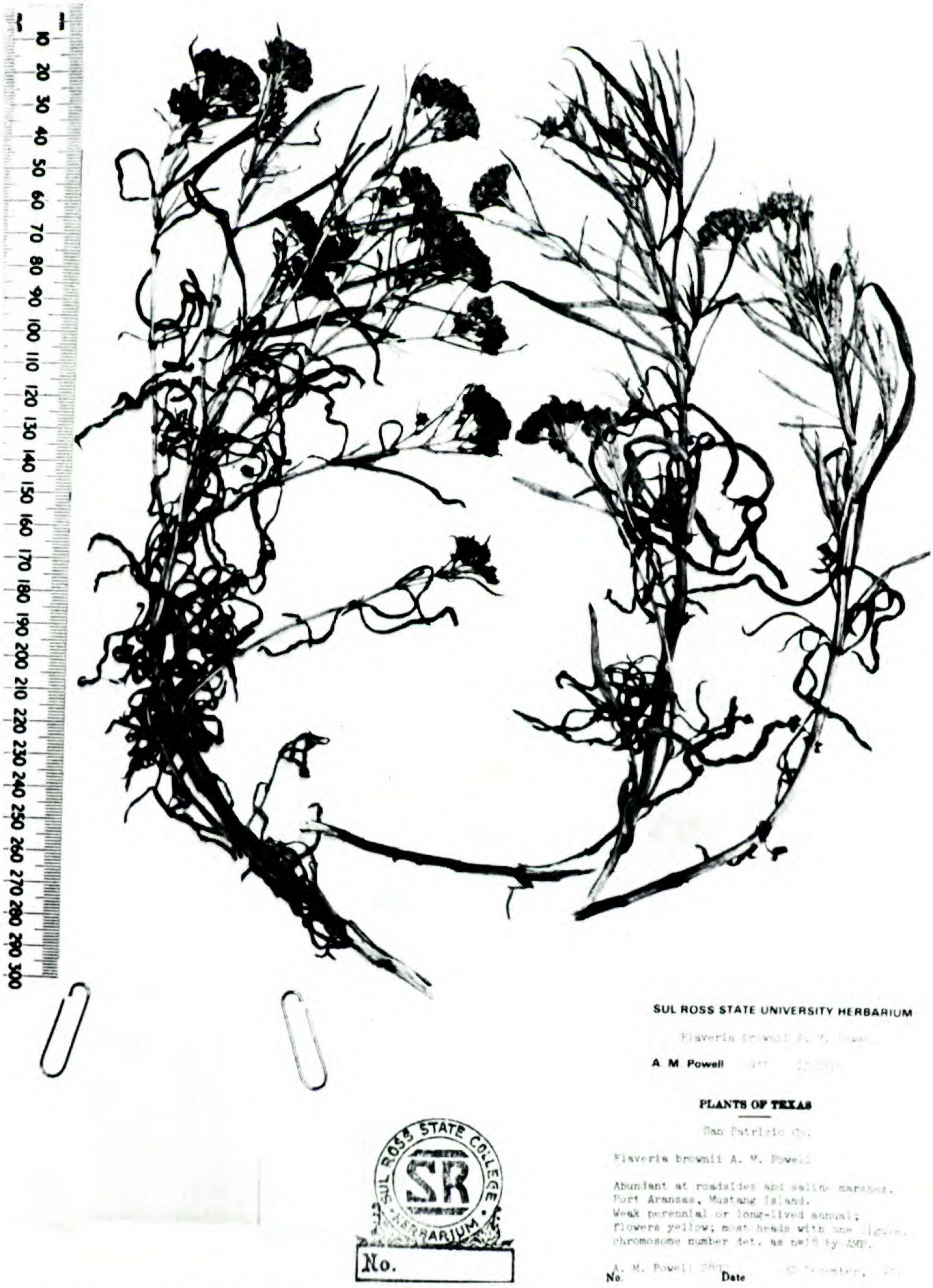

FIGURE 4. Phototype of *Flaveria brownii* A. M. Powell.

florets with the ligules ca. 2 mm long, oblong-elliptic; disc florets 5–10, the corollas 2.5–3 mm long, the tubes 0.8–1.2 mm long, the throats 1.2–1.5 mm long, the upper half expanded and funnelform, the lobes 0.5–1, acute; anthers 1.5 mm long; achenes linear, 1.5–2 mm long, the ray achenes longer; pappus absent; chromosome number, $n = 18$.

Saline, sandy, and marshy areas of the coastal flats and islands of the lower Texas Gulf Coast (Fig. 2).

REPRESENTATIVE SPECIMENS: UNITED STATES. TEXAS: Aransas Co., Aransas Refuge, *Cory 45791* (TEX). Rockport, *Tharp 4620* (TEX, US). Brooks Co., 21.7 mi SE of Hebbronville, *Cory 16950* (GH). Calhoun Co., below Seadrift, *Tharp s.n.* (TEX). Port O'Connor, *Tharp & Brown 48-179* (TEX). Kenedy Co., King Ranch, *Johnston 53·280·36* (TEX). 4.4 mi S of Armstrong, *Johnston 542265* (TEX). 6.7 mi N of Noria, *Stuessy & Roberts 3624* (OS). Kleberg Co., Riviera, *Reed 981* (US). Nueces Co., Mustang Island, *Gillespie 307* (TEX). Corpus Christi, *Tharp s.n.* (TEX). Padre Island, *Urbatsch 1547* (TEX). San Patricio Co., Aransas Pass, *Cory 51238* (MICH, NY). Willacy Co., Raymondville, *Shiller 786* (US).

This newly described species has long been confused in herbaria with *F. oppositifolia* to which it is superficially similar, but from which it is readily distinguished by its radiate heads among the discoid ones in each capitulescence. *Flaveria brownii* is probably most closely related to *F. floridana* of the Florida west coast as judged by their similar morphologies and ability to form seemingly fertile artificial F_1 and F_2 hybrids (Table 1). Synthetic hybrids also are readily formed with *F. oppositifolia*. *Flaveria brownii* also resembles *F. linearis*, especially those populations in Yucatán, Quintana Roo, and Cuba where the lower leaves of the plants tend to wither in spirals at senescence. Among the four species mentioned above, all somewhat related in the 5-phyllary line, *F. brownii* is the only one which has evolved C_4 photosynthesis (Fig. 1).

The occurrence of C_4 metabolism in *F. brownii* raises the question as to whether the phenomenon arose independently in the 5-phyllary line, as appears to be the case, or whether this species is actually derived from the original C_4 line which includes the annual species (Fig. 1). There is little morphological suggestion that *F. brownii* could have evolved from *F. vaginata* or the C_4 annuals. Morphologically *F. brownii* is closely tied to members of the 5-phyllary line, strongly suggesting that its C_4 capabilities were evolved at least as a second such event in the genus.

The specific epithet honors the late Walter V. Brown, an unusually perceptive investigator of the Kranz syndrome in Gramineae and other taxa, including *Flaveria*. In *Flaveria* he was particularly excited about the existence, in certain taxa, of Kranz morphology intermediates which suggest the active evolution of C_4 metabolism in the genus.

5. **Flaveria floridana** J. R. Johnston, Proc. Amer. Acad. Arts 39: 291. 1903. TYPE: United States, Florida, Lee Co., Sanibel Island, 29 Jan. 1896, *H. J. Webber 175* (US, holotype, not seen; F, MO, isotypes). Florida, Hog Island, 24 Nov. 1901, *S. M. Tracy 7341* (F, GH, MO, NY, US, WIS, syntypes). Florida, Manatee, *J. H. Simpson s.n.* (NY, US [2], syntypes).

F. linearis Lag. var. *latifolia* J. R. Johnston, Proc. Amer. Acad. Arts 39: 289. 1903, pro parte. TYPE: United States, Florida, Palm Beach Co., shore of Lake Worth, near Palm Beach, 31 Aug. 1895, *A. H. Curtiss 5524* (GH, holotype; GA, KSC, MO, NY, UC, US, isotypes).
F. latifolia (J. R. Johnston) Rydb., N. Amer. Fl. 34: 145. 1915, pro parte.
F. pinetorum Black, Bull. Torrey Bot. Club 50: 204. 1923 TYPE: United States, Florida, Lee Co., vicinity of Ft. Myers, 14 Dec. 1919, *P. C. Standley 18909* (US, holotype, not seen).
F. × *latifolia* (J. R. Johnston) Long & Rhamstine, Brittonia 20: 249. 1968, pro parte.

Plants herbaceous perennials, or perhaps annuals, 50–120 cm high, branching from the base, erect, essentially glabrous except sparsely pubescent on the upper peduncles; leaves opposite, connate or barely so, 5–14 cm long, 0.4–1.7 cm wide, linear, lanceolate, rarely subelliptic, the margins entire or minutely serrate or spinulose; capitulescence of corymbose panicles with numerous heads densely aggregated in subscorpioid clusters; heads radiate and discoid; involucres 3.6–4.5 mm long, suburceolate, oblong-angular, the phyllaries 5–6(–9), oblong or ovate-orbicular, obtuse or acute, an outer bract somewhat swollen and keeled basally, with 0–3 linear, hyaline, chafflike inner bracts; calyculate bracts linear, 0.3–1.5 cm long, often exceeding the length of the involucral bracts, and with modified upper peduncular leaves, visible above the top of the corymbs; ray florets with the ligules 2–2.8 mm long, 1.5–2 mm wide, obovate-spatulate, notched; disc florets 9–14, the corollas 2.7–3.2 mm long, the tubes 0.8–1 mm long, sparsely pubescent, the throats 1.3–1.5 mm long, funnelform, gradually tapering from the tube or more dilated distally, the lobes ca. 0.6 mm long, acute; anthers ca. 1.5 mm long; achenes of ray and disc florets of similar size, 1.2–1.8 mm long, oblong-oblanceolate or linear; pappus absent; chromosome number, $n = 18$.

This species is "restricted to saline, white sand near the beaches of brackish marshes" (Long & Rhamstine, 1968), lower Gulf Coast of Florida, especially common in the Tampa Bay area (Fig. 5).

REPRESENTATIVE SPECIMENS: UNITED STATES. FLORIDA: Charlotte Co., Punta Gordo, *Cornman 2091* (ARIZ, MO, US). Lee Co., Sanibel Island, *Brumbach 6538* (US). Captiva Island, *Brumbach 8159* (US). Little Gasperilla Island, *Fleak & Kreisel 1814* (NY). 5 mi E of Ft. Myers, *Kral 7546* (USF). Pine Island, *Lakela 30607* (USF). Hillsborough Co., 6 mi SE of Tampa, *Blanton 6483* (DS, LL, TEX, UC). Bahia Beach, *Lakela 24832* (LL, TEX, USF). Manatee Co., Longboat Key, *Long & Lakela 24582* (USF). Terra Ceia Island, *Shuey s.n.* (USF). Casey Key, *Ward & Burch 3161* (USF). Monroe Co.? keys of S Florida, *Chapman 2387* (US). Sneed's Island, *Tracy 6356* (GH, NY, US).

Flaveria floridana is distinguished from the other perennial species of Florida, *F. linearis*, by its long calyculate bracts that extend beyond the involucres and are visible above the corymbs (on herbarium sheets), larger heads with 10–15 florets, and funnelform disc corollas. Long & Rhamstine (1968) suggested that *F. floridana* was related to *F. oppostifolia*, but I believe that the species is closest to *F. brownii* of the lower Texas Gulf Coast. The two taxa are similar in their annual or weak perennial habits and both occupy similar habitats in limited coastal and coastal island areas. Among other traits the taxa are distinguished by leaves (and stems) in *F. floridana* which are darker green and thicker in texture. Presumably the Kranz anatomy of *F. brownii* results in a lighter coloration of the leaves.

6. **Flaveria linearis** Lag., Gen. & Sp. Nov. 33. 1886. TYPE: Cuba, Havana (not seen).

F. maritima H. B. K., Nov. Gen. Sp. Pl. 4: 285. 1820. TYPE: Cuba (not seen).
Selloa nudata Nutt., Amer. J. Sci. 5: 300. 1822.
Flaveria tenuifolia Nutt., J. Acad. Nat. Sci. Philadelphia 7: 81. 1834. TYPE: United States, East Florida, *Mr. Peale* (not seen).
Gymnosperma nudatum DC., Prodr. 5: 312. 1836.
Flaveria × *latifolia* (J. R. Johnston) Long & Rhamstine, Brittonia 20: 249. 1968, pro parte.

Plants herbaceous perennials, 30–80 cm high, the stems often purplish, erect, branching from the base, glabrous or pubescent mostly on the upper peduncles; leaves opposite, connate or barely so, 5–10(–13) cm long, 0.1–0.4(–1.5) cm wide, linear, the margins entire or serrulate-spinulose; capitulescence of flat-topped, corymbose panicles with numerous heads aggregated in clusters; heads radiate and discoid; involucres 3.3–4.5 mm long, oblong-angular, the phyllaries 5(–6), linear or oblong, obtuse-acute, the outer 2–3-keeled; calyculate bracts linear, 1–2.5 mm long; ray florets with the ligules 2–3 mm wide, oval or obovate-spatulate, 1–3-toothed; disc florets (2–)5–7(–8), the corollas 2.5–3.3 mm long, the tubes 0.8–1.2 mm long, glabrous or sparsely pubescent, the throats 1–1.5 mm long, tubular at the base, dilated to funnelform-campanulate above, the lobes ca. 0.5 mm long, acute; anthers 1.3–1.5 mm long; achenes of ray and disc florets of similar size, 1.2–1.8 mm long, linear; pappus absent; chromosome number, $n = 18$.

Near the coast and on offshore islands, Yucatán Peninsula, Mexico, widespread in the West Indies, and the most common *Flaveria* in Florida, "found in a wide variety of habitats" near the peninsular coast, including "in old fields, in roadside areas, margins of hammocks, in wet-cypress-pineland associations, in littoral communities, along canals, in mangrove swamps, etc." (Long & Rhamstine, 1968) (Fig. 5). In southern Florida the species frequently occurs in low, flat, rocky pineland in association with *Samolus*, *Bigelowia*, and *Borrichia*. Flowering throughout the year.

REPRESENTATIVE SPECIMENS: UNITED STATES. FLORIDA: Brevard Co., Melbourne Beach, *Lakela 28676* (GH). Broward Co., 10 mi W of Deerfield, *McCart 11262* (USF). Citrus Co., Shell Island, *Long 1308* (USF). Collier Co., Marco Island, *Lakela 27511* (USF). Dade Co., Coral Gables, *Demaree 10202* (DS, MO, US). Hendry Co., 4 mi W of LaBelle, *Henderson 63-1609* (TEX). Hernando Co., Bayport, *Cooley 5456* (USF). Hillsborough Co., *Blanton 6868* (CAS). Indian River Co., 5 mi N of Vero Beach, *Webb et al. 3612* (USF). Lee Co., Sanibel Island, *Cooley 904* (USF). Martin Co., near Indian Town, *Burch 20* (F, GH, MO, NY, TEX, UC, US). Monroe Co., Big Pine Key, *Almeda & Lakela 1934* (USF). Orange Co., Orlando, *Rhoades 6714* (F, UC). Osceola Co., Kissimmee Prairie, *McFarlin 3779* (MICH). Palm Beach Co., Lake Worth, *O'Neill 839* (MO, US). Pasco Co., Aripeka, *O'Neill 1045* (US). Pinnellas Co., Clearwater Beach, *McFarlin 3696* (MICH). Polk Co., Anastasia Key, *Jennings s.n.* (USF). St. Lucie Co., near Ft. Pierce, *Lakela 25238* (GH, USF). Volusia Co., Daytona Beach, *Ray 11131* (GH, USF). Wakulla Co., St. Marks Refuge, *Norris 663* (TEX).

BAHAMA ISLANDS. Andros Island, Kemp Bay, *Brace 5027* (F, NY). New Providence, *Britton 3150* (F, GH, NY).

CUBA. MATANZAS: *Alain 3049* (NY). PINAR DEL RÍO. *Britton & Cowell 9979* (NY).

MEXICO. QUINTANA ROO: Cozumel Island, *Steere 2985* (MICH). YUCATÁN: Progreso, *Gaumer 1147* (A, CAS, F, GH, MICH, MO, US). Perez Island, *Millspaugh 1753* (F, NY).

Long & Rhamstine (1968) noted that the Florida populations of *F. linearis*

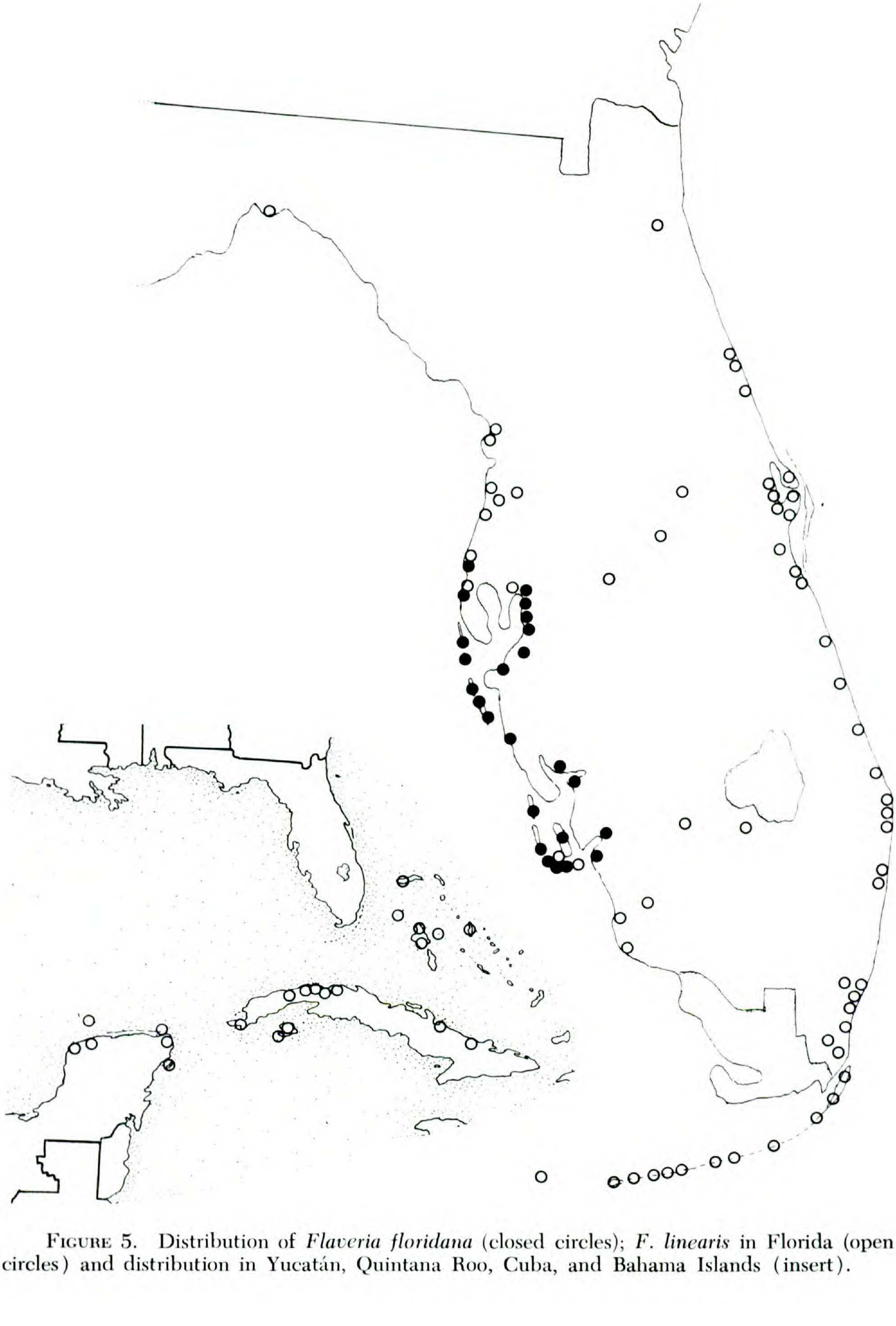

FIGURE 5. Distribution of *Flaveria floridana* (closed circles); *F. linearis* in Florida (open circles) and distribution in Yucatán, Quintana Roo, Cuba, and Bahama Islands (insert).

are more variable, particularly in leaf shape and size, than are those from the Bahamas, and they suggested that this variation originated through introgression from *F. floridana.* I also have found that the populations of *F. linearis* outside Florida in Quintana Roo, Yucatán, Cuba, and the Bahamas, are more homogeneous, and usually with narrower leaves. As in Florida, however, occasional plants from the West Indies and Mexico have broad leaves much like those which are theorized by Long and Rhamstine to have come from introgression in Florida.

My observations have shown that the populations of *F. linearis* from Yucatán and Cuba have a slightly different aspect than plants from Florida or the Bahamas. In general the Yucatán-Cuba plants appear slightly more robust, perhaps larger-stemmed, with shorter internodes, and with early senescent, twisting lower leaves, so that healthy leaves are on the middle and upper stems. The latter leaf trait also is characteristic of *F. brownii.* Plants of *F. linearis* from the Yucatán Peninsula have slightly larger heads, approaching those of *F. brownii.* The latter morphological features and distributional considerations (Fig. 5) suggest that *F. linearis* might have originated in Mexico, the distributional center of *Flaveria,* and then spread eastward through the West Indies and eventually into Florida. *Flaveria brownii* could have evolved as a C_4 adapted species and Texas Gulf Coast offshoot from the Yucatán population of *F. linearis.* Distributional and morphological considerations then might suggest that *F. floridana* evolved in the Tampa Bay area as an offshoot of *F. brownii.* It does not follow, however, that the C_3 taxon, *F. floridana,* would have originated from the C_4 *F. brownii* in that the latter condition is usually thought of as derived (Brown, 1977). Another possibility regarding the origin of *F. floridana* is that it became established as an offshoot of Mexican *F. linearis* at the same time as *F. brownii. Flaveria floridana* and *F. linearis* are ecologically isolated in Florida, and they could have coexisted there or not, in evolutionary history.

The source of variability in Florida populations of *F. linearis* is not fully understood. It is highly possible that hybridization with *F. floridana* and subsequent introgression is responsible for the variation, as Long & Rhamstine (1968) believed. Experimentally the two species are interfertile (Table 1), but further study of the situation in the field remains to be accomplished.

In addition to hybridization and introgression between *F. linearis* and *F. floridana,* Long & Rhamstine (1968) proposed the existence of a stable species, *F.* × *latifolia,* of the same hybrid origin. The hybrid species is supposedly intermediate morphologically, except sometimes with wider leaves, and was said by Long and Rhamstine to occur in a type of hybrid habitat, i.e., fill material dredged from the ocean and used in land development, and also "in dune and strand vegetation along the lower Gulf Coast." Artificial *F. linearis* × *F. floridana* hybrids (Table 1) conform morphologically with specimens annotated by Long and Rhamstine as *F.* × *latifolia.* Thus experimental evidence supports the possibility that natural hybridization has occurred between *F. linearis* and *F. floridana.*

At this time, however, I am not able to recognize the hybrid species *F.* × *latifolia.* My observations suggest that hybridizations between *F. linearis* and

F. floridana have occurred, but that the events were uncommon and sporadic, and that there exists no stable population worthy of specific status. Furthermore, my studies show that *F. floridana* is restricted to the lower Gulf Coast of Florida (Fig. 5) while *F. linearis* is essentially allopatric and widespread over much of the peninsula, although the distributions do overlap in Hillsborough, Pinellas, and Lee counties (Fig. 5). Long & Rhamstine (1968) show one locality of *F. floridana* in Palm Beach County on the East Coast, and they show *F. linearis* to be regionally sympatric with *F. floridana* in the vicinity of Tampa Bay and south along the Gulf Coast. Richard P. Wunderlin (pers. comm.) is of the opinion that *F. linearis* and *F. floridana* are sympatric somewhere in south Florida and that hybridization probably occurs between them. Further studies will be necessary to resolve the exact distributions of the two species, to clarify the extent of their ecological isolation, and to evaluate the extent to which hybridization might have contributed to the variability of *F. linearis* in Florida. If hybrids exist, then one would expect to find them in areas of sympatry and not scattered over the peninsula as indicated by Long & Rhamstine (1968), unless the "hybrids" are progeny of a stabilized species of hybrid origin as proposed by the latter authors.

Distinguishing characters of *F. linearis* include: usually narrow, linear leaves; rather short, linear calyculate bracts; oblong-angular involucres; heads rather small, with 5–8(–9) florets; throats of disc corollas tubular at base and abruptly expanded distally to funnelform-campanulate. Long & Rhamstine (1968) report that an extensive population of *F. linearis* was found growing with *F. bidentis* on Malabar Cape, Brevard County, but with no indication of hybridization.

7. **Flaveria sonorensis** A. M. Powell, sp. nov. TYPE: Mexico, Sonora, Agua Caliente, N of Alamos, 2 Nov. 1939, *H. S. Gentry 4852* (UC, holotype; DS, MICH, NY, isotypes).

Herbae perennes ad 1 m altae. Folia 6–14 cm longa 0.3–1.5 cm lata glabra linearia vel lanceolata margine spinuloso-serrata. Capitula radiata aut discoidea, 5–7-flora; phyllaria 4–5. Achaenia 1.2–1.5 mm long. Chromosomatum numerus $n = 18$.

Plants herbaceous perennials, to 1 m high; leaves barely connate, 6–14 cm long, 0.3–1.5 cm wide, glabrous, linear or lanceolate, the margins serrate or spinulose-serrate; capitulescences of flat-topped panicles with numerous heads in each cluster; heads radiate and discoid; phyllaries (4–)5, linear; disc florets 5–7, the corollas 2.5–3 mm long; achenes 1.2–1.5 mm long, the ray achenes slightly longer than some disc achenes, equal to others; pappus absent; chromosome number, $n = 18$.

Watershed of the Río Mayo, southern Sonora, short-tree forests of tropical Sonora, often close to warm mineral springs, 160–1,000 m, and near Batopilas in adjacent Chihuahua (Fig. 2).

REPRESENTATIVE SPECIMENS: MEXICO. CHIHUAHUA: near Batopilas, *Goldman 240* (GH, NY, US). SONORA: San Bernardo and vicinity, *Arguelles 82* (LL, TEX, US). Salitral, Río Mayo, *Gentry 1274* (F, GH, MICH, NY, TEX, UC). Aguas Calientes, *Kuntze 23481* (NY, UC). Rancho Salitral near San Bernardo, *Martin 5* (ARIZ).

This previously undescribed entity was discovered among borrowed specimens of *F. robusta*, which *F. sonorensis* resembles in capitulescence and floral aspects. *Flaveria sonorensis* is delimited by its rather narrow spinulose-serrate or serrate leaves, (4–)5 linear phyllaries, 5–7 florets per head, and distribution. The relationship of *F. sonorensis* is not clear, but its heads with five phyllaries suggest that it may not belong with *F. robusta* and the 3-phyllary line, even though these species are of similar habit and distribution (Fig. 3). Instead, *F. sonorensis* may be related to *F. linearis*, a radiate species of the 5-phyllary line with a propensity for coastal and inland distribution.

8. **Flaveria angustifolia** (Cav.) Pers., Syn. Pl. 2: 489. 1807.

Milleria angustifolia Cav., Icon. Pl. 3: 12. 1794. TYPE: Mexico, "Nova Hispania," (K, lectotype).
Flaveria integrifolia Moç. & Ses. in DC., Prodr. 5: 635. 1836, pro syn.
F. radicans Moç. & Ses. in DC., Prodr. 5: 635. 1836, pro syn.
F. elata Klatt, Leopoldina 23: 146. 1887. TYPE: Mexico, Tehuacán, *Leibman 267* (not seen).

Plants herbaceous perennials, 0.5–1 m high, erect and spreading; leaves opposite, connate, the upper ones 8–12 cm long, 1–2.2 cm wide, glabrous, linear-lanceolate, the margins serrulate-spinose to minutely so, rarely entire; capitulescence of corymbose panicles with numerous heads aggregated in dense scorpioid clusters; heads radiate and discoid with a ray floret in most heads; involucres 4.3–5 mm long, oblong-angular, the phyllaries 3–4, boat shaped, oblong and acute, usually with an outer phyllary enclosing the ray floret, the phyllary shorter, broader, usually with a prominent, curved, swollen corky keel at maturity, the 2 other main phyllaries, if mature, may be corky keeled on the lower half, an inner 4th phyllary smaller, linear; calyculate bracts 2–3 mm long, sublinear or subovate, somewhat cupped- and sickle-shaped; ray florets with the ligules (1.5–)2–3 mm long, linear-oblong, 2–3-toothed; disc florets 5–7, the corollas 3–3.5 mm long, the tubes 1–1.3 mm long, moderately villous, the throats 1.5–1.7 mm long, the lower half tubular, the upper half expanded into a campanulate shape, the lobes ca. 0.5 mm long, acute; anthers ca. 1.5 mm long; achenes of the ray and disc florets the same size, (1–)1.5–2(–2.5) mm long, linear or narrowly oblanceolate, rarely nearly obovate; pappus absent; chromosome number, unknown.

Sandy or loamy soils in open fields and in sclerophyllous scrub, Puebla and Oaxaca, to Mexico (Distrito Federal) and Guerrero (Fig. 3).

REPRESENTATIVE SPECIMENS: MEXICO. DISTRITO FEDERAL: Chapultepec, *Schaffer 16* (GH). GUERRERO: Coyuca-Tinajas, *Hinton 5844* (K, MO, US). OAXACA: Ca. 1 mi N of Tamazulapan, *King 2930* (DS, MICH, NY, TEX, UC, US). Cerro Solo, 7 km NE of Tepelmeme de Morelos, *Cisneros 2419* (MICH). PUEBLA: Puebla, *King 2623* (DS, MICH, NY, TEX, UC, US). Fields near Puebla, *Pringle 4749* (GH, MICH, MO, NY, UC, US). Near Tehuacán, *Rose & Hay 5871* (US).

Flaveria angustifolia is closely related to *F. pringlei* and the taxa have often been confused by superficial examination of herbarium specimens, but *F. angustifolia* can be delimited easily by its radiate heads. The species is also distinguished usually by its mostly sessile, linear-lanceolate leaves with serrulate-spinulose margins, distally expanded throats of the disc corollas, and corky-keeled phyllaries. Leaf measurements and observations in the descriptions of *F. angustifolia* and related shrubby species were taken from the upper portions of the plants that were preserved as specimens.

9. **Flaveria pringlei** Gandoger, Bull. Soc. Bot. Fr. 65: 42. 1918. TYPE: Mexico, Puebla, fields at Tehuacán, 20 Dec. 1895, *C. G. Pringle 7369* (P? holotype; US, isotype).

Plants perennial herbs, shrubs with many erect stems from the base, or small trees, 1–4 m high; leaves opposite, the lower leaves petioled (0.5–1 cm) and barely connate, the upper leaves sessile and connate or short petioled, 7–13 cm long, 1.5–4.5 cm wide, glabrous, lanceolate-elliptic to broadly so or ovate, the margins entire; capitulescence of corymbose panicles with numerous heads densely aggregated in clusters; heads discoid, or rarely with a seemingly abortive ray floret enclosed by the outer phyllary, the ligule erect and not extending from the bract; involucres 4–5 mm long, tubulo-angular, the phyllaries 3–4, with 2 outer and 2 inner ones, the outer phyllaries boat shaped; calyculate bracts 1.5–3 mm long, subdeltoid, linear, rarely boat shaped; disc florets 7–9, the corollas 3–4 mm long, the tubes 1.5 mm long, sparsely villous or naked, the throats 1–1.5 mm long, funnelform, the lobes ca. 1 mm long, acute; anthers 1.5–2 mm long; achenes (1.2–)1.5–2 mm long, linear or narrowly oblanceolate; pappus absent; chromosome number, n = 18, 36.

Rather arid and at least sometimes gypseous habitats, scattered localities, waste places, cultivated fields, roadsides, deciduous woods, in and near the Tehuacán Valley, Puebla and Oaxaca, west to Guerrero (Fig. 3).

REPREENTATIVE SPECIMENS: MEXICO. GUERRERO: 7 mi N of Chilpancingo, *King 4174* (F, MICH, NY, UC, US). Ca. 35 km NNW of Chilpancingo, *McVaugh 22198* (DS, LL, MICH, NY, TEX). OAXACA: 6 mi NW of Huajuapan de León, *Dillon 681* (LL, TEX). Ca. 7 mi N of Huajuapan de León, *King 2532* (DS, MICH, TEX). 54 mi SE of Puebla-Oaxaca border, *King 6439* (MO, US). 30 mi NNW of Huajuapan de León, *Turner P-50* (TEX). PUEBLA: 18–20 km NW of the Oaxaca-Puebla border, *Anderson & Anderson 5647* (MICH). 5 mi SW of Tehuacán, *Breedlove 14188* (CAS, MICH, NY). 1 mi SE of Tehuacán, *Cronquist & Sousa 10388* (NY). 16 mi S of Esperanza, *Hartman et al. 3834* (LL). 3 mi N of the Oaxaca-Puebla border, *King 2534* (DS, MICH, TEX). S of Petlalcingo, *Langman 4152* (US). 5 km NW of Petlalcingo, *Rzedowski 28942* (MICH, TEX). 1 mi S of Rija, 16 mi S of the Morelos border, *Walker 72009* (NY).

On herbarium sheets *F. pringlei* is readily distinguished from the closely related and morphologically similar *F. angustifolia* by its discoid heads. The former species also differs by its usually broader, ovate leaves with entire margins, disc corollas with funnelform throats, and somewhat thickly keeled outer phyllaries.

Abortive ray florets were seen in two collections of *F. pringlei*, the type collection and *King 2533* (Puebla, near Petlalcingo). In certain heads the florets with very small, erect ligules were found enclosed by an outer (shortest) phyllary, not at all evident except by dissection. I believe that *F. pringlei* evolved from the radiate *F. angustifolia*. The only instances of polyploidy (n = 36) known in *Flaveria* were found in two collections of *P. pringlei* (*Dillon 681*; *Hartman et al. 3834*). The known distributions of *F. pringlei*, *F. angustifolia*, and *F. vaginata* are somewhat overlapping (Fig. 3), and it is possible that hybridization has occurred among the taxa.

10. **Flaveria vaginata** B. L. Robinson & Greenman, Proc. Amer. Acad. Arts 32: 48. 1896. TYPE: Mexico, Oaxaca, between Coixtlahuaca and Tamuzulapan, 2,300–2,600 m, 12 Nov. 1894, *E. W. Nelson 1933* (GH, lectotype; K, isolectotype).

Plants shrubby perennials, ca. 1 m high, the stems several, erect, with short grayish woolly pubescence especially on the peduncles; leaves opposite, sessile, connate, often fascicled in the axils, 3–8 cm long, 0.2–0.6 cm wide, pale green, rather densely short pubescent, linear-subulate, the margins entire, ciliated; synflorescence of corymbose-paniculate, hemispherical glomerules, with numerous heads tightly aggregated in simulation of normal composite heads, the ligulate heads mostly peripheral; heads radiate and discoid; involucres 3.5–4 mm long, oblong-angular, the phyllaries 3(–4), boat shaped, hyaline; calyculate bracts 1.5–3 mm long, ovate-orbicular or sickle shaped; ray florets with the ligules 2–4 mm long, oblong-elliptic, 2–3-toothed; disc florets 5–8, the corollas 3.2–3.5 mm long, the tubes ca. 1 mm long, moderately pubescent or naked, the throats ca. 1 mm long, the upper half expanded to a subcampanulate shape, the lobes ca. 0.5 mm long, acute; anthers ca. 1.5 mm long; ray achenes ca. 2 mm long, the disc achenes ca. 1.5 mm long, both linear or narrowly oblanceolate; pappus absent; chromosome number, unknown.

Known only from the type collection and the one other specimen cited (Fig. 3).

REPRESENTATIVE SPECIMEN: MEXICO. PUEBLA: 7 mi W of Izúcar de Matamoros, *King 2922* (DS, MICH, NY, TEX, UC, US).

The type specimens of *F. vaginata* are distinctive in the densely pubescent upper herbage, sessile linear-subulate leaves, and heads aggregated into hemispherical glomerules with peripheral radiate heads. The *King 2922* collection shows minor differences in the disc corollas but otherwise compares favorably with the types. The species is closely related to *F. angustifolia* and *F. pringlei* of the same general distribution.

The shrubby habit, rather thick leaves, and radiate heads of *F. vaginata* and *F. angustifolia* suggest primitiveness in the 3–4-phyllary line of Puebla-Oaxaca species (Fig. 1), but the glomerulate heads (synflorescence) and C_4 metabolism of *F. vaginata* suggest a more derived lineage. In fact, it is from *F. vaginata* that the C_4 annual species (Fig. 1), all with radiate synflorescences, may be derived.

11. **Flaveria cronquistii** A. M. Powell, sp. nov. TYPE: Mexico, Puebla, 6 mi NW of Teotitlán and 33 mi SE of Tehuacán, 1,100 m, 22 Oct. 1965, *A. Cronquist & M. Sousa 10385* (NY, holotype; CAS, F, GH, KSC, MICH, TEX, US, WIS, isotypes).

Frutex 1–1.7 m altus. Folia 7–10 cm longa 0.3–1.5 cm lata, succulenta glabra linearis vel lanceolata petiolis 0.6–1.3 cm longis. Capitula eradiata 7-flora; phyllaria 3. Achaenia 1.5–1.8 mm longa. Chromosomatum numerus $n = 18$.

Plants shrubs and small trees, 1–1.7 m high; leaves opposite, barely connate, 7–10 cm long, 0.3–1.5 cm wide, slightly succulent, glabrous, linear or lanceolate, the margins entire, the petioles 0.6–1.3 mm long; capitulescence of rather open, corymbose, flat-topped panicles, with numerous heads rather loosely aggregated in each cluster; heads discoid; involucres ca. 4 mm long, subcylindrical-angular, the phyllaries 3, boat shaped, obtuse; calyculate bracts linear, ca. 1 mm long; disc florets 7, the corollas 3–3.5 mm long, the tubes 1–1.2 mm long, the throats 1.2–1.5 mm long, tubular or slightly funnelform, the lobes 0.5–1 mm long, reflexed, linear; anthers ca. 1.5 mm long; achenes 1.5–1.8 mm long, nearly linear or narrowly oblanceolate; pappus absent; chromosome number, $n = 18$.

Rocky limestone (possibly gypseous) areas of the Tehuacán Valley, usually in thorn-scrub vegetation, Puebla-Oaxaca, Mexico (Fig. 3).

REPRESENTATIVE SPECIMENS: MEXICO. OAXACA: 8 km SE of Teotitlán, *Cronquist 11240* (MO, US). PUEBLA: 8 mi SE of Coxcatlán, *Anderson & Anderson 5341* (MICH). 5 mi SW of Tehuacán, *Breedlove 14189* (CAS, MICH, NY). Amatitlán, *Miranda 2516* (GH). Tehuacán, *Purpus 5626* (F, NY, UC, US).

Flaveria cronquistii is delimited from other species of the Tehuacán Valley region by its subcylindrical discoid heads arranged in rather loose, flat-topped corymbs, linear (or lanceolate) leaves, pubescent and indistinct tips of the style branches, and barely funnelform throats of the disc corollas. The taxon perhaps most closely resembles *F. robusta* of Colima-Michoacán, but its shrubby habit, semisucculent leaves, small heads, and distribution also suggest a relationship with *F. angustifolia* and allies. Both *F. cronquistii* and *F. vaginata* exhibit C_4 metabolism (Fig. 1) suggesting an ancestral connection on this basis, although the radiate glomerulelike inflorescence of *F. vaginata* is not at all like that of *F. cronquistii.*

The *Miranda 2516* collection from Puebla is here assigned to *F. cronquistii* although it is anomalous in the following characters: leaves broadly lanceolate, longer (to 13 cm) and wider (to 3.2 cm); calyculate bracts ovate and obtuse; florets 3; disc corollas slightly shorter with tubular throats; style branches glabrous with sharply defined tips; achenes smaller, 1.2–1.3 mm long.

The specific epithet of this newly described species is intended to honor Dr. Arthur Cronquist of the New York Botanical Garden who has collected the species and other Flaverias, and who is widely recognized for his contributions to the systematics of Asteraceae.

12. **Flaveria robusta** Rose, Contr. U.S. Natl. Herb. 1: 337. 1895. TYPE: Mexico, Colima, 27–28 Feb. 1891, *E. Palmer 1299* (GH, lectotype; K, MO, NY, UC, isolectotypes).

Plants perennial herbs or shrubs, (60–)100–200 cm high, the stems essentially glabrous; leaves opposite, connate or nearly so, 5–14 cm long, 0.8–3.4 cm wide, somewhat fleshy, glabrous, lanceolate, lance-elliptic, linear-lanceolate, or linear, the margins serrate or minutely so, or entire, the petioles 1–2.5 mm long; capitulescence of rather open corymbose, flat-topped panicles with numerous heads in each cluster; heads radiate and discoid; involucres ca. 3 mm long, oblong-angular or subcylindrical, the phyllaries usually 3, boat shaped or linear; calyculate bracts linear, ca. 1 mm long; ray florets with the ligules 2–2.5 mm long, oblong-obovate, notched apically; disc florets usually 3, the corollas 2.5–3 mm long, the tubes ca. 1 mm long, glabrous or sparsely glandular, the throats ca. 1.5 mm long, funnelform, the lobes ca. 0.8 mm long, reflexed, linear; anthers 1–1.7 mm long; achenes of the disc florets ca. 1.2 mm long, those of the ray florets ca. 1.5 mm long, subobovate or oblanceolate; pappus absent; chromosome number, $n = 18$.

Gypsum and slate, sandy clay, deciduous woodland, or open rocky slopes, often weedy at roadsides, or with cacti and bromeliads, 340–500 m, Colima and adjacent Michoacán (Fig. 3).

REPRESENTATIVE SPECIMENS: MEXICO. COLIMA: 20 mi S of Colima, *Alava & Cook 1693* (MICH, UC). Armeria, *Jones 276* (US). Ca. 11 mi SSW of Colima, *McVaugh & Koelz 1044* (LL, MICH, TEX). 10 mi SSW of Colima, *McVaugh 15529* (MICH, US). 5–10 mi N of Tecomán, *Thompson & Fields 321* (TEX). MICHOACÁN: Ca. 5 km SW of Coahuayana, *Feddema 2732* (CAS, MICH, TEX).

The large habit, small heads with three phyllaries and geographical considerations suggest that *F. robusta* is related to *F. angustifolia* and allies, and derived therefrom. The species is distinguished by its showy radiate heads arranged in rather open panicles, leaf shape and size, various floral characters, and distribution.

13. **Flaveria bidentis** (L.) Kuntze, Rev. Gen. 3: 148. 1898.

Ethulia bidentis L., Mant. 110. 1767. TYPE: "India"? (LINN, not seen).
Eupatorium chilense Molina, Sagg. Chile 142. 1789.
Milleria chiloensis Juss., Gen. Pl. 187. 1789, pro syn.
Flaveria chilensis Juss.; J. F. Gmel., Syst. Nat. 2: 1269. 1791.
Milleria contrayerba Cav., Icon. 1: 2. 1791.
Vermifuga corymbosa Ruiz & Pavón, Syst. Veg. Fl. Per. 216. 1798.
Flaveria contrayerba Pers., Syn. Pl. 2: 489. 1807.
F. capitata Juss.; Smith, in Rees, Cycl. 14: 1810. *Flaveria* no. 1.
F. bonariensis DC., Prodr. 5: 635. 1836.
F. bidentis var. *angustifolia* Kuntze, Rev. Gen. 3: 148. 1898. TYPE: South America, Argentina, Córdoba (not seen).

Plants delicate or robust annuals, (15–)25–100 cm high, the stems often purplish, sparsely-villous; leaves opposite, rather light green, 5–12(–18) cm long, 1–2.5(–7) cm wide, glabrous or densely short-pubescent, lanceolate-elliptic, serrate or spinulose-serrate, the petioles of the main leaves 0.3–1.5 cm long, the bases nearly connate, the blades of the upper leaves usually connate; capitulescence of tightly aggregated heads in scorpioid cymes, the heads alternate on short axes; heads obscurely radiate; involucres ca. 5 mm long, oblong and angular, the phyllaries 3(–4), concave and rounded or obtuse apically; calyculate bracts 1–2; ray corollas short, 1–2 mm long, pale yellow, the ligule not or barely protruding from the closed bracts, erect, ovate-oblique, acute, ca. 1 mm long or less; disc florets (2–)3–8, the corollas ca. 2.3 mm long, the tubes ca. 0.8 mm long, the throat ca. 0.8 mm long, funnelform, the lobes ca. 0.5 mm long, acute; anthers ca. 1 mm long; achenes of the disc florets ca. 2 mm long, those of the ray florets ca.

FIGURE 6. Distribution of *Flaveria bidentis* in South America.

2.5 mm long, larger, oblanceolate or subclavate; pappus absent; chromosome number, $n = 18$.

A weed in moist places on waste ground, near rivers, streams, and barrancas, in fields, pastures, disturbed ground, near streets and sidewalks in towns, clay-gravel, or sand, 250–2,800 m. South America (Fig. 6); ballast and waste ground

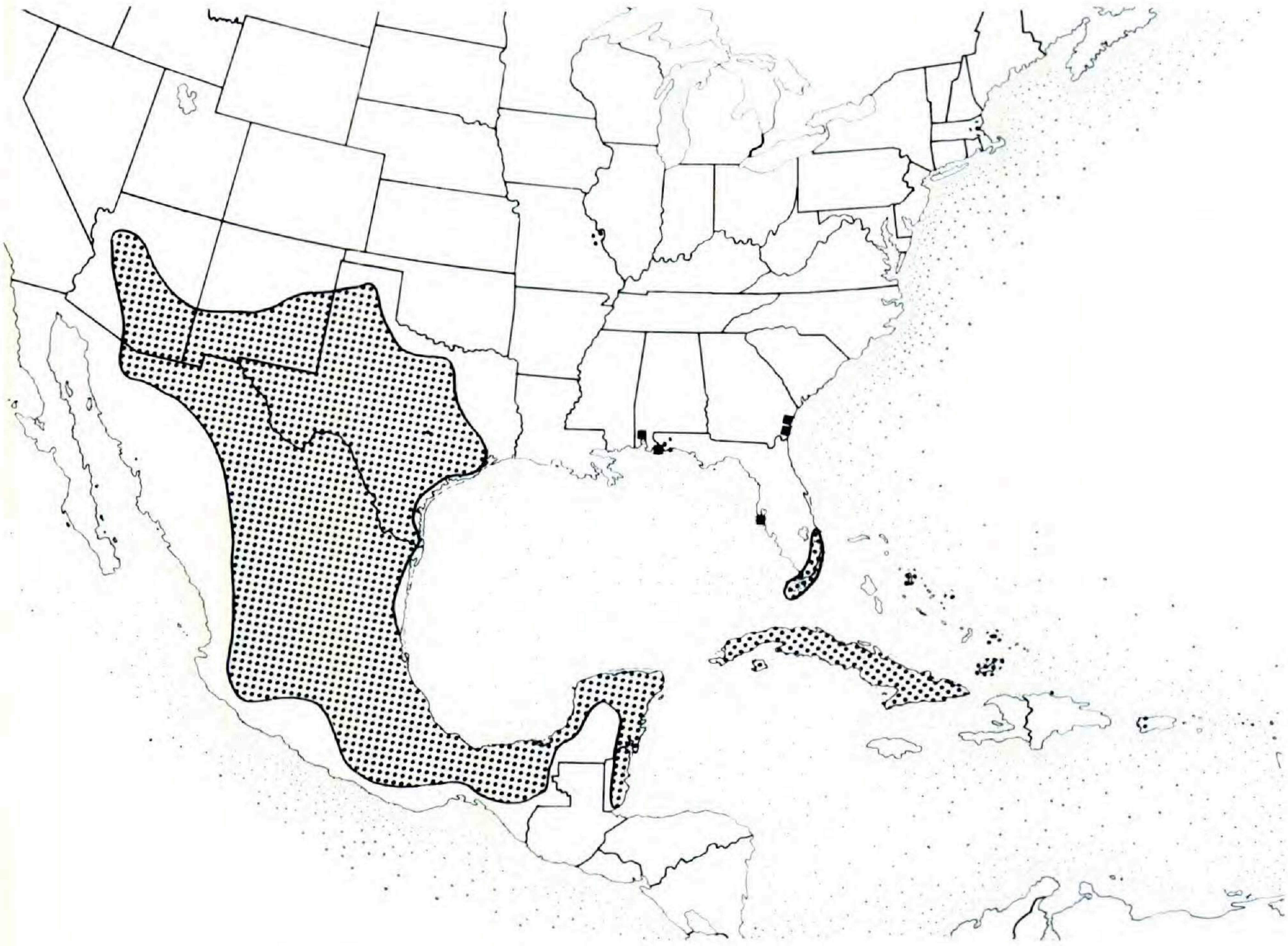

FIGURE 7. Generalized distribution of *Flaveria trinervia* in North America, Central America, and the West Indies (dots); Old World distribution of *F. trinervia* not plotted; distribution of *F. bidentis* in the United States (squares).

near wharfs and the shore, southeastern Gulf Coast, United States (Fig. 7); a weed in Great Britain, the West Indies, Egypt, and southern Africa.

REPRESENTATIVE SPECIMENS: ARGENTINA. BUENOS AIRES: Saladillo, *Cabrera 6426* (US). CATAMARCA: Belen, *Cabrera 1195* (LL, TEX). CHACO: Presidente de la Plaza, *Malvarez 862* (DS). CÓRDOBA: Córdoba, *Huidobro 461* (US). CORRIENTES: Saladas, *Schwarz 9573* (TEX). FORMOSA: Pilcomayo River, *Morel 8339* (US). JUJUY: Humahuaca, *Venturi 8773* (GH, US). LA PAMPA: Catriló, *Furtuna s.n.* (A). LA RIOJA: Famatina, *Paz s.n.* (A, F, UC). MENDOZA: Godoy Cruz, *Leal 8390* (A, UC). MISIONES: Apostoles, *Huidobro 4699* (TEX). NEUQUEN: General Roca, *Fischer 249* (F, GH, MO, NY, US). SALTA: Mira Flores, *Huidobro 551* (US). SAN JUAN: Jachál, *Cuezzo 1920* (F). SAN LUIS: San Martín, *Varela 521* (F). SANTIAGO DEL ESTERO: Río Salado, *Job 1102* (NY). TUCUMÁN: Tucumán, *Venturi 332* (A, US).

BOLIVIA. CHUQUISACA: La Loma, *Espinosa 494* (F). COCHABAMBA: Cochabamba, *Bang 968* (F, GH, MO, NY, US). LA PAZ: Río Palca Valley, *Julio 20* (US). SANTA CRUZ: Cabezas, *Peredo 396* (A). TARIJA: Tarija, *Fiebrig 2227* (GH).

BRAZIL. MATO GROSSO: Corumbá, *Robert 786* (K).

CHILE. ATACAMA: Copiapó, *Johnston 5000* (GH, US). SANTIAGO: Santiago, *Claude-Joseph 2233* (US). TARAPACÁ: Arica, *Jaffuel 1064* (GH). VALPARAÍSO: Quillota, *Bridges 491* (K).

ECUADOR. IMBABURA: Between Ibarra and Salinas, *Asplund 10449* (CAS, NY, US). LOJA: Loja, *Espinosa 494* (NY). MANABI: Zapallo, *Eggers 15704* (F, US).

PARAGUAY. BOQUERÓN: Gran Chaco, *Pride s.n.* (K). CONCEPCIÓN: Sierra de San Luis, *Kurtz 8551* (NY).

PERU. AMAZONAS: Valley of Río Utcubamba, *Wurdack 2065* (F, US). APURIMAC: Andahuaylas, *Herrera 1486* (GH). AREQUIPA: Arequipa, *Rose 18816* (US). CUZCO: *Bues s.n.* (F, GH). HUÁNUCO: 5 km N of Huánuco, *Canne et al. 211* (ASU, OS, US). ICA: Ica, *Lauderman 4023* (K). LA LIBERTAD: Chicama Valley, *Smith 16* (US). LIMA: San Lorenzo Island, *Anderson s.n.* (US). Chosica, *Grant 7407* (GH). TACNA: Near Tacna, *Metcalf 30348* (GH, MO, US).

UNITED STATES. ALABAMA: Mobile Co., *Mohr s.n.* (US). FLORIDA: Escambia Co., Pensacola, *Curtiss 6495* (DS, GH, K, MO, NY, UC, US). Hillsborough Co., Mullet Key, *Long 1261* (DS). GEORGIA: McIntosh Co., Durien, *Biltmore? 6723* (US). Glynn Co., Brunswick, *Harper 1521* (F, GH, MO, NY, US).

GREAT BRITAIN. Gloucester, *Sandwith 5744* (K).
ANTIGUA. *Box 1022* (F, MO, UC, US).
CUBA. *Wright s.n.* (K).
DOMINICAN REPUBLIC. Barahona, *Liogier 18314* (NY, US).
PUERTO RICO. MAYAGUEZ: Guanica, *Liogier 10436* (NY).
BOTSWANA. 5 mi S of Palapye, *Leach & Noel 268* (K).
EGYPT. *Pfund 1586* (US).
ETHIOPIA. *Pappi 2193* (F).
RHODESIA. *Wild 2784* (K).
LESOTHO. *Clirhaiulan 717* (K).
SOUTH AFRICA. NATAL: Zululand, *Ward 2451* (K). TRANSVAAL: Pretoria, *Strey 3095* (A).
SOUTH WEST AFRICA. *Meyer 1115* (UC).
SWAZILAND. *Compton 40919* (K).

The weedy species *Flaveria bidentis* is widespread and well established in South America, and probably should be regarded as native to that country. In floral structure *F. bidentis* is perhaps least advanced of the annual species. The capitulescence is somewhat scorpioid, but contracted, as though it were derived from *F. angustifolia*. *Flaveria bidentis* also is characterized by pubescent stems, lanceolate-elliptic, bluish green leaves (thinner in texture than in *F. trinervia*), 3(–4) phyllaries, 2–8 florets per head, and reduced ray corollas.

Flaveria bidentis perhaps evolved as an annual C_4 prototype in Mexico from the perennial *F. vaginata* (C_4) line (Fig. 1), and reached South America as a self-compatible colonizer during the Pliocene or Pleistocene, a time much other bicontinental distribution was taking place (Raven, 1963). The species then must have flourished in South America, subsequently spreading as a weed to other parts of the world. Some specimens of *F. bidentis* from the West Indies and other areas are smaller, thinner plants with narrow leaves and more lax capitulescences, but these are seemingly ecological variances without taxonomic significance. The taxon is related to *F. campestris* and *F. trinervia.*

14. **Flaveria campestris** J. R. Johnston, Proc. Amer. Acad. Arts 39: 287. 1903. TYPE: United States, Missouri, near Courtney, 10 Sep. 1890, *B. F. Bush 51* (US, lectotype).

Flaveria angustifolia A. Gray, Mem. Amer. Acad. Arts, n.s., 4: 88. 1849. Hyponym., Coult., Contr. U.S. Natl. Herb. 2: 234. 1892, non *F. angustifolia* Pers. 1807.

Plants delicate or robust annuals, 18–70 cm high, the stems mostly erect, often purplish, glabrous except tufted-pubescent in the axils; leaves opposite, barely connate, 3–9 cm long, 0.6–2.2 cm wide, glabrous, lanceolate or linear-lanceolate, the margins serrate to weakly so, or spinulose-serrate; capitulescence of tightly aggregated heads in subglomerules; heads radiate or discoid, the radiate heads peripheral; involucres 6–7 mm long, urceolate or oblong, angular, the phyllaries 3, boat shaped, keeled, elliptic, obovate or oblong-obovate, acute;

calyculate bracts 2, 1–3 mm long, unequal, linear-lanceolate; ray florets with the ligules yellow, 1.5–2.5 mm long, ovate, notched; disc florets 5–6(–8), the corollas 2.5–3.5 mm long, the tubes 0.8–1.3 mm long, the throats 1.2–1.7 mm long, funnelform, the lobes 0.5–0.8 mm long, acute; anthers 1–1.5 mm long; achenes 2.8–3.6 mm long, those of the ray florets noticeably larger and longer by ca. 0.2 mm, oblanceolate, linear, or oblong; pappus absent; chromosome number, $n = 18$ (9).

Seemingly always in saline soils, at the margins of lakes, ponds, streams, in flood plains, or in disturbed pastures, 1,000–1,600 m, Missouri southwest to Kansas, Colorado, New Mexico, and to Arizona, and south of Oklahoma and north Texas (Fig. 2).

REPRESENTATIVE SPECIMENS: UNITED STATES. ARIZONA: Navajo Co., 5 mi SE of Winslow, *Crutchfield 912* (LL). COLORADO: Bent Co., Las Animas, *Osterhout 4138* (NY). Mesa Co., Grand Junction, *Cowen 2903* (MO, NY, US). Otero Co., E of Lajunta, *Drouet et al. 4073* (F). Prowers Co., 4 mi W of Lamar, *Lindstrom 1660* (KSC). Pueblo Co., Lake Minnequa near Pueblo, *Myers s.n.* (F). KANSAS: Barber Co., Medicine Lodge, *Smyth 292* (NY, US). Barton Co., Pawnee Rock, *Lowell 45* (GH). Clark Co., *Hitchcock s.n.* (KSC). Edwards Co., *Hitchcock s.n.* (KSC). Finney Co., 0.5 mi S of Garden City, *McGregor 2183* (KSC). Gray Co., *Hitchcock s.n.* (KSC). Hamilton Co., S of Kendall, *Gates 16091* (KSC, WIS). Kearney Co., S of Lakin, *Anderson 2585* (DS, FSU). Kiowa Co., near Belvidere, *Ward s.n.* (GH, US). Marion Co., *Norton s.n.* (KSC). Meade Co., below Lake Larrabee, *Horr 3659* (US). Reno Co., near Sylvia, *Brownlee s.n.* (KSC). Rice Co., Sterling, *Anderson 2810* (FSU). Sedgwick Co., Wichita, *Smyth 735* (NY). Seward Co., Cimarron River bottom, *Gates 16245* (KSC). Shawnee Co., Topeka, *Smyth s.n.* (KSC). Stafford Co., 6 mi E of Hudson, *McGregor 13692* (F, NY). Wyandotte Co., Argentine, *MacKensie 1307* (K, KSC, MO, NY). MISSOURI: Jackson Co., Courtney, *Bush 8190* (GH, NY, US). Marion Co., Hannibal, *Davis 3249* (MO). NEW MEXICO: Bernalillo Co., along the Rio Grande, *Palmer 31131* (GH). Chaves Co., Lake Van, 1.4 mi SE of Dexter, *Pinkava et al. 3092* (ASU). Colfax Co., Cimarron River, *Fendler 536* (GH, K, MO, UC). Doña Ana Co., 9 mi N of Las Cruces, *Munz 13271* (LL, TEX, UC). Eddy Co., Carlsbad, *McKechnie 553* (MO). Guadalupe Co., Santa Rosa, *Dittmer 8479* (NMU). Sandoval Co., Bernalillo, *Arsène 19440* (F, LL, TEX, US). Socorro Co., Rio Grande bottom, *Ferris 1176* (DS). Valencia Co., near Belen, *Anderson 3229* (FSU). OKLAHOMA: Alfalfa Co., *Carleton 505* (US). Beckham Co., near Sayre, *Goodman 2352* (CAS, MO, NY). Blaine Co., 3 mi W of Watonga, *Waterfall 2386* (GH, NY). Canadian Co., flood plain of the Canadian River, *Waterfall 2506* (ARIZ). Cleveland Co., Norman, *Emvig 526* (US). Ellis Co., near Shattuck, *Stevens 2722* (GH). Harmon Co., near Hollis, *Stevens 1113* (DS, GH, NY). Harper Co., 20 mi E of Buffalo, *Smith 123* (TEX). Woods Co., near Alva, *Stevens 2808* (DS, GH, MO, US). Woodward Co., Woodward, *Locke 54* (US). TEXAS: Bailey Co., Coyote Lake, *Ferris & Duncan 3463* (CAS, DS, NY). Baylor Co., Seymore, *Reverchon 506* (NY, US). Childress Co. (TEX). Culberson Co., Rustler Springs, *Cory 2763* (GH). Dallam Co., Mustang Spring, *Havard 13* (NY, US). Donley Co., Lelia Lake, *Whitehouse 17260* (GA, MICH, NY, UC). Garza Co., Post, *Palmer 14574* (MO). Hemphill Co., Canadian River, *Rowell 5838* (TEX). Hockley Co., *Hams 47* (US). Howard Co., near Big Spring, *Reverchon 13* (GH). Hutchinson Co., Canadian River breaks, *Drake 173* (TEX). Lubbock Co., near Lubbock, *Reed 3145* (US). Motley Co., Roaring Springs, *Cory 16097* (TEX). Wheeler Co., N fork Red River, *Tharp & Tyson s.n.* (TEX). Wilbarger Co., near Vernon, *Eggert s.n.* (MO). UTAH: Grand Co., lower Courthouse Wash, near Colorado River, Arches Natl. Monument, *Welsh & Moore 2751* (NY, WIS).

Flaveria campestris is characterized by its annual habit, linear-lanceolate leaves with serrate or spinulose-serrate margins, contracted but not completely glomerulate capitulescence, 3-keeled phyllaries, 5–6(–8) florets per head, and distribution. The larger heads, less contracted capitulescence, and habit of *F. campestris* suggest that the taxon might have originated as an early, north-migrating offshoot of *F. bidentis*.

The localized distribution of *F. campestris*, restricted by saline and at least seasonally wet conditions, evidently fluctuates considerably from year to year. In Kansas, Anderson (1972) was not able to recollect from an exact site after six years. I have visited numerous precise localities of previous collections without finding the plants. In 1928 *F. campestris* was collected at Rustler Springs (*Cory 2763*), a permanently wet site in the gypsum plains of Culberson Co., Texas. When I visited the site in 1976, both *F. trinervia* and *F. chloraefolia* were abundant, but *F. campestris* was absent.

15. **Flaveria trinervia** (Spreng.) C. Mohr, Contr. U.S. Natl. Herb. 6: 810. 1901. TYPE: Botanical Garden, Halle, cultivated (not seen).

Oedera trinervia Spreng., Bot. Gard. Halle 63. 1800.
Brotera contrayerba Spreng., J. Bot. Schrad. 1800. *pl.* 5. 1801, non *Flaveria contrayerba* Pers., 1807.
Nauenbergia trinervata Willd., Sp. Pl. 3: 2393. 1804.
Brotera trinervata Pers., Syn. Pl. 2: 498. 1807.
Flaveria repanda Lag., Gen. & Sp. Nov. 33. 1816. TYPE: Mexico (not seen).
Brotera sprengelii Cass., Dict. Sci. Nat. 34: 306. 1825.
Flaveria trinervata Baillon, Hist. Pl. 55. 1882.

Plants delicate or robust annuals, 15–80 cm to more than 2 m high and nearly as broad, the stems often purplish, essentially glabrous; leaves opposite, 3–15 cm long, (0.7–)1–4 cm wide, essentially glabrous, lanceolate, oblanceolate, to elliptic or subovate, the margins serrate, serrate-dentate, or spinulose-serrate, the petioles of the main leaves 1–2 cm long, the petiole bases nearly connate, the blades of the upper leaves usually connate; capitulescence of glomerulelike, tightly clustered secondary heads, 1–2.5 cm wide, sessile, axillary, subtended by smaller cauline leaves; receptacles of glomerules with long, slender, membranous, chafflike setae; heads radiate or discoid, the florets usually 1, rarely 2; radiate heads mostly peripheral in glomerules; involucres 3.8–4.5 mm long, oblong and cylindrical or angular, the phyllaries usually 2, concave and rounded apically, closely investing and falling with mature achenes; ray corollas short, ca. 1.5 mm long, seemingly vestigial, pale yellow or whitish, the ligule barely protruding from the closed bracts, the ligule oblique or suborbicular, 0.5–1 mm long; disc corollas 2–2.5 mm long, the tubes 0.5–1.4 mm long, pubescent, the throats, 0.5–0.8 mm long, pubescent, campanulate, the lobes ca. 1 mm, acute; anthers ca. 1 mm long; achenes 2–2.6 mm long, oblanceolate or subclavate, the ray achenes longer; pappus absent; chromosome number, $n = 18$.

A weedy species even more widespread than *F. bidentis*, in a variety of habitats, usually saline, gypseous, and disturbed, usually near ephemeral or permanent water sources; throughout most of Mexico; Texas to Arizona in the United States, and other scattered localities, including Hawaii; Central America, British Honduras; Brazil, Ecuador, Peru, and Venezuela of South America, seemingly not in competition with *F. bidentis*; West Indies (Fig. 7); Africa; India; Middle East.

REPRESENTATIVE SPECIMENS: MEXICO. AGUASCALIENTES: Aguascalientes, *McVaugh & Rzedowski s.n.* (MICH, MO). CAMPECHE: Champotón, *King 6855* (MO, US). CHIAPAS:

Near Soyatitán, *Ton 3138* (MICH, NY). CHIHUAHUA: 3 mi W of Camargo, *Powell & Tomb 2658* (TEX, US). COAHUILA: 4 mi N of Monclova, *Flyr 239* (TEX). DISTRITO FEDERAL: San Angel, *Smyth 91* (US). DURANGO: Vicinity of Durango, *Palmer 481* (MO, NY, UC, US). GUANAJUATO: Near San Miguel Allende, *Kenoyer 2175* (GH). GUERRERO: Coyuca, *Hinton 7284* (GH, K, MICH, NY, UC). HIDALGO: Near Ixmiquilpan, *Quintero 2832* (DS, MICH, TEX). JALISCO: 4.5 mi W of Juanacatlán, *McVaugh 22089* (LL, MICH, NY, TEX). MORELOS: 10 mi NW of Cuantla, *Lyons 147* (MICH). NUEVO LEÓN: Laguna de Labradores, *Chase 7707* (ARIZ, F, GH, MICH, MO, NY). OAXACA: 1 mi N of Tamazulapan, *King 2937* (DS, MICH, NY, TEX, UC, US). QUERETARO: Cerro de las Campanas, *Arsène 10063* (F, MO, US). SAN LUIS POTOSÍ: Matehuala, *Shreve 8703* (ARIZ, MICH). SONORA: Magdalena, *Drouet & Richards 3799* (F). TAMAULIPAS: Vicinity Tampico, *Palmer 57* (CAS, F, GH, MO, NY, US). TLAXCALA: Hueyotlipan, *Nicolas s.n.* (GH). VERACRUZ: Veracruz, *Muller 150* (NY). YUCATÁN: Progreso, *Millspaugh 1653* (F). ZACATECAS: Hacienda de Cedros, *Lloyd 168* (US).

UNITED STATES. ARIZONA: Greenlee Co., Duncan, *Davidson 391* (GH). FLORIDA: Dade Co., Miami, *Burch 54* (GH). HAWAII: Oahu, *Egler 37-232* (LL, UC, US). MASSACHUSETTS: Middlesex Co., *Fletcher s.n.* (GH). MISSOURI: St. Louis Co., *Sherff 797* (F). NEW MEXICO: Chaves Co., 20 mi S of Roswell, *Earle & Earle 304* (K, MO, NMSU, NY, US). TEXAS: Culberson Co., 25 mi W of Orla, *Powell 2221* (TEX).

BELIZE. BELIZE: *Lundell 1884* (MICH, TEX, US).
BRAZIL. GOIÁS: Brasilia, *Riedel 938* (K).
ECUADOR. *Eggers 15704* (K).
PERU. CARAVELI: Near Lima, *Hutchinson 1293* (UC).
VENEZUELA. DISTRITO FEDERAL: Near Caracas, *Alston 5247* (NY, US).
BAHAMA ISLANDS. Great Inagua Island, *Dunbar 135* (A).
CUBA. LA HABANA: Near Havana, *Curtiss 545* (F, GH, MO, NY, US).
JAMAICA. Rose Hall, *Proctor 35286* (MO).
PUERTO RICO. *Liogier 10883* (GH, US).
ETHIOPIA. Harar, *Burger 1313* (US).
KENYA. Kisumu, *Tweedie 2358* (K).
RHODESIA. Salisbury, *Whellan 1845* (K).
SOMALIA. Northwest, *Gillett 4552* (K).
TANZANIA. Zanzibar, *Vaughan 1707* (K).
ZAMBIA. Monze, *Fanshawe 6873* (K).
MASCARENE ISLANDS. Mauritius, *Collector* (K).
INDIA. Tamil Nadu, *Gamble 16429* (K).
IRAQ. Baghdad, *Agnew 1867* (K).
SAUDI ARABIA. *Smith & Lavranos 33* (K).
YEMEN. *Woodford 1* (K).

Flaveria trinervia is perhaps the most derived species in the genus, along with the closely related *F. australasica*, in that many of the floral features are reduced from those which characterize the supposedly ancestral *F. bidentis* lineage. In *F. trinervia*, and *F. australasica*, the heads are very tightly aggregated into axillary glomerules, obviously in *Flaveria* a type of reduced capitulescence. Additionally the phyllaries are reduced to 2, there are 1(–2) florets per head, and the ligules are usually less than 1 mm long.

16. **Flaveria australasica** Hook., in Mitchell's J. Exped. Trop. Australia. 118. 1848. TYPE: Australia, Banks of Balook, subtropical New Holland, 6 Apr. 1846, *T. L. Mitchell 100* (K, lectotype).

Plants delicate or robust annuals, 15–80 cm to more than 2 m high, essentially glabrous; leaves opposite, 2–10 cm long, 0.4–1.3 cm wide, lanceolate, the margins serrate, serrate-dentate, or spinulose-serrate; capitulescence of axillary glomerules; receptacles of glomerules with long, slender, membranous, chafflike setae; heads radiate or discoid, florets usually 1, rarely 2; involucres 3.8–5 mm long, the phyllaries usually 2; ray florets with the ligule barely protruding from the closed bracts, 0.5–1 mm long; disc corollas 2–2.5 mm long; achenes (2.3–)2.5–4.5 mm long; chromosome number, $n = 18$.

Often in saline conditions, near rivers, streams, drainage canals, cultivated areas, or in coastal dune sand, Australia; distribution not mapped; flowering April–September.

REPRESENTATIVE SPECIMENS: AUSTRALIA. NEW SOUTH WALES: 50 mi N of Broken Hill, *Norris 2478* (NY). Mt. Browne, *Prayer 20833* (CAS). NORTHERN TERRITORY: E of Mataranks, *Blake 17512* (K). Victoria River, *Mueller s.n.* (GH, K). Brickerton Island, *Specht 536* (US). QUEENSLAND: 10 mi SE of Roma, *Johnson 2073* (K). Darling Downs, *Norman s.n.* (K). SOUTH AUSTRALIA: Flinders Range, *Koch s.n.* (K). WEST AUSTRALIA: Ashburton River, *Morrison s.n.* (K). Kimberly District, *Mueller s.n.* (NY). Monte Bello Island, *Purry 4* (K). Gascoyne Jnct., *Turner 5404* (TEX).

Flaveria australasica is exceedingly close to *F. trinervia* and probably is of only recent derivation from an Australian founder of the latter species. The taxa are so similar morphologically that when attempting to identify herbarium specimens, reference to distribution is often the most reliable method. In fact, it might be acceptable to recognize the Australian population as a variety of *F. trinervia*. Living greenhouse specimens of *F. australasica*, however, are readily distinguished from *F. trinervia* by their taller, more slender habit and narrower, lanceolate leaves. The Australian plants also exhibit slightly longer involucres, somewhat thicker phyllaries, slightly larger disc corollas, and longer achenes.

17. **Flaveria palmeri** J. R. Johnston, Proc. Amer. Acad. Arts 39: 290. 1903. TYPE: Mexico, Coahuila, San Lorenzo de Laguna, 94–114 km SW of Parras, 1–10 May 1880, *E. Palmer 684* (GH, holotype; F, K, NY (2), US, isotypes).

Plants delicate or robust annuals (5–)10–75 cm high, to 0.5–1 m wide, glabrous or sparsely pilose, or tufted, especially in the axils; leaves opposite, often appearing whorled, 3–8 cm long, 0.4–1.4 cm wide, essentially glabrous, lanceolate to broadly so, or linear, weakly serrate, sessile or subsessile; capitulescence of tightly aggregated heads extended alternately on very short, modified peduncles giving a subscorpioid effect; heads radiate or discoid, the radiate heads mostly peripheral; involucres 4–5 mm long, 1–2 mm wide, cylindrical to suboblong and somewhat flattened or angular, the phyllaries 3(–4), ovate-lanceolate or elliptic, boat shaped, the apex minutely lacerate, rounded or obtuse; calyculate bracts 1–2 linear, ca. 2 mm long; ray florets with the ligules yellow, ca. 2 mm long, ovate to orbicular, notched; disc florets (3–)5–8, the corollas 2.5–3 mm long, the tubes 0.8–1 mm long, the throats 1.2–1.5 mm long, narrowly funnelform, 0.4–0.5 mm long, acute; anthers ca. 1.8 mm long; achenes (1.7–)2–2.5(–2.8) mm long, those of the ray florets longer (by 0.5 mm), narrowly oblanceolate to linear; pappus absent; chromosome number, $n = 18$.

Gypsum flats and knolls, or clay-loam soils probably with dilute gypsum, bolsons near lagunas, distributed areas near roads and fields, mostly in south-central Coahuila (Fig. 2).

REPRESENTATIVE SPECIMENS: MEXICO. COAHUILA: 76.3 mi W of Cuatro Ciénegas, *Bacon & Leverich 1168* (TEX). 3 mi E of Torreón, *Fisher 44151* (CAS, GH, MO, NY). Near Matrimonio Sta., *Johnston 9373* (GH, LL, TEX). Rancho Acatita, *McGill & Keil 8054* (ASU). Puerto Salada, *Pinkava et al. 5439* (ASU). Just SW of Cuatro Ciénegas, *Powell & Tomb 2621* (TEX, US). 39 mi N of San Pedro, *Powell & Tomb 2611* (TEX, US). Just N of Matamoros, *Sikes et al. 838* (TEX, US). 15 mi E of Cuatro Ciénegas, *Sikes et al. 851* (TEX, US). Laguna del Rey, *Stewart & Santos 3021* (GH). 25 mi W of El Oro, *White 2020* (ARIZ, GH, MICH, US). 25 mi E of Americanos, *Wynd 755* (ARIZ, GH, K, US). NUEVO LEÓN: Monterrey, *Arsène 10090* (US).

The distinctive annual, *F. palmeri*, a C_4 species commonly found between Torreón and Cuatro Ciénegas, Coahuila, is probably an early offshoot of the *F. bidentis* line. In overall morphology, phyllary number, and floret number, *F. palmeri* is similar to *F. bidentis* and *F. campestris*, but the former species differs in its self-incompatibility, usually narrower leaves, more open capitulescence, and in several floral traits. *Flaveria palmeri* is most closely related to *F. intermedia.* Both *F. trinervia* and *F. chloraefolia* occur sporadically within the range of *F. palmeri,* but these taxa are evidently ecologically and reproductively isolated.

18. **Flaveria intermedia** J. R. Johnston, Proc. Amer. Acad. Arts 39: 287. 1903. TYPE: Mexico, Durango, plains near Yermo, 17 Oct. 1896, *C. G. Pringle 7359* (GH, holotype; F, US, isotypes).

Plants erect annuals, 16–25 cm high, glabrous or sparsely pilose, tufted in the axils; leaves opposite, sessile, 2–4 cm long, 2–4.5 mm wide, essentially glabrous, lanceolate or linear, weakly serrate; capitulescence of tightly aggregated heads, giving a subcorymbose effect; heads radiate or discoid; involucre ca. 4 mm long, oblong-angular, the phyllaries 3, ovate-elliptic; ray florets with the ligules 1.5–2 mm long, ovate-elliptic, notched or acute; disc florets 5, the corollas 2–2.9 mm long, the tubes ca. 1 mm long, the throats ca. 1 mm long, tubular below, abruptly expanding to broadly funnelform or campanulate above, the lobes acute; achenes of the disc florets ca. 2 mm long, the ray achenes 2.8–3 mm long, narrowly oblanceolate to linear; pappus absent; chromosome number, unknown.

Known only from the type locality (Fig. 2).

Flaveria intermedia is exceedingly close to *F. palmeri* and the two might eventually be considered as conspecific. Here I have retained *F. intermedia* as a species because it is known only from the disjunct type locality, and because several minor character differences are exhibited in the collection. In describing both *F. intermedia* and *F. palmeri*, Johnston (1903) failed to note their close relationship. *Flaveria intermedia* differs from *F. palmeri* in the following traits: usually smaller habit; usually smaller leaves; shorter phyllaries; shorter ligules, acute or notched at the apex; shorter achenes; and perhaps most conspicuously, the basally tubular disc corollas are expanded distally to a broadly tubular-campanulate throat. During field studies I was not able to relocate *F. intermedia* in the type locality vicinity, and it is possible that the plant is no longer extant.

19. **Flaveria anomala** B. L. Robinson, Proc. Amer. Acad. Arts 27: 178. 1892. TYPE: Mexico, San Luis Potosí, plains, Vanegas, Sept. 1890, *C. G. Pringle 3669* (GH, lectotype; F, isolectotype). San Luis Potosí, in route from San

Luis Potosí to San Antonio, Texas, Aug. 1878, *C. C. Parry 500* (F, GH, MICH, NY, syntypes).

Plants delicate or robust annuals, (6–)15–75 cm high, to 0.5–1 mm wide, the stems rather lax or densely clumped, often purplish, essentially glabrous except with tufted hairs in the axils; leaves opposite, sessile, 3.5–10 cm long, 0.2–1 cm wide, glabrous, linear, lanceolate, or oblanceolate, the margins entire and subundulate or weakly serrate; capitulescence of tightly aggregated heads, with several clusters exhibiting a corymbose effect, the central heads discoid, the peripheral heads uniligulate, giving the effect of a single radiate, composite head; involucres 2.5–4.5 mm long, including the beaked apices, the phyllaries 2–3(–4), boat shaped and beaked, at maturity one or all swollen and corky below the beaks, the gibbous phyllaries also often winged, each phyllary enclosing an achene or not, the whole involucre closely investing and falling with the achenes; ray florets with the ligules 3.5–5 mm long, 2–3 mm wide, elliptical, rounded or emarginate at the apices; disc florets usually 1, often 2, rarely 3, the corollas 2.5–3 mm long, the tubes ca. 1 mm long, the throats 1–1.2 mm long, abruptly expanded into a funnelform campanulate shape, the lobes ca. 0.5 mm long, acute; anthers ca. 1.2 mm long; achenes 1.3–2.2 mm long, those of the ray florets larger and longer by 0.2–0.4 mm, narrowly oblanceolate to linear; pappus absent; chromosome number, $n = 18$.

High gypsum plains, often in disturbed sites, desert scrub or pine forests, 1,500–2,100 m, southern Coahuila south to Zacatecas and San Luis Potosí, east to Tamaulipas where plants may occur at 50 m elevation (Fig. 2).

REPRESENTATIVE SPECIMENS: MEXICO. COAHUILA: 6 mi N of La Ventura, *Johnston 7647* (CAS, GH). 26.5 mi N of Concepción del Oro, *Powell & Tomb 2599* (TEX, US). NUEVO LEÓN: 8 mi S of Galeana, *Correll & Johnston 19867* (TEX). 7.5 mi S of San Roberto Jnct., *Powell & Tomb 2559* (TEX, US). 34.4 mi S of San Roberto Jnct., *Powell & Tomb 2566* (TEX, US). 40 mi N of Matehuala, *Waterfall 15757* (F). SAN LUIS POTOSÍ: 9 mi NW of Ciudad Maíz, *Graham & Johnston 4473* (TEX). 1 mi N of Matehuala, *Powell & Tomb 2568* (TEX, US). Presa de Guadalupe, *Rzedowski 6755* (MICH). Near Salado, *Shreve 9354* (ARIZ, GH, MICH, UC). TAMAULIPAS: 0.5 mi S of Santander Jiménez, *Graham & Johnston 4818* (MICH, TEX). 4 mi S of Jaumave, *Stanford et al. 2227* (CAS, DS, MICH, NY, UC, US). ZACATECAS: 8.5 mi NE of Concepción del Oro, *Powell & Tomb 2594* (TEX, US). Sierra Hermosa, *Shreve 8591* (ARIZ, MICH, US).

The most distinctive features of *F. anomala* include the boat-shaped, beaked phyllaries which at maturity may become swollen and corky basally, closely investing and falling with the fruit; usually 1(–3) flower per head. Also, in *F. anomala* the radiate heads (each with a conspicuous ligule) have peripheral arrangement in the capitulescence clusters, and more than any other *Flaveria* thus display the effect of a typical radiate composite head.

Flaveria anomala and its related species *F. ramosissima* are the only annual taxa of the genus with C_3 metabolism. The morphologies of these species suggest that they are of ancestry similar to that of the C_4 annual species, which means that *F. anomala* and *F. ramosissima* were perhaps derived from the C_3 *F. angustifolia* line (Fig. 1).

The weedy *F. trinervia* grows intermixed with *F. anomala* throughout much of its range, but without any apparent hybridization. Experimental data (Table 1) suggest that the two distinct taxa are reproductively isolated. The ranges of *F. anomala* and *F. palmeri* are proximal but spatially isolated (Fig. 2) at present. Experimental data (Table 1) indicate that the *F. anomala* and *F. palmeri* are so strongly isolated reproductively that hybridization could not succeed if future distributional changes should bring them into contact. Indeed, the two contiguous annual species probably evolved strong reproductive barriers in response to characteristic *r*-selection strategy (Gadgil & Solbrig, 1972).

20. **Flaveria ramosissima** Klatt, Leopoldina 23: 146. 1887. TYPE: Mexico, Puebla, Tehuacán, *Liebmann 456* (K, lectotype; GH, isolectotype, fragment). *Liebmann 457* (K, US, paratypes, on the sheet with *Liebmann 456*).

F. angustifolia Schultz Bip. ex Klatt var. *ramosissima* Klatt, Leopoldina 23: 146. 1887.

Plants annual, 12–50 cm high, erect, the stems diffuse, often purplish, glabrate to sparsely hairy below, becoming sparsely villous above; leaves opposite, connate, 2.5–5 cm long, 0.2–0.6 cm wide, glabrous, linear or linear-lanceolate, entire or minutely serrate; capitulescence of numerous heads rather tightly aggregated in subscorpioid, corymbiform clusters; heads radiate or discoid; involucres ca. 3 mm long, angular-urceolate, the phyllaries 5, oblong-ovate or boat shaped; calyculate bract 1, linear, ca. 1 mm long; ray florets with the ligules ca. 3 mm long, 1.5–2 mm wide, oblong-orbicular; disc florets 5–8(–10), the corollas ca. 2 mm long, the tubes 0.6–0.7 mm long, the throats 0.7–0.9 mm long, funnelform, the lobes ca. 0.5 mm long, acute; anthers ca. 1 mm long; ray achenes 1.3–1.5 mm long, the disc achenes ca. 1 mm long, oblanceolate or linear; pappus absent; chromosome number, $n = 18$.

Sandy-clay bottoms, along dry washes, fields and roadsides, possibly in gypseous soils, thorn-scrub vegetation, 800–1,700 m, Tehuacán Valley area, Puebla and Oaxaca, Mexico (Fig. 3).

REPRESENTATIVE SPECIMENS: MEXICO. OAXACA: 12 km SSE of Teotitlán, *Cronquist 11235* (MO, US). PUEBLA: 8 mi SE of Coxcatlán, *Anderson & Anderson 5340* (MICH). 2.5 mi NW of Teotitlán, *Cronquist & Sousa 10381* (CAS, GH, MICH, NY, TEX, US). Tehuacán, *Matuda 32279* (US).

This annual species is characterized by its diffuse, low branching habit, narrow leaves, rather open, somewhat scorpioid capitulescence, showy radiate heads with ligules 3 mm long, small achenes and disc corollas, and distribution. *Flaveria ramosissima* probably has affinity with the *F. angustifolia* line, but seems more closely related to *F. anomala*, also a C_3 species.

21. **Flaveria mcdougallii** Theroux, Pinkava & Keil, Madroño 24: 13. 1977. TYPE: United States, Arizona, Mohave Co., Grand Canyon National Park, Cove Canyon (174.2 mi below Lee's Ferry), 27 Jan. 1976, *M. E. Theroux 1675* (US, holotype; ARIZ, ASC, ASU, DES, GCNP, GH, MNA, NY, RSA, SRSU, TEX, UC, isotypes).

Plants suffrutescent, ca. 50 cm high, the stems erect, glabrous; leaves opposite, weakly connate basally, 5–11 cm long, 2–7 mm wide, glabrous, linear-lanceolate, the margins entire; capitulescence corymbose, with the heads arranged in several small clusters; heads discoid; involucres turbinate, ca. 3 mm long, the phyllaries 2–6, oblong, 2–3 mm long, ca. 0.7 mm wide; calyculate bracts 1–2 mm long; disc florets 2–6, the corollas 3.5 mm long, exserted conspicuously from the involucre, the tubes ca. 1 mm long, the throats 1.5 mm long, the lobes ca. 1 mm long; achenes ca. 1.5 mm long, linear; pappus a crown of fringed scales, ca. 0.3 mm long; chromosome number, $n = 18$.

Known only from near saline springs at the mouths of two remote tributary canyons in the Grand Canyon (Theroux et al., 1977), (Fig. 2).

PARATYPES: UNITED STATES. ARIZONA: Coconino Co., Grand Canyon National Park, Matkatamiba Canyon (148.8 mi below Lee's Ferry), 1 Oct. 1975, *M. E. Theroux 1519* (MNA). Mohave Co., Grand Canyon National Park, Cove Canyon, 5 Oct. 1975, *M. E. Theroux 1567* (MNA).

Flaveria mcdougallii was thoroughly discussed by Theroux et al. (1977). The delimiting characters of this species include: linear leaves with entire margins; 2–6 phyllaries; discoid heads with 2–6 florets; glabrous corollas; achenes with (or without) double hairs; pappus crown of scales; and distribution. The morphological and experimental data accumulated so far suggest that *F. mcdougallii* might well stand alone as a monotypic genus (see Hybridizations). For the present, however, I prefer to retain the species in *Flaveria* while additional studies are conducted, particularly crosses with additional species of *Flaveria.*

EXCLUDED SPECIES

For a list of excluded species see Rydberg, 1915.

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Index of Latin Names

Numbers in **boldface** refer to main taxonomic entries; numbers in *italic* refer to synonyms; numbers followed by *k* refer to entries in key; numbers followed by *f* refer to figures; numbers in roman type only refer to all other references.