

# CYTOTAXONOMIC AND EVOLUTIONARY STUDIES IN THE NORTH AMERICAN SPECIES OF *GUTIERREZIA* (COMPOSITAE)<sup>1</sup>

*Gutierrezia* is an American genus of *Compositae-Astereae* found in western America, Mexico, and southern and western South America. The genus is poorly known botanically. Several species have been described, but no intensive taxonomic study of them has ever been made. Morphological and cytological studies are also lacking.

The principal objective has been to study the genus from various approaches, such as cytology, morphology, distribution, ecology, including detailed investigations of populations in nature. Unfortunately the problem of transportation to the different localities where *Gutierrezia* grows, as well as lack of time, has prevented the author from studying all species with the same degree of intensity. This applies particularly to the South American representatives, which had to be excluded from this study for these reasons.

This work is therefore not primarily a systematic study, although a taxonomic revision of the North American species is attempted. Nevertheless it is hoped that this study, incomplete as it is, will help to clarify the taxonomy of the genus and furnish some information about the life-history of its species.

### ACKNOWLEDGMENTS

Professor Lincoln Constance gave invaluable help during the course of this investigation and the preparation of the manuscript. Hours of conversation relating to subjects botanical and otherwise gave me a better and wiser understanding of science. Professor Herbert G. Baker's advice was very helpful in providing other dimensions and outlooks to the problems encountered and so was the help received from Professor G. Ledyard Stebbins, Jr. To all three of them I express my sincere thanks.

A large number of persons have aided this work in various ways. Drs. H. Arnott, R. Bacigalupi, Marion S. Cave, D. S. Correll, F. W. Gould, R. H. Miller, R. Ornduff, P. Raven, Helen Sharsmith, L. Shiners, B. C. Tharp, G. W. Thomas, R. K. Vickery, Jr., U. T. Waterfall, W. A. Weber, Messrs. J. Swanson and E. C. Twisselmann and Miss Francia Chisaki obtained seeds or living material of *Gutierrezia* and/or provided other information or help towards a better understanding of the problems. I am very grateful to all of them.

A "James Gowey Fellowship in Botany" from the University of

<sup>1</sup> Revised from a thesis submitted, in partial fulfillment of the requirements for the degree of Doctor of Philosophy, to the Graduate Division of the University of California, Berkeley.



California, Berkeley, permitted me to devote full time to research during the last year of graduate work. Grants in aid from the "Associates in Tropical Biogeography" and the "Patent Fund" of the University of California made field work in Mexico, South America, and the United States possible.

I have studied material from the following herbaria, to whose curators I wish to express my appreciation for making this possible: Academy of Natural Sciences of Philadelphia; California Academy of Sciences; Chicago Natural History Museum; Gray Herbarium and Arnold Arboretum of Harvard University; Jepson Herbarium, University of California; Missouri Botanical Garden; New York Botanical Garden; Pomona College; Rancho Santa Ana Botanical Garden; Rocky Mountain Herbarium, University of Wyoming; Southern Methodist University; United States National Herbarium; University of California, Berkeley; University of California, Los Angeles; University of New Mexico; University of Washington; and Washington State University.

#### HISTORY OF THE GENUS

The genus *Gutierrezia*, with the one species, *G. linearifolia*, was described in 1806 by Lagasca. It is dedicated to a member of the Spanish noble family Gutierrez. The type-material is unknown, since no specimens named by Lagasca exist and the original description is so general that it fits several modern species. Lagasca indicated the type locality only as "Hab. in N. H." (Habitat in "Nova Hispania"?). The only other use of the name *G. linearifolia* Lag. known to me is that by Hooker and Arnott (1835) for plants collected by Darwin in South America. The description and the localities given suggest that they referred to what we know today as *G. Gilliesii*. Asa Gray (1884) noted that, "*G. linearifolia* Lag., the original species (of which no specimen named by Lagasca is extant) . . . may with the highest probability be referred to a Chilean species, the *Brachyris* [*Gutierrezia*] *paniculata* D.C." This species is closely allied to *G. Gilliesii* and its characters correspond to Lagasca's description.

Pursh (1814) described specimens collected by Lewis "on the plains of the Missouri" as *Solidago sarothrae*. Nuttall (1818), unaware of Lagasca's paper, described the new genus *Brachyris* and the species *B. euthamiae* based on material collected by himself and on *Solidago sarothrae*. A second species of *Brachyris*, *B. divaricata*, was described by the same author in 1841. Sprengel (1825) changed *Brachyris* into *Brachyachyris*; he stated no reason for this change,



but it is supposed that it was purely etymological<sup>2</sup>.

De Candolle (1836) was the first to study the totality of the material then known. He accepted Nuttall's *Brachyris*, dividing it into two sections, *Eubrachyris* and *Amphiachyris*. Under *Eubrachyris* he placed *B. euthamiae* Nutt. and five species newly described by himself; in *Amphiachyris* he placed another new species, *B. dracunculoides* DC. In addition he established the genus *Hemiachyris*, with one species, *H. texana* DC., and the genus *Odontocarpa* for a new species from Chile, *O. Poeppigii*, and placed this last genus in the tribe *Vernoniae*, its clearly asteroid characters notwithstanding.

Hooker and Arnott (1841) recognized that *Gutierrezia* and *Brachyris* were congeneric and further remarked, "We are far from certain if the *B. paniculata*, *euthamiae*, *californica* and *texana* are not all forms of the *G. linearifolia* Lag." This seems to indicate that Lagasca's species was not included among those specifically named. If this is so, the original material must come from South America, since, aside from the species indicated above, no other North American species fit the original description.

Torrey and Gray, in the "Flora of North America" (1841-43), did not include in their treatment of *Gutierrezia*, *Amphiachyris dracunculoides*, which had been elevated to generic rank by Nuttall (1841). However, they did include *Gutierrezia texana* (DC.) T. & G. In their study they recognized fewer species than did De Candolle; Asa Gray's treatment in the "Synoptical Flora" (1884) does not differ appreciably from that of 1841.

Hoffmann, in his monograph of *Compositae* (1897), for Engler's "Pflanzenfamilien", divided *Gutierrezia* into three sections, *Brachyris*, *Amphiachyris*, and *Hemiachyris*. His characterization of the sections is similar to that of De Candolle, who had described *Hemiachyris* as a genus.

No monographic study of *Gutierrezia* has been attempted since De Candolle, and the North American species were treated for the last time by Gray in 1884. Nevertheless, more than 50 species have been described from North and South America since then by various authors, particularly E. L. Greene, R. Philippi, J. Lunell, P. A. Rydberg, and more

<sup>2</sup> In the original description Nuttall derived the name *Brachyris* from *Brachys*: short, and *Achyris*: chaffy scale.



recently S. F. Blake, A. Nelson, and A. L. Cabrera. The genus has been studied on several occasions for different local floras; the various authors differ in their treatments, but they coincide in placing in synonymy a large number of the described taxa.

#### CYTOLOGY AND GENETICS

The investigation of chromosome number and morphology as an aid to taxonomy and evolutionary understanding is a well known technique. The analysis of artificially obtained interspecific hybrids has also been used widely enough to necessitate no introductory emphasis. Both of these approaches have been used in the present investigation.

#### CROSSES AND RESULTS

Plants were grown in the greenhouse of the Department of Botany of the University of California at Berkeley in the spring and fall of 1956, from seed obtained partly by the author and partly by various correspondents. The seeds were germinated in two-inch pots and the plants were later transferred to four-inch pots. A second transplantation was performed, usually a year later, to eight-inch pots. Several plants were grown from each seed collection. In the fall of 1957 a large number of the plants were transplanted to the experimental area of the University of California Botanical Garden in Strawberry Canyon.

To perform crosses, the maternal plants were decapitated with a razor blade just before the tubular flowers opened, and were then washed for several minutes with a thin jet of luke-warm water from a plastic squeezing-bottle. The washing was repeated twice a day until the stigmas came out. To avoid accidental pollination by insects, the heads were covered with a net of cheesecloth. The heads were pollinated by hand and pollination was also effected by tying together heads from the parent plants under the cheesecloth net.

All the crosses were done reciprocally between both parents and were repeated several times in each case. Control tests were run with unpollinated decapitated heads which did not set seed in any case, and with non-decapitated heads covered with the cheesecloth net, which did set some seed. This was taken as an indication of self-compatibility.

A few words about seed setting in *Gutierrezia* species



might be appropriate here. It has been observed that a large amount of *Gutierrezia* seed collected in the field does not germinate. This might be due to a lack of optimal conditions in the laboratory, but since morphological examinations indicated a large amount of shrunken and apparently inviable seed, it seems likely that the species of *Gutierrezia* are poor seed producers. It is assumed that poor pollination is accountable for this, but it is likely also that the physiological

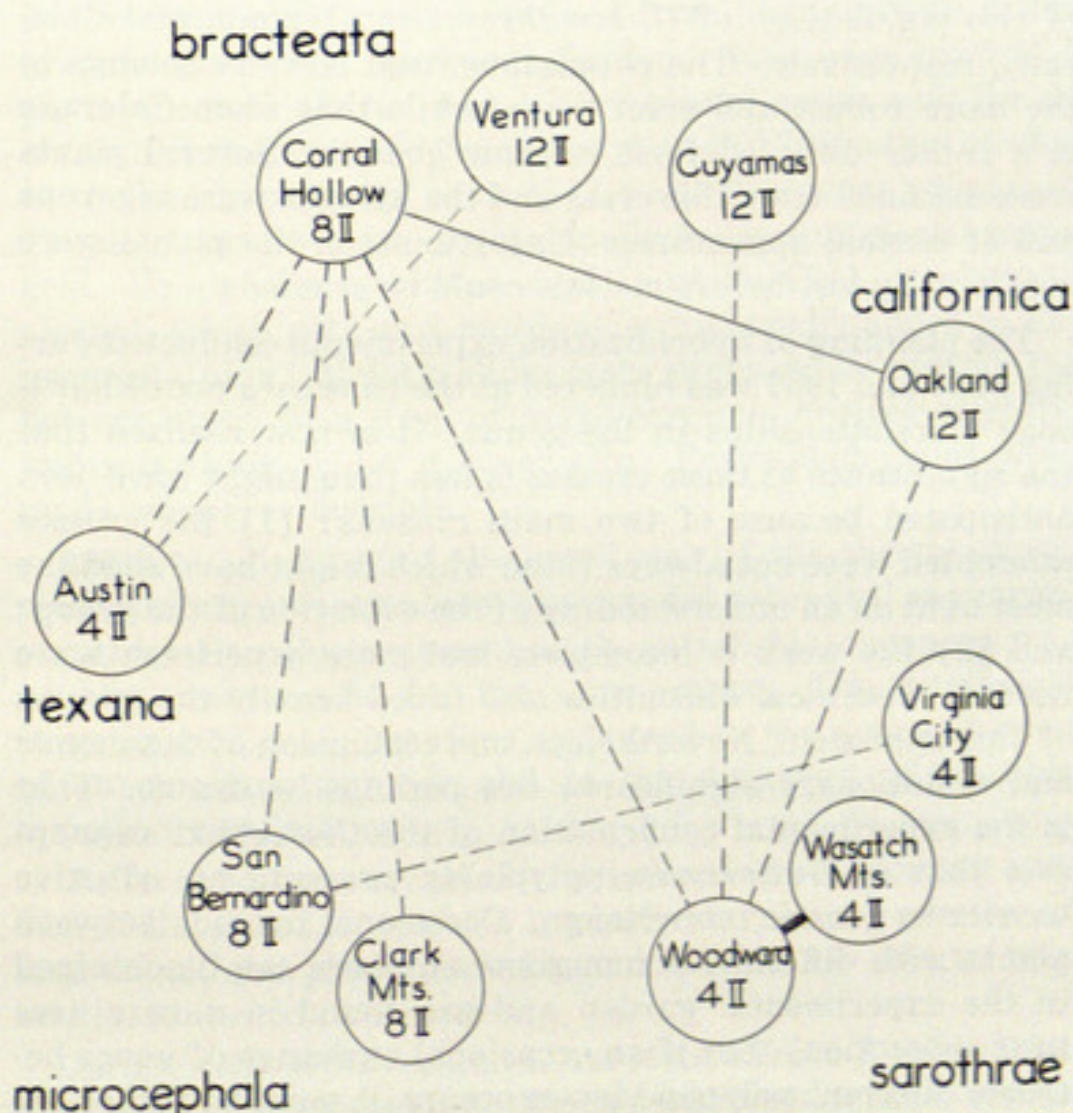


FIG. 1. Attempted artificial crosses between species of *Gutierrezia*. A thick full line represents a presumably fertile cross; a thin full line indicates a sterile hybrid; a dotted line indicates that no hybrid was obtained.

balance needed for seed production is very delicate and easily upset. The possibility therefore exists that the failure of the crosses attempted is attributable to physiological and not genetical causes.

In figure 1 are depicted the crosses attempted and the results obtained. As can be seen, in only one case was a cross



between two different levels of ploidy successful. The hybrid plant obtained from several attempted crosses between *G. californica* ( $n = 12$ ) and *G. bracteata* ( $n = 8$ ), was very slow growing and abnormal in appearance. The plant was sterile and the meiotic analysis revealed that division of PMC's was arrested at metaphase I and consequently no pollen was formed.

The only other successful cross was one between members of two populations of *G. sarothrae* from Nevada and Colorado, respectively. The population from Nevada belongs to the more robust and erect form, while that from Colorado is a rather dwarfed form of slow growth. Several plants were obtained from this cross and the hybrids were vigorous and of normal appearance. Unfortunately, the plants were accidentally lost before meiosis could be studied.

The planning of hybridization experiments conducted during 1956 and 1957 was hindered at the time by a poor knowledge of relationships in the genus. It is now realized that the significance of these crosses is less than might have been anticipated because of two main reasons: (1) the crosses attempted were not always those which might have shed the most light on an understanding of the evolution of the group; and (2) the work is incomplete and more experiments are needed. Technical difficulties also taxed heavily the success of this approach. Nevertheless, one conclusion of taxonomic and evolutionary significance can perhaps be drawn. That is the experimental confirmation of the theoretical assumption that in *Gutierrezia*, polyploidy presents an effective barrier to genetic interchange. Occasional hybrids between plants with different chromosome numbers can be obtained in the experimental garden and are found in nature (see next subsection), but if an occasional exchange of genes between different polyploid levels occurs, it must be rather exceptional and of little evolutionary significance. A mechanism for an interchange of genes between different levels of ploidy, as discovered by Zohary and Nur (1959) in *Dactylis*, is not likely.

#### CYTOLOGY

**TECHNIQUE.** Studies were made of mitosis in root tips and of meiosis in dividing pollen mother cells.

Root tips were obtained both from germinating seeds and



from growing seedlings and fixed in Carnoy's fixative, or in any one of several modifications. The root tips were then macerated in the usual way with 1 N HCl or a mixture of concentrated HCl and 95% ethyl alcohol and then placed in a drop of aceto-carmin or aceto-orcin on a slide and squashed under a cover glass. Some root tips were processed according to the Feulgen technique.

Most floral buds used for the study of meiosis were fixed in the field; others were obtained from plants grown in the greenhouse or the Botanical Garden. Buds were fixed in 3 parts absolute alcohol and 1 part glacial acetic acid for 24 hours and then washed twice and stored in 70% ethyl alcohol in the refrigerator at near 0° C. until they were processed. Propionic acid was used occasionally in place of glacial acetic acid. Drops of a saturated solution of  $\text{Fe}(\text{OH})_3$  in absolute alcohol, which acts as a mordant, were usually added to improve staining. Meiotic slides were prepared by teasing the flowers apart in a drop of aceto-carmin, heating slightly, and squashing under a cover slip. Permanent slides were made whenever possible.

**RESULTS.** Because of the small size of the chromosomes, studies of chromosomal morphology did not reveal any structural details. Pretreatment with paradichlorobenzene was equally unsuccessful for the same reason. The cytological investigation was therefore restricted to the determination of chromosome number and to the discovery of possible meiotic irregularities.

*Gutierrezia texana* and *G. glutinosa*, the only annual species of the genus, revealed a haploid chromosome number of four in all the plants investigated (Table 1). No irregularities in meiosis were noted.

*Gutierrezia sarothrae* and *G. serotina* (Table 1) both have four pairs of chromosomes. Meiosis was regular in all plants investigated. Four of the populations of *G. sarothrae* studied have eight pairs of chromosomes. Meiosis in these plants, as far as it has been possible to detect, is perfectly normal and no multivalents have been found.

Eight or twelve pairs were found in populations belonging to the *Gutierrezia bracteata* complex. Meiosis was usually normal, but some irregularities were discovered in several instances. Anaphase bridges were common, but no frag-



ments could be detected, which indicates that the bridges were of the "sticky" type. Two plants belonging to different populations are remarkable enough to merit more detailed description.

TABLE 1. CHROMOSOME NUMBERS IN SPECIES OF GUTIERREZIA

Species	Locality	Collector	n	2n
<i>G. sarothrae</i>	12.6 mi. E. of Ash Fork, Arizona	Solbrig	2801	4
	0.8 mi. E. of Hyde Park, Arizona	"	2805	4
	12.3 mi. W. of Aguanga, California	"	2760	4
	9.9 mi. S. of Santa Ysabel, California	"	2763	4
	2 mi. W. of Temecula, California	"	2758	4
	9.8 mi. S. of Santa Ysabel, California	"	2765	4
	1.6 mi. W. of Rancho Sta. Fe, California	"	2769	4
	8.5 mi. E. of Chula Vista, California	"	2766	4
	6.2 mi. E. of Chula Vista, California	"	2768	4
	11.1 mi. E. of Idyllwild, California	"	2773	4
	Fort Collins, Colorado	A. Weber		4
	Virginia City, Nevada	R. H. Miller	4	8
	Mt. Rose, Nevada	"		4
	Field Creek, Oregon	R. Ornduff		4
	Wasatch Mts., Utah	R. K. Vickery Jr.	4	
	Wasatch Mts., Utah	"		4
	5 miles N. of Payson, Arizona	Solbrig	2794	8
	9.8 mi. W. of Seligman, Arizona	"	2802	8
	19.8 mi. N. of Roosevelt Dam, Arizona	"	2792	8
	Jct. Payson-Phoenix and Hwy. 488, Arizona	"	2793	8
	17 mi. E. of Tucson, Arizona	"	2777	4
<i>G. serotina</i>	Silver Canyon, White Mts., California	Rancho Santa Ana Bot. Gard.	9389	8
<i>G. microcephala</i>	Morongo, San Bernardino Co., California	"	8382	8
	10 mi. E. of Roswell, New Mexico	G. W. Thomas		8
	5 mi. W. of Bronco, Texas	"		8
	Hondo, New Mexico	"		8
	Douglas, Arizona	Solbrig	2789	16
	Cuyama Valley, California	"	2166	12
	Padres Nat. Forest, California	"	2167	12
	22.5 mi. E. of Idyllwild, California	"	2774	12
	1.4 mi. N. of Jct. Hidden Valley & Parkfield roads, California	"	2830	12 24
	Kern & S. Luis Obispo Co. line, California	"	2753	12
	Tahquitz Canyon, California	"	2775	12
<i>G. bracteata</i>	Corral Hollow, California	"	2159	8 16
	Cache Creek, Yolo Co., California	Rancho Santa Ana Bot. Gard.	8	16
	La Panza, California	Solbrig	2751	8
	7.2 mi. W. of Patterson, California	"	2743	8
	Oakland Hills, California	"	2154	12
<i>G. californica</i>	Red River St., Austin, Texas	B. C. Tharp		4
<i>G. texana</i>	Austin Chalk, Austin, Texas	B. C. Tharp		4
	Dallas, Texas	L. Shimmers		4
<i>G. glutinosa</i>	Matehuala, San Luis Potosí, Mexico	Solbrig &		
	San Luis Potosí, San Luis Potosí, Mexico	Ornduff	4590	4
		"		4



The first is from a population in San Luis Obispo County, California. Most of the cells have eight pairs. Nevertheless we find a small number of multivalents (2%) and also univalents (8%). Supernumeraries, easily distinguishable by their size and disposition at meiosis, were also present. We are possibly in the presence of a small translocation here, but there may be also some homologies between non-sister chromosomes.

The other plant is from near Coalinga, Fresno County, California. In this area both eight- and twelve-chromosome populations occur, sometimes in the same locality. In this plant, most cells showed nine pairs of chromosomes, although it varied from nine to eleven. Univalents and multivalents were also present. The most plausible explanation is that this plant might be a hybrid between eight- and twelve-chromosome *Gutierrezia bracteata*, as the presence of 10 pairs in some cells would indicate, the tenth chromosome having been lost in a pre-meiotic division. The existence of cells with eight pairs and even eleven indicates the possibility of irregular division prior to meiosis. This does not rule out the origin of this plant through a back-cross, but this possibility seems to me to be remote.

*Gutierrezia californica* has 12 pairs of chromosomes in all the plants studied, and meiosis was regular.

The picture presented by the *Gutierrezia microcephala* complex is a very different one. The first plants investigated came from seed received from the Rancho Santa Ana Botanical Garden, and proved to have eight pairs of chromosomes at metaphase. It was observed at the time that there were very few PMC's undergoing meiosis in each preparation. This was attributed at the time to the fact that there are only one or two flowers per head with pollen. In the fall of 1958 buds were gathered from several populations in California and Arizona. These plants showed very irregular meiosis with little or no fertile pollen. Most cells which could be counted showed eight pairs of chromosomes, but some had 16 or even 32 chromosomes. One population of *Gutierrezia microcephala* showed 16 pairs of chromosomes and a regular meiosis.

As a result of these studies we may conclude that: (1) *Gutierrezia* is a polyploid complex with a base number of



$x = 4$ ; and (2) different levels of ploidy are genetically isolated.

#### DISTRIBUTION AND ECOLOGY

*Gutierrezia sarothrae* is the most widely distributed of all North American species of the genus. It is found throughout the region extending from northern Mexico to southern British Columbia and Alberta in Canada, between the Sierra Madre Occidental and Sierra Nevada-Cascades in the west and the Great Plains on the east. It grows also in southern California and in Baja California, Mexico (fig. 2). *Gutierrezia californica* is restricted to the area of San Francisco Bay, California, while *G. bracteata* grows in the central and

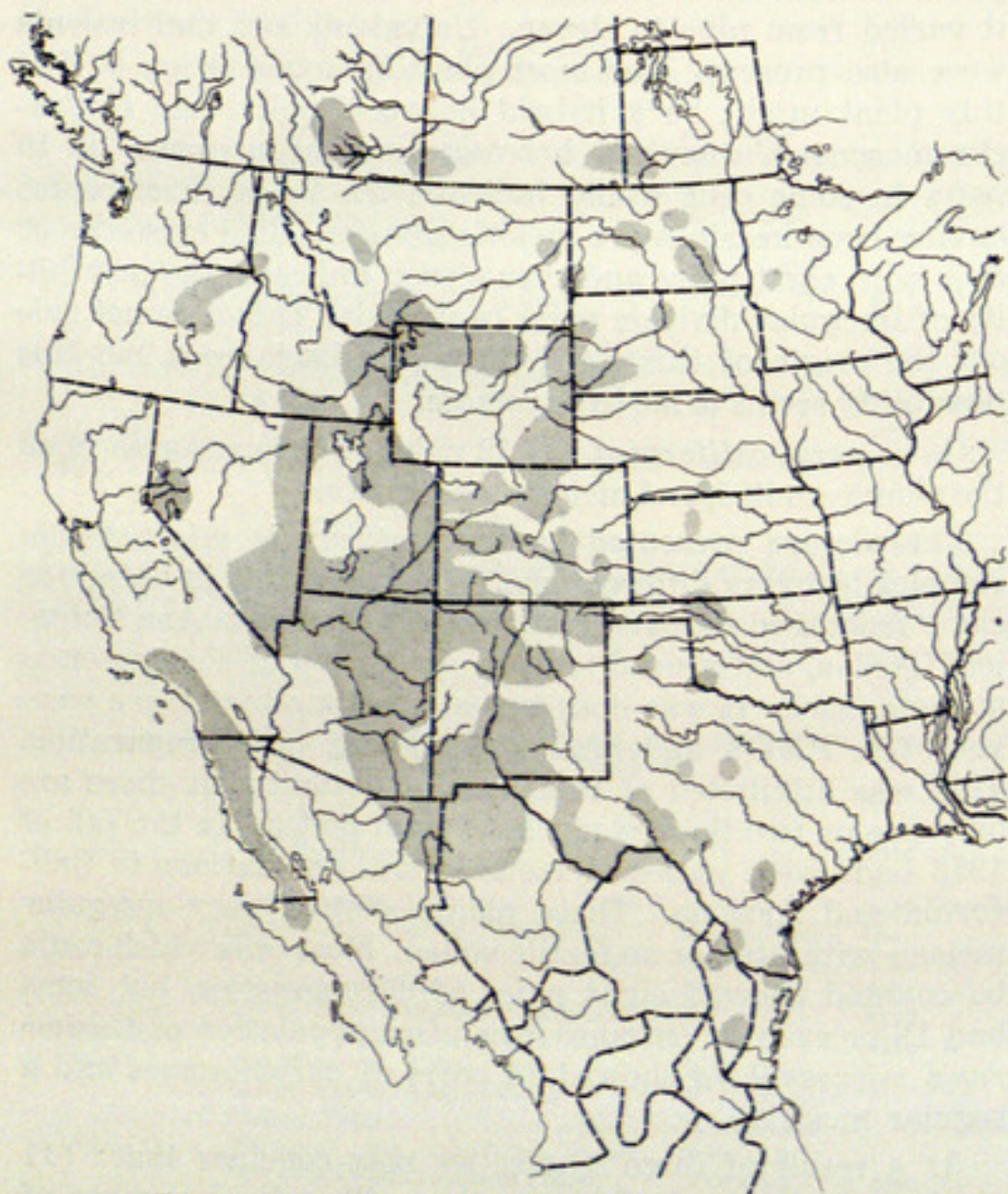


FIG. 2. Distribution of *Gutierrezia sarothrae* (dotted area).



south Coast Ranges and from Inyo County to the Tehachapi Range and occasionally southward to about Baja California, Mexico (fig. 3). *Gutierrezia serotina* grows in an area

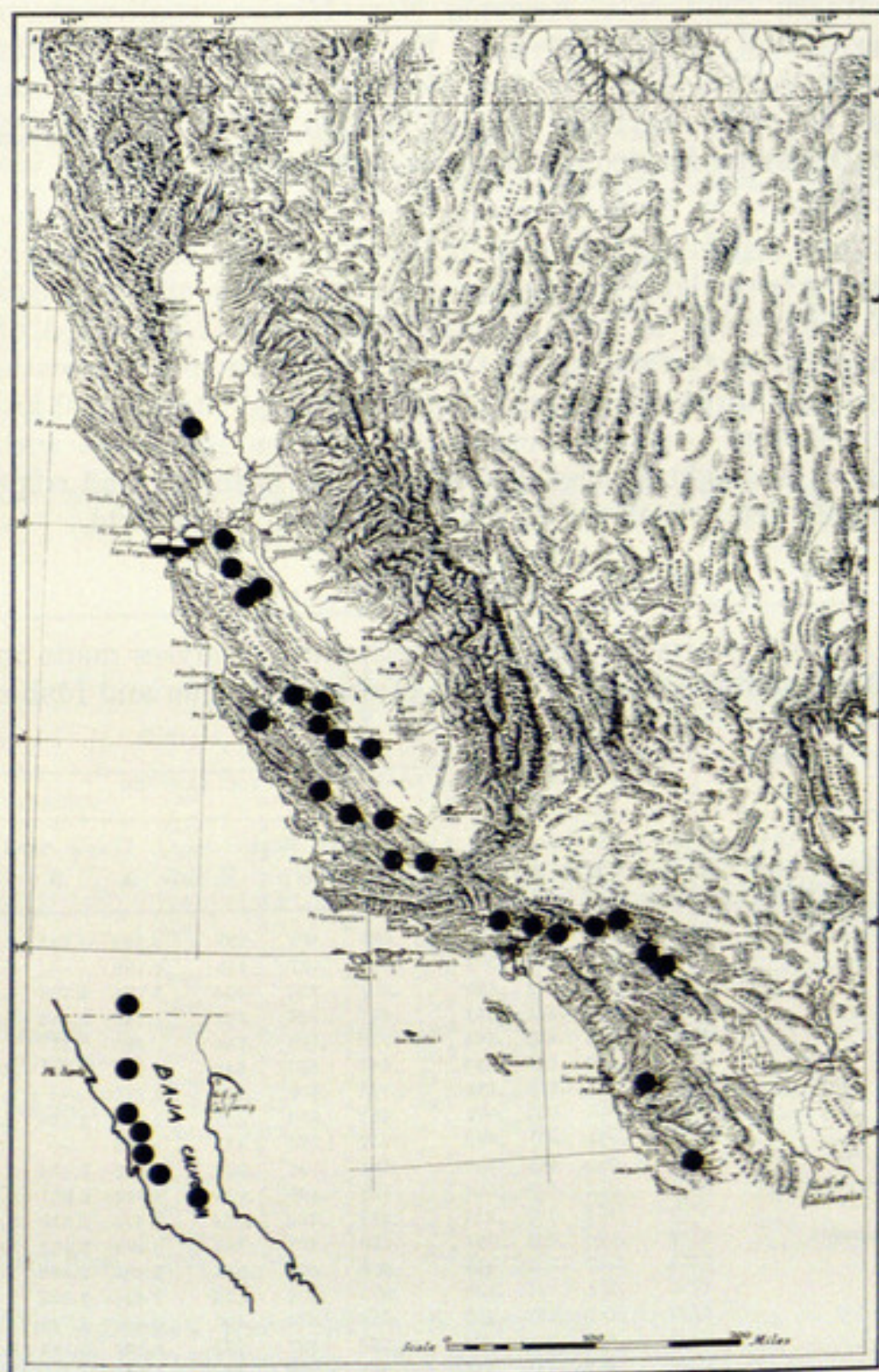


FIG. 3. Distribution of *Gutierrezia californica* (half-full dots) and *G. bracteata* (full dots). Physiographic map of California used by special permission of Ginn and Company. Copyright by Ginn and Co.



around Tucson, Arizona, and occasionally southward into Mexico. *Gutierrezia microcephala*, on the contrary, is more widely distributed, being found in a belt extending through southern California, Arizona, New Mexico, southwestern Texas, and northern Mexico (fig. 4). Finally, *Gutierrezia texana* ranges from northern Mexico to southern Oklahoma, and *G. glutinosa* from central Mexico to Texas, through northeastern Mexico and eastern New Mexico (fig. 5).

In order to discover whether or not environmental conditions determine this distributional pattern, it was necessary to investigate the ecology and distribution of the species of *Gutierrezia* in more detail. These studies consisted of careful observations of the type of distribution and growth, ecological preferences, and plant associates. Mechanical analyses were performed on 19 soil samples associated with six of the eight species, and several pH readings and some nitrate determinations of soils were made in the field.

#### SOIL STUDIES

Table 2 shows the results of mechanical analyses made on 19 soil samples from California, Arizona, Oregon and Idaho.

TABLE 2. MECHANICAL ANALYSIS OF 19 SOIL SAMPLES

Species	Coll. No.	Moisture <sup>1</sup>			Organic Matter			Coarse Sand		
		A	B	$\bar{x}$	A	B	$\bar{x}$	A	B	$\bar{x}$
<i>G. sarothrae</i>	2756	.060	.052	.056	.395	.401	.398	4.184	4.221	4.202
	2763	.224	.183	.203	.455	.432	.443	4.196	—	4.196
	2766	.242	.694	.468	.515	.394	.454	4.721	4.578	4.649
	2769	.326	.337	.331	.917	.806	.861	1.146	2.481	1.813
	2801	.556	.451	.503	.755	.707	.731	.390	.357	.373
	2905	.500	.360	.430	.647	.651	.649	1.664	2.257	3.417
	2912	.128	.118	.123	.739	.702	.720	2.579	—	2.579
	2792	.094	.090	.092	.312	.584	.448	2.970	2.750	2.860
	2794	.033	.051	.042	1.522	1.363	1.442	1.485	—	1.485
	2777	.069	.063	.066	.284	.291	.287	5.452	5.394	5.423
<i>G. serotina</i>	2807	.024	.009	.016	.123	.147	.135	6.793	6.981	6.887
<i>G. microcephala</i>	2789	.122	.107	.114	.657	.652	.654	2.773	2.839	2.806
<i>G. bracteata</i>	2722	.034	.034	.034	.450	.427	.438	3.475	3.552	3.513
	2604	.042	.074	.057	.304	.361	.332	2.487	2.940	2.713
	2755	.211	.147	.179	.575	.472	.523	1.638	1.942	1.790
	2723	.207	.173	.190	.511	.476	.493	4.646	4.799	4.722
	2748	.036	.010	.023	.164	.182	.173	6.462	5.786	6.124
	2743	.162	.142	.152	.625	.646	.635	1.986	—	1.986
<i>G. californica</i>	2428	.234	—	.234	1.605	—	1.605	3.420	3.297	3.358

<sup>1</sup> All measurements expressed in grams



TABLE 2 (cont.)

Fine Sand			Clay			Silt			Total		
A	B	$\bar{x}$	A	B	$\bar{x}$	A	B	$\bar{x}$	A	B	$\bar{x}$
4.132	4.766	4.449	.998	.506	.752	.100	.061	.080	9.869	10.007	9.937
4.319	—	4.319	.805	—	.805	.056	—	.056	10.055	—	10.022
3.089	3.564	3.326	.909	.863	.886	.103	.091	.097	9.579	12.114	10.846
3.541	3.328	3.434	3.305	2.952	3.128	.151	.146	.148	9.386	10.050	9.718
3.577	3.551	3.564	4.537	4.500	4.518	.105	.136	.120	9.921	9.702	9.809
3.225	3.321	3.273	1.938	3.280	2.609	.130	.158	.144	8.296	9.931	9.113
5.851	—	5.851	.294	—	.294	.152	—	.152	9.743	—	9.719
4.202	4.667	4.434	1.668	1.447	1.557	.053	.089	.071	9.299	9.627	9.463
4.921	4.549	4.735	1.159	.988	1.073	.056	.095	.075	9.179	—	8.852
3.021	3.233	3.127	.717	.691	.704	.058	.055	.056	9.601	9.727	9.664
2.708	2.547	2.627	.109	.076	.092	.100	.100	.100	9.854	9.860	9.857
4.195	4.173	4.184	1.696	1.509	1.552	.103	.071	.087	9.446	9.371	9.351
4.211	2.455	3.333	.774	.857	.815	.063	.054	.058	9.007	7.379	8.191
4.640	4.688	4.664	.685	.873	.779	.083	.070	.076	8.241	9.005	8.621
5.661	5.262	5.461	1.990	1.836	1.913	.256	.134	.195	10.331	9.793	10.061
2.580	2.634	2.607	1.413	1.520	1.466	.050	.060	.055	9.407	9.662	9.533
2.709	3.446	3.077	.373	.380	.376	.099	.099	.099	9.843	9.903	9.872
5.483	—	5.483	1.213	—	1.213	.113	—	.113	9.582	—	9.582
3.085	2.881	2.983	1.832	1.940	1.886	.095	.082	.088	10.271	—	10.154

TABLE 2 (cont.)

Species	Coll. no.	% Moisture	% Organic Matter	% Coarse Sand	% Fine Sand	% Clay	% Silt	Soil Type
<i>G. sarothrae</i>	2756	0.6	4.0	42.0	44.5	7.5	1.0	Sand
	2763	2.0	4.4	42.0	43.2	8.0	0.6	Sand
	2766	14.7	4.5	46.5	33.3	8.7	1.0	Sand
	2769	3.3	8.6	18.1	34.3	31.3	1.5	Sandy-Clay-Loam
	2801	5.0	7.3	3.7	35.6	45.2	1.2	Sandy-Clay
	2905	4.3	6.5	16.6	33.3	26.1	1.4	Sandy-Clay-Loam
	2912	1.2	7.2	24.2	59.0	3.0	1.5	Sand
	2792	0.9	4.5	28.6	44.3	15.6	0.7	Sandy-Loam
	2794	0.4	14.4	14.9	47.4	10.7	0.8	Sand
<i>G. serotina</i>	2777	0.7	2.9	54.2	31.3	7.0	0.6	Sand
<i>G. microcephala</i>	2807	0.2	1.4	68.9	26.3	0.9	1.0	Sand
	2789	1.1	6.5	28.1	41.8	15.5	0.9	Sand
<i>G. bracteata</i>	2722	0.3	4.4	35.1	33.3	8.2	0.6	Sand
	2604	0.6	3.3	27.1	46.6	7.8	0.8	Sand
	2755	1.8	5.2	17.9	54.6	19.1	2.0	Sandy-Loam
	2723	1.9	4.9	47.2	26.1	14.7	0.6	Sand
	2748	0.2	1.7	61.2	30.8	3.8	1.0	Sand
	2743	1.5	6.4	19.9	54.8	12.1	1.1	Sand
<i>G. californica</i>	2428	2.3	16.1	33.6	29.8	18.7	0.8	Sandy-Loam

The samples were taken in localities supporting a good growth of *Gutierrezia*. The soil surface was scraped clean of debris and vegetation, and the sample was taken from the upper layers where the bulk of the roots of the *Gutier-*



*rezia* plants were found. In every case only one horizon was involved.

The technique in the analysis of particle-size followed is the so called "Beaker method" as described by Piper (1942). The analyses were run on 10 grams of the soil sample after it had been passed through a 5-mm. screen and thoroughly mixed. Each analysis was repeated twice unless otherwise indicated.

The analysis was intended as a rough guide to detect possible gross requirements of the different species in relation to soil texture. As can be seen, the results are rather uniform, the variation in soil type is not great from sample to sample, and the differences cannot be correlated with the occurrence of any one of the species. This does not rule out variations in tolerance to different soil types by the species, especially to heavy soils, but this is still to be shown experimentally.

Table 3 indicates the results of pH readings performed in the field. A Beckmann portable pH meter was used in most cases, the readings being made directly from a soil solution extracted with distilled water. A few of the readings were obtained by a colorimetric method. The reason for making

TABLE 3. PH DETERMINATIONS MADE ON SOILS SUPPORTING GUTHIERREZIA

Species	Locality	pH
<i>G. bracteata</i>	Corral Hollow, Alameda County, California	7.5
	Patterson, Santa Clara County, California	7.6
	La Panza, San Luis Obispo County, California	8.5
<i>G. sarothrae</i>	Idyllwild, Riverside County, California	6.4
	Temecula, San Diego County, California	6.2
	John Day, John Day County, Oregon	7.1
	Hansen, Twin Falls County, Idaho	9.2
	Ash Fork, Coconino County, Arizona	8.0
<i>G. serotina</i>	Tucson, Pima County, Arizona	8.0

these readings was the same as that which led to the undertaking of soil analyses, and the results were similarly uniform. Table 4 shows the results of a few determinations of the content of nitrates in the soil. The nitrate was determined colorimetrically by the diphenylamine method from a soil solution extracted with a weak acid, with the aid of a commercial field soil kit known as the "La Motte Field Soil Kit". Since no significant differences were obtained, it was deemed unnecessary to perform more of these determinations.



Even though the analytical soil data failed to reveal any ecological differences between species, they provide some indication of the over-all requirements of the genus as a whole. The North American species of *Gutierrezia* seem to grow on loose, sandy, alkaline or neutral soils, and apparently those also with a low content of organic matter and nitrates.

A careful chemical analysis of the principal elements of the soil does not fall within the scope of this work. A chemical analysis *per se*, in the present state of our knowledge about the complex soil-plant relations, would not have been very significant in any case if it had not been complemented by experiments to determine the importance of trace elements, differential absorption of different soil constituents, etc. Nevertheless, it would be helpful if such data were to be available some day, especially in relation to *Gutierrezia californica sensu stricto* (see page 50). This species is of interest in this connection because of its restriction to the San Francisco Bay area and because it grows on serpentine soils.

TABLE 4. NITRATE NITROGEN DETERMINATIONS ON SOILS SUPPORTING GUTIERREZIA

Species	Locality	Nitrate p./million
<i>G. bracteata</i>	Patterson, Santa Clara County, California	1.5
	La Panza, San Luis Obispo County, California	1.5
<i>G. sarothrae</i>	Temecula, San Diego County, California	1.5

It is known that many species of plants cannot grow on serpentine, while others are restricted to it. Finally, a third group can grow either on or off serpentine (Kruckeberg, 1951, 1954, 1957). The reasons for this behaviour are not altogether clear; several authors have investigated this fascinating problem and various explanations have been suggested (Walker, 1954).

None of the species of *Gutierrezia* can be classed as a so-called "serpentine species" with the possible exception of *G. californica*. In northern California, where serpentine outcrops are rather common, the author knows of only four populations of *Gutierrezia* which grow unmistakably on serpentine: the Oakland Hills, Point Bonita, and Angel Island populations of *Gutierrezia californica* and the large serpentine outcrops of New Idria in the central Coast Ranges, where both eight- and twelve-chromosome populations of *G. bracteata* are found.



A few preliminary experiments were performed in order to determine tolerance to serpentine in different populations of *Gutierrezia californica* and *G. bracteata*. Seeds of the Oakland Hills population of *G. californica* and of the Corral Hollow and Cache Creek populations of *G. bracteata* (both of these last with eight pairs of chromosomes) were sown

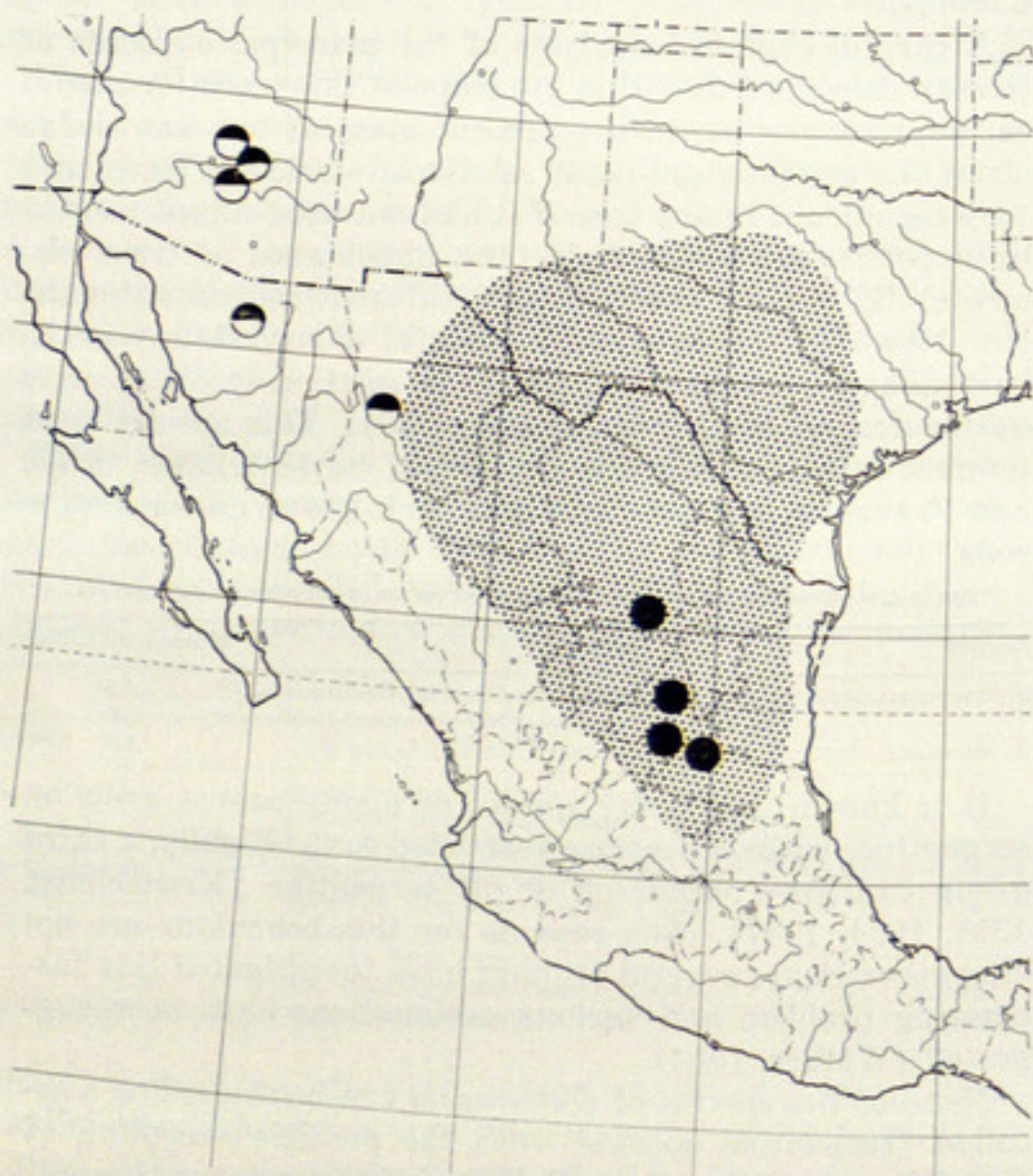


FIG. 4. Distribution of *Gutierrezia glutinosa* (dotted area), *G. serotina* (half-shaded circles), and *G. grandis* (full shaded circles). Goode Base Map used by special permission, Dept. of Geography, Univ. of Chicago. Copyright by the University of Chicago.

in two different pots, one with pure serpentine soil, and the other with a mixture of equal parts of sand and greenhouse top-soil. In each case both sets of seeds germinated normally and no difference could be detected relating to speed of ger-



mination or number of seedlings. The seedlings were later transplanted to individual pots and grown to maturity with the same type of soil as that in which they had been germinated. In all three cases the plants on soil grew slightly better than those on serpentine, notwithstanding the fact

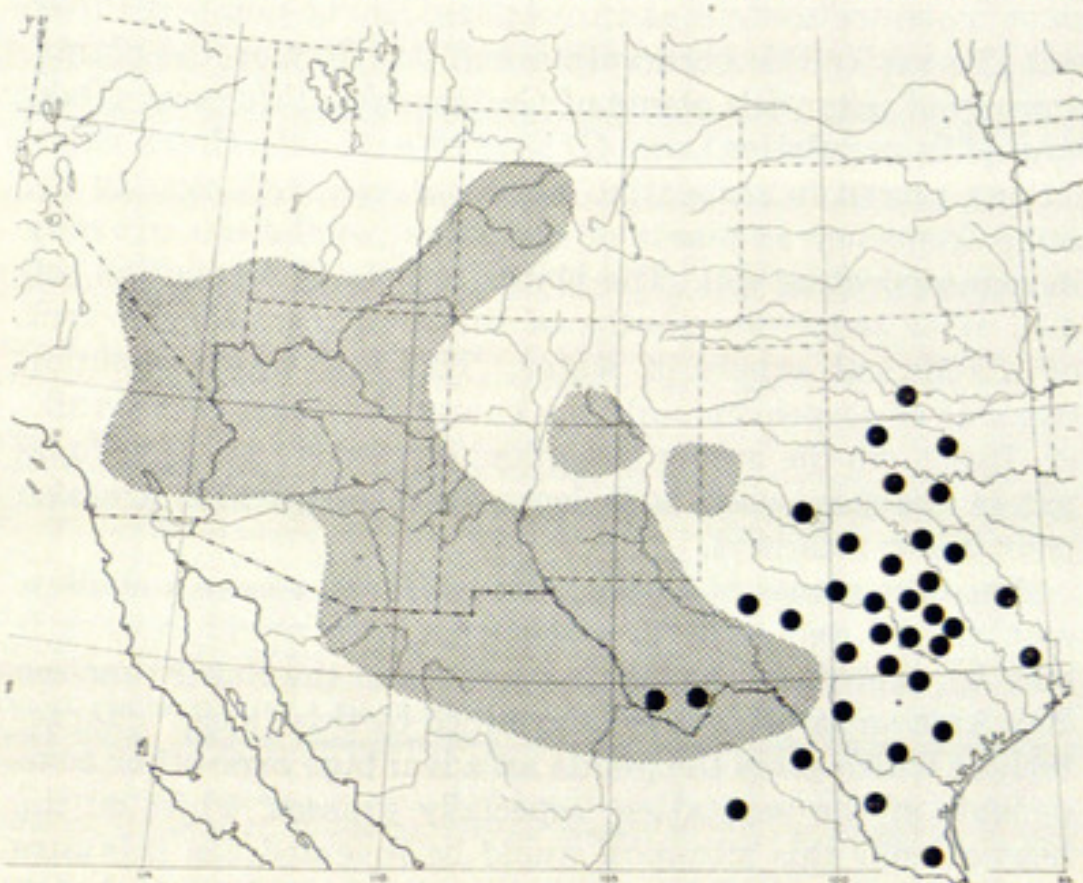


FIG. 5. Distribution of *Gutierrezia microcephala* (crosshatched area) and *G. texana* (black dots). Goode Base Map used by special permission, Dept. of Geography, Univ. of Chicago. Copyright by the University of Chicago.

that one set of seeds (Oakland Hills) came from plants growing on serpentine in nature.

This experiment, aside from showing that *Gutierrezia californica* can grow off serpentine under experimental conditions, also demonstrates that there is no element in serpentine deleterious by itself to the growth of those plants of *G. bracteata* which normally do not occur on serpentine.

In addition to the experiments just reported, plants from the Oakland Hills and Angel Island populations of *Gutierrezia californica* and from the New Idria population of *G. bracteata* (12-chromosome type) were grown in pots in the greenhouse and also in the Botanical Garden in common agricultural soil without any visible effect on them, aside from the production of larger and more vigorous specimens



because of the greater care (mainly freedom from competition) and watering they enjoyed.

While performing these rough experiments the author observed that the pots which contained serpentine required more frequent watering in order to maintain in them the same moisture content as in pots containing non-serpentine soil. To verify this observation and its effect on the plants, a group of pots with plants of *Gutierrezia californica* (Oakland Hills population) and *G. bracteata* (Cache Creek population) grown in serpentine were watered with exactly the same frequency as plants of the same populations growing in non-serpentine soil. The plants in pots of serpentine soil died after some two months of this treatment, due to lack of a sufficient supply of water. This low water-retention capacity of serpentine soils is a known characteristic (Walker, 1954). In the author's opinion, serpentine soils are to be put in the same class with loose sand soils, which are also poor water retainers.

Since the plants of *Gutierrezia californica* have a shallow root system and grow in association with mesic grasses it may be, therefore, that their presence in the San Francisco Bay Area on serpentine is determined by this "loose" characteristic which gives the plants an advantage over other components of the vegetation, especially grasses, while on the heavier soils this situation would be reversed. In this case it may be that the low water-retention capacity of serpentine, rather than its mineral content, accounts for the growth of *Gutierrezia* on it.

#### FIELD OBSERVATIONS

The various species of *Gutierrezia* usually grow in company with perennial grasses and shrubs in the open broad-leaf shrub communities. Munz and Keck (1949), in their study of California plant communities, characterize *Gutierrezia sarothrae* as a member of the Shad-Scale Scrub. Nevertheless, after visiting and studying populations of all the species from central Mexico to Idaho, it has been observed that the species of *Gutierrezia* are not restricted to defined communities. This is not to say that they are not characteristic in a certain area of a certain type of vegetation, or that their tolerances are so broad that they grow under almost any conditions. This is certainly not the case: limitations of soil and climate are as important to them as to any other plant



species. But aside from certain broad physiographic and ecological characteristics, in the many localities visited, *Gutierrezia* was the only conspicuous element present in all.

Whenever possible, a list was made of the species growing in association with *Gutierrezia* (table 5). Unfortunately, when the genus blooms in late summer or fall, most of the herbaceous vegetation is dried up and not easily identifiable. The list of table 5 is therefore tentative and incomplete, and is presented only as a guide to the type of vegetation which may be expected to occur in association with *Gutierrezia*.

TABLE 5. PLANTS GROWING IN ASSOCIATION WITH VARIOUS SPECIES OF GUTIERREZIA

**A. *Gutierrezia sarothrae*.** — *Pinus ponderosa* Dougl., *P. cembroides* Zucc., *Juniperus communis* L., *Avena fatua* L., *Bromus tectorum* L., *B. brizaeformis* L., *B. japonicus* L., *Poa* sp., *Allium* sp., *Atriplex canescens* (Pursh) Nuttall, *Chenopodium* sp., *Salsola kali* L., *Polygonum aviculare* L., *Erigonum umbellatum* Torr., *Erigonum* sp., *Alyssum alyssoides* (L.) L., *Potentilla flabelliformis* Lindl., *Rosa woodsii* Lindl., *Melilotus officinalis* (L.) Lam., *Astragalus* sp., *Epilobium paniculatum* Nutt., *Lomatium* sp., *Phlox douglasii* Hook., *Penstemon pratensis* Greene, *Castilleja* sp., *Scutellaria antirrhinoides* Benth., *Helianthus annuus* L., *Solidago* sp., *Cirsium vulgare* (Savi) Tenore, *C. undulatum* (Nutt.) Spreng., *Xanthium canadense* L., *Grindelia* sp., *Lactuca scariola* L., *Chrysothamnus nauseosus* (Pall.) Britt., *Artemisia tridentata* Nutt., *Senecio canus* Hook., *Achillea lanulosa* Nutt., *Blepharipappus scaber* Hook.

**B. *Gutierrezia californica*.** — *Pellaea andromedaefolia* Fée, *Polypodium scolieri* H. & G., *Koeleria cristata* (L.) Pers., *Chlorogalum pomeridianum* (Ker) Kunth, *Quercus agrifolia* Née, *Eriogonum nudum* Dougl., *Umbellularia californica* Nutt., *Rhamnus crocea* Nutt., *Rhus diversiloba* T. & G., *Silene gallica* L., *Eschscholtzia californica* Cham., *Arabia glabra* (L.) Bernh., *Dudleya* sp., *Lathyrus vestitus* Nutt., *Lupinus albus* Benth., *Sidalcea malvaeflora* Gray, *Sanicula bipinnatifida* Dougl., *Monardella villosa* Benth., *Achillea lanulosa* Nutt., *Artemisia californica* Less.

**C. *Gutierrezia bracteata*.** — *Pinus sabiniana* Dougl., *Juniperus communis* L., *Avena fatua* L., *A. sativa* L., *Festuca* sp., *Quercus douglasii* H. & A., *Q. lobata* Née, *Yucca whipplei* Torr., *Eriogonum* sp., *Grayia spinoza* (Hook.) Moq., *Adenostoma fasciculatum* H. & A., *Astragalus* sp., *Euphorbia peplus* L., *Eriodictyon californicum* (H. & A.) Greene, *Arctostaphylos* sp., *Monardella villosa* Benth., *Scutellaria* sp., *Grindelia* sp., *Madia* sp., *Trichostemma* sp., *Artemisia californica* Less., *Lepidospartum squamatum* Gray, *Chrysothamnus* sp.

**D. *Gutierrezia serotina*.** — *Eriogonum* sp., *Cercidium microphyllum* (Torr.) Rose & Johnston, *Prosopis juliflora* (Swartz) DC., *Carnegie gigantea* (Engelm.) Britt. & Rose.

#### OTHER OBSERVATIONS

*Gutierrezia* has a shallow root system which puts it in direct competition with shallow-rooted herbaceous plants, especially grasses. Since it blooms in the fall, it is in a vegetative state all through the summer, a season of very little or no rainfall throughout its range. Water relations therefore become critical and no doubt play an important role in the distribution of the species, both in determining the range and the localities within the range.

The author has observed that wherever one finds a population there is some kind of physical accident in the environment which presupposes a higher moisture content in the



soil than in the surrounding area, such as a depression, a gulch, sometimes even a creek bed, or running water. Exposure also plays an important role and it is not uncommon to find plants growing only on north or northeast slopes. This is probably due to the north-facing slopes having less sun exposure, with less evaporation and less transpiration by the plants.

It has already been mentioned that *Gutierrezia* must compete with grasses, especially perennial ones. The competition here is believed to be mainly for the available water supply in the ground. Xerophytic grasses are better adapted morphologically and anatomically than *Gutierrezia* and apparently eventually crowd it out of better soils. In poorer soils, on the other hand, the situation appears to be reversed, and a possible explanation may be the requirement by grasses of more fertile soils (Tisdale, personal communication, and my own field observations).

This dynamic balance between grasses and *Gutierrezia* is expressed most clearly when the natural equilibrium is disturbed. One frequent cause of disturbance is overgrazing. Grasses are eaten avidly by both cattle and sheep while *Gutierrezia* is eaten very little. In such cases the latter plants spread rapidly, to the point that throughout their range both *Gutierrezia sarothrae* and *G. microcephala* are considered, wherever they grow abundantly in rangelands, to be indicators of overgrazing. A second frequent case of unbalance is produced when the soil is disturbed by road construction or some similar accident. *Gutierrezia* plants may frequently be seen growing in the barren slopes where the subsoil has been exposed, while the grasses rapidly take over the better spots.

The distribution of rainfall also plays an important role in determining the area of distribution. The concentration of species and abundance of individuals in the southwestern United States and northern Mexico seems to be directly correlated with late summer and fall rains. *Gutierrezia bracteata* is, of course, an exception to this, since, after the spring rains have ceased, it receives very little or no rain before September-October. It is interesting, therefore, to note that *Gutierrezia bracteata* is the latest bloomer, by about a month, of all the species of the genus.



These field observations are substantiated by those made on the cultures in the Botanical Garden at Berkeley. Plants of *Gutierrezia californica* (Oakland Hills and Angel Island, California, populations), *G. bracteata* (Yolo County, Corral Hollow, Temblor Range, and Cuyama Valley, California, populations), *G. sarothrae* (Fort Collins, and Grand Junction, Colorado; Wasatch, Nevada; and Lake Elsinore, California, populations), *G. microcephala* (Clark Mts., Nevada, population), *G. glutinosa* (San Luis Potosí, Mexico, population) and *G. texana* (Austin, Texas, population), were grown together. Water was provided in amounts sufficient so that it never became a limiting factor. All the plants attained much greater stature than they normally do in nature, but their flowering time was similar to that which had been observed in the field. The first to bloom were the Colorado populations of *G. sarothrae*, about mid-June. A month later all populations of *G. sarothrae* were in full bloom. In August, *G. microcephala* and *G. glutinosa* began blooming; toward the end of the month the Texas populations of *G. texana* and the populations of *G. bracteata* and *G. californica* were in anthesis. By October all but these last two species had passed their blooming period. Finally, in December *G. bracteata* and *G. californica*, especially the latter, were still blooming, while the Grand Junction population of *G. sarothrae* was flowering for a second time.

If we correlate these observations with rainfall, we see that the Colorado plants come from a region where the summer rains start first, and the California plants from the region which gets its rain latest. Undoubtedly, environmental conditions can hasten or retard flowering time but, as the experiments of Clausen, Keck, and Hiesey (1940, 1945, 1948) and Clausen and Hiesey (1958) have shown, flowering time seems to be determined genetically.

#### VARIATION STUDIES

Preliminary herbarium studies revealed among the perennial North American species the existence of an over-all morphological similarity; no clear-cut qualitative differences could be detected. In addition all those characters, which classically had been used to separate the species of *Gutierrezia*, showed some degree of variation. Field studies confirmed these observations and also showed a higher degree



of inter-than intra-population variation. These preliminary observations were restricted mainly to such characters as size of heads and number of flowers, which have usually been employed to characterize the various species.

In order to evaluate the amount of variation and to find correlations, if any, with specific taxonomic units, it was decided to study and measure the largest possible number of characters. Another object of this investigation was to determine the validity of the morphological characterization of the species.

An approach different from the mere study of herbarium specimens was thought to be important since studies of this kind in the past had failed to produce satisfactory results in *Gutierrezia*. It was decided therefore to study the variation of populations in nature with the aid of simple standard statistical methods. This, it was hoped, would produce a better understanding of the population dynamics.

#### MATERIAL AND METHODS

Eleven characters were selected after some preliminary inquiry. These are the following: height of plant; height and width of involucre; length and width of achenes of both ligulate and tubular flowers; length of pappus of both ligulate and tubular flowers; and number of ligulate and tubular flowers per capitulum.

A total of 17 populations, belonging to five species, from the states of Oregon, Idaho, California, and Arizona was studied. These populations were chosen at random. Lack of time and transportation facilities precluded the study of populations in other states. A sample of 50 individuals was selected from each population. In order to randomize, each population was measured as to length and width and a rough outline of it was drawn on paper. A rectangle was then circumscribed around it and each side was divided into six equal parts, and a grid consisting of 36 equal divisions was constructed. The vertical columns and horizontal bars were then numbered from one to six, so that each square of the grid was identified by two numbers. Finally with the aid of two different colored dice, ten squares in the grid were selected. Taking a corner of the rectangle circumscribing the population as an origin, five plants of each of the selected squares nearest to the origin were then chosen. After the



height of the plant had been measured, one head of each plant was collected and deposited in an envelope, for subsequent measurement and study in the laboratory. It is not therefore possible to establish any correlation between a single measurement of height of plant and any of the other characters, although it is possible to do so for any of the other characters.

This laborious sampling method has been followed in order to try to eliminate any kind of voluntary or involuntary bias, so as to obtain a true random sample from which meaningful statistical conclusions can be drawn. It is also hoped that randomization has largely changed systematic errors such as possible differences in soil, moisture, exposure, etc. within the population, into fluctuating errors, and that these have been subsequently made negligible by the use of the common standard statistical methods used in this study. If the sources of bias and systematic errors have been taken care of, and we may rather safely assume so, the samples are a true representation of the phenotypes of the populations studied.

*Gutierrezia californica* was not included in this study initially. By the time it had become apparent that data from this species would be of interest, its flowering season had passed. Consequently, the largest number of herbarium specimens of two populations well known to the author were gathered and one head from each available plant was removed and studied. This sample is less reliable than those obtained directly in the field, since it is very possible the collectors selected specimens for their vigour, size, or some other special characteristic. Another source of error is introduced by the fact that they were collected in different years and hence under different seasonal climatic conditions. Nevertheless, since both populations are small, the data may have comparative value and certain meaningful preliminary conclusions may perhaps be drawn from this material.

**STATISTICAL METHOD.** Hubbs and Perlmutter (1942) have provided a graphic method for the rapid comparison of representative samples of several populations. This method is a modification of that of Dice and Lleraas (1936) and consists in plotting in a graph the range and the mean of the sample and in addition one standard deviation and two



standard errors on each side of the mean. If the ranges of the four-standard errors so plotted do not overlap or just barely touch, and provided that the ratio between them is no greater than two, the mean of the two samples can be assumed to be significant ( $P=0.01$  to  $0.005$ ). If there is overlap, when it is no more than 33% of the length of the shorter of the two four-standard errors rectangles com-

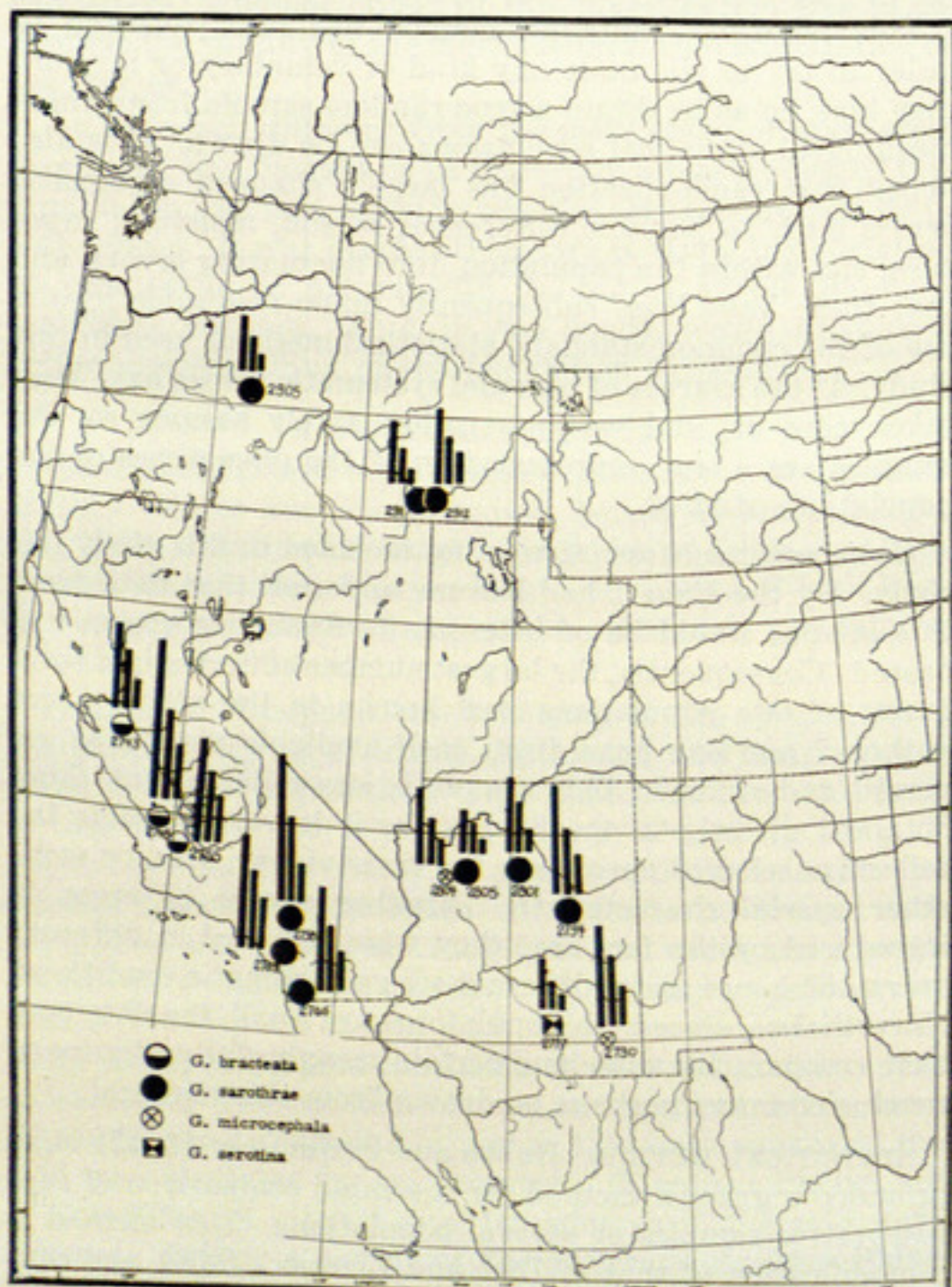


FIG. 6. Maximum (left bar), minimum (right bar), and mean (central bar) plant height measurements of fifteen populations of *Gutierrezia*.



pared, Hubbs and Perlmutter present tables ( $t$  values) which show that the mean still can be significant ( $P = 0.05$ ). In cases where the larger four-standard errors rectangle is two to four times longer than the shorter, an overlap of 50% or even 75% still can be somewhat significant ( $P = 0.072$  for 50% overlap and a ratio of 2/1;  $P = 0.089$  for 75% overlap and a ratio of 4/1).

This method has been used in comparing the means of six characters: length and width of achene of tubular and ligulate flowers and length of pappus of tubular and ligulate flowers (fig. 9-14).

On the other hand, a frequency distribution was thought to be more meaningful for comparing the number of both ligulate and tubular flowers, since in this case actual number rather than mathematical mean is the important feature. Measurements of the involucre were combined in a pictorial diagram so that width, length and shape can be compared. Finally, size of plant was plotted on a map in relation to the geographical location of the population.

#### RESULTS

**PLANT HEIGHT.** Nine populations of *Gutierrezia sarothrae*, three of *G. bracteata*, two of *G. microcephala*, and one of *G. serotina* were investigated as to this character. Fifty plants were measured in every case with exception of a population of *G. sarothrae* from San Diego County, California (Solbrig 2769) which consisted of only 35 plants.

Measurements were taken in the field with the aid of a steel measuring tape. The height recorded is that between the base of the plant and the tip of the longest branch. All measurements of plant height are expressed in inches, since no tape marked in meters could be found, and converting inches to centimeters would have introduced a source of inaccuracy.

There was an appreciable difference in the size of the plants both between and within populations. The mean height of the populations also varied widely, as did the range and the standard deviation. No meaningful correlations could be detected between the variation of these parameters and any definite geographic or specific character.

The mean heights of the populations of *G. bracteata* and *G. microcephala* are situated in the upper range of the dis-



tribution; the only population of *G. serotina* investigated has the smallest mean height, while the populations of *G. sarothrae* range from values not significantly larger than those of *G. serotina* to some which fall well within the range of *G. bracteata*.

INVOLUCRE. Size and shape of involucre is an important character in the separation of genera in Astereae, and it also has been employed in the delimitation of species of *Gutierrezia*. It is important, therefore, to know to what extent this structure may provide reliable taxonomic characters.

TABLE 6. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF PLANT HEIGHT

Species	Locality	Pop. No.	n	s	Mode	Min.	Max.	Range	s	$\sqrt{s}$
<i>G. sarothrae</i>	Temecula, Calif.	2758	50	22.4	22	10	38	28	13.90	1.966
	Chula Vista, Calif.	2766	50	17.3	16	10	27	17	9.70	1.371
	Rancho Santa Fe, Calif.	2769	35	20.3	20	13	29	12	7.48	1.263
	Payson, Arizona	2794	50	17.3	17	10	28	18	5.74	.811
	Hyde Park, Arizona	2805	50	7.8	8	4	11	7	3.18	.450
	John Day, Oregon	2905	50	9.3	9	4	14	10	4.84	.684
<i>G. bracteata</i>	Hansen, Idaho	2911	50	9.1	11	4	16	12	4.92	.695
	Patterson, Calif.	2743	50	15.0	15	7	22	18	6.62	.936
	Pond Ranch, Calif.	2748	50	23.7	23	14	31	17	9.88	1.397
<i>G. microcephala</i>	Tembler Range, Calif.	2755	50	18.5	19	12	27	15	6.90	.975
	Saint David, Arizona	2790	50	17.8	17	10	26	16	6.74	.953
<i>G. serotina</i>	Hyde Park, Arizona	2804	50	12.6	10	7	20	13	6.00	.848
	Tucson, Arizona	2777	50	7.7	7	4	13	9	4.24	.599

All measurements expressed in inches.

Figure 7 shows the shape and the mean dimensions of the involucre in the populations of *Gutierrezia* studied for this structure. The range of dimensions is illustrated by means of two superimposed crosses, the larger being proportional to the maximal sizes and the smaller to the minimal ones; the range is the difference between the largest and the smallest cross. In both crosses the vertical bar represents height and the cross bar indicates width.

Two populations may be singled out easily from the rest: population No. 2777, representing *G. serotina*, and population No. 2804, which belongs to *G. microcephala*. The shape and also the proportion between length and width (almost as high as broad in *G. serotina* and several times longer than broad in *G. microcephala*) are so characteristic that the two



species can be identified readily by these characters.

The involucre of *G. californica* is of approximately the same shape as that of *G. bracteata* and *G. sarothrae*. The mean dimensions of the former are larger than those of the latter species. In spite of a slight overlap in range with *G. bracteata* it is believed that this character is of some taxonomic value.

TABLE 7. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF HEIGHT OF INVOLUCRE

Species	Locality	Pop. No.	n	s	Mode	Min.	Max.	Range	s	$\sqrt{x}$
<i>G. sarothrae</i>	Temecula, Calif.	2758	50	43.6	45	49	35	14	5.64	.797
	Chula Vista, Calif.	2766	50	35.1	31	45	25	20	2.35	.332
	Rancho Santa Fe, Calif.	2769	50	34.3	35	39	27	12	6.00	.848
	Payson, Arizona	2794	50	56.5	55	65	45	20	8.52	1.205
	Ash Fork, Arizona	2801	50	37.3	39	43	27	16	1.61	.227
	Hyde Park, Arizona	2805	50	39.2	40	49	35	14	2.58	.364
	John Day, Oregon	2905	9	39.3	*	45	33	12	8.58	3.031
	Hansen, Idaho	2911	3	47.0	*	*	*	*	*	*
<i>G. bracteata</i>	Patterson, Calif.	2743	50	51.2	51	59	40	19	3.40	.480
	Pond Ranch, Calif.	2748	50	51.6	51	58	46	12	2.25	.318
	Temblor Range, Calif.	2755	50	55.7	59	63	49	14	8.60	1.216
<i>G. microcephala</i>	Hyde Park, Arizona	2804	50	35.9	35	41	17	24	8.38	1.185
<i>G. serotina</i>	Tucson, Arizona	2777	50	28.6	29	45	19	26	8.78	1.241
<i>G. californica</i>	Angel Island, Calif.	2428	10	57.0	*	*	*	*	*	*
	Oakland, Calif.	2154	19	52.1	*	*	*	*	*	*

\* Data insufficient

All measurements expressed in mm.  $\times 10$ .

TABLE 8. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF WIDTH OF INVOLUCRE

Species	Locality	Pop. No.	n	s	Mode	Min.	Max.	Range	s	$\sqrt{x}$
<i>G. sarothrae</i>	Temecula, Calif.	2758	50	24.8	25	19	29	10	2.68	.379
	Chula Vista, Calif.	2766	50	18.5	19	13	27	14	2.69	.380
	Rancho Santa Fe, Calif.	2769	50	21.5	19	15	25	10	4.12	.582
	Payson, Arizona	2794	50	21.2	20	18	28	10	2.48	.350
	Ash Fork, Arizona	2801	50	19.6	19	13	25	12	2.34	.330
	Hyde Park, Arizona	2805	50	16.7	17	11	27	16	2.52	.356
	John Day, Oregon	2905	9	30.1	*	25	35	10	7.16	2.530
	Hansen, Idaho	2911	3	31.3	*	*	*	*	*	*
<i>G. bracteata</i>	Patterson, Calif.	2743	50	33.9	32	29	42	13	3.56	.503
	Pond Ranch, Calif.	2748	50	33.0	32	26	48	22	3.25	.459
	Temblor Range, Calif.	2755	50	26.1	29	19	35	16	7.30	1.032
<i>G. microcephala</i>	Hyde Park, Arizona	2804	50	10.0	10	5	16	11	2.49	.352
<i>G. serotina</i>	Tucson, Arizona	2777	50	26.5	25	19	35	16	7.46	1.055
<i>G. californica</i>	Angel Island, Calif.	2428	10	42.0	*	*	*	*	*	*
	Oakland, Calif.	2154	19	37.7	*	*	*	*	*	*

\* Data insufficient.

All measurements expressed in mm.  $\times 10$ .



*Gutierrezia sarothrae* and *G. bracteata* cannot be separated on the basis of involucral characters alone, even though in the populations studied the involucres of *G. bracteata*

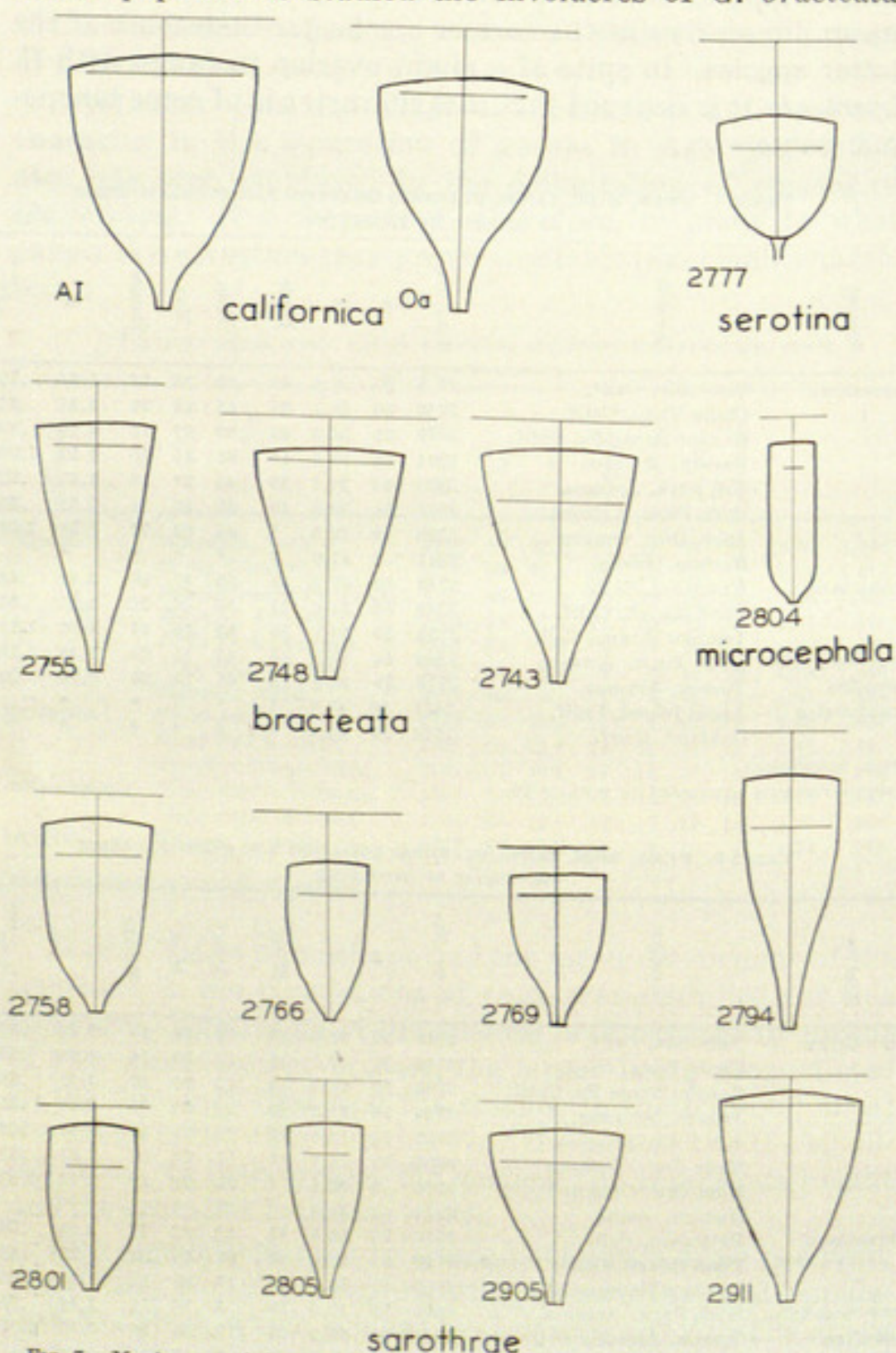


FIG. 7. Maximum, minimum, and mean of height and width of the involucre. Each outline drawing is proportional to the mean dimensions; the larger vertical and transversal bars represent the maximum dimensions; the smaller inner bars the minimum dimensions.



were slightly larger than those of *G. sarothrae*. The overlap is so large and consequently the chances of error so great that, even if we were to assume that size were a valid difference, the use of this character would lead to confusion rather than to clarification.

Nevertheless, certain trends can be pointed out: (1) the trend toward larger involucre in *G. bracteata* (see above); (2) the relatively narrower involucre of *G. sarothrae*; (3) the funnellform involucre of *G. bracteata* in contrast to the more turbinate ones of *G. sarothrae*. These slight differences in shape can be correlated with a tendency in the involucre bracts of *G. bracteata* to reflex slightly and consequently to loosen the involucre somewhat, while in *G. sarothrae* the involucre bracts are closely appressed at anthesis.

Aside from the differences noted above between populations belonging to different species, figure 7 shows also that populations of the same species differ from one another not only in the mean of the characters considered but also in the range. Population No. 2794 of *Gutierrezia sarothrae* is of interest in this respect. As may be seen in figure 7, the involucre are larger, although not broader, than in all the other populations studied of the same species. It is thought to be significant that this population is a polyploid with  $n = 8$ , while all the others are diploid with  $n = 4$ . It is also of interest that the mean length of the involucre of population No. 2794 approaches that of the 8-chromosome populations of *G. bracteata*.

**NUMBER OF FLOWERS.** This character is very important because it has been used extensively to separate species. In this case it is believed that frequency distribution and range are more meaningful than mean and standard deviation, and therefore the latter will not be considered (although it has been calculated and the interested reader is referred to tables 9 and 10).

Figure 8 shows the distribution of the frequencies of ligulate and tubular flowers of 14 populations of *Gutierrezia*. In most cases the mode class has a frequency of about 50%. An exception to this is the only population of *G. microcephala* studied, which shows a greater frequency for the modal class and far less variation than all the other populations investigated. Herbarium studies appear to confirm this observation.



A second feature which may be observed is that the range between the lowest and highest values observed is not great. The Oakland Hills population of *G. californica* might be an exception to this, but since the representativeness of the sample is questionable (see page 25) this cannot be confirmed.

Another characteristic is that different populations of the

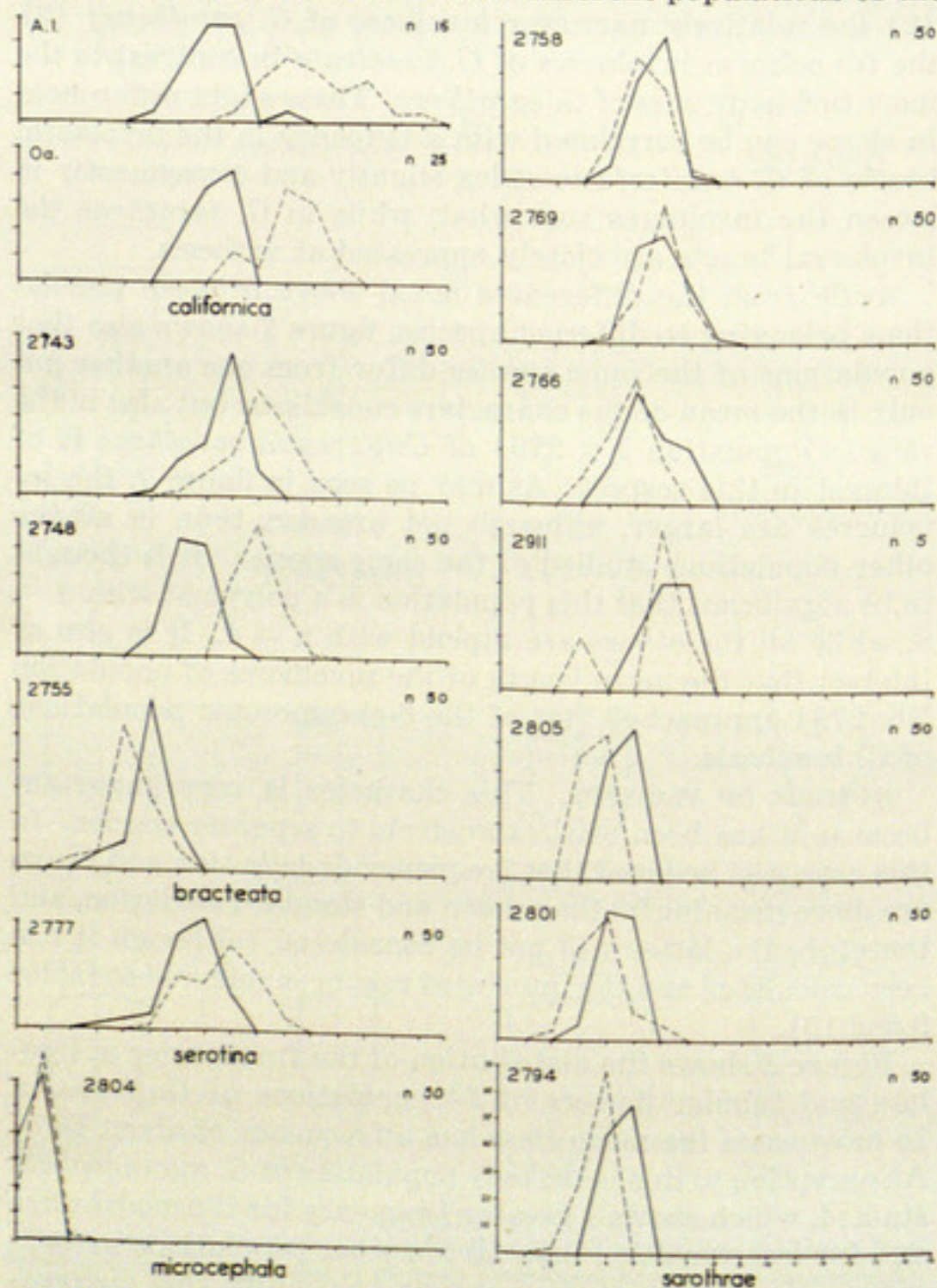


FIG. 8. Frequency distribution of number of ligulate (full line) and tubular flowers (broken line) in one head.



same species have different modal classes and also vary in the range. This finding is believed to be important because all the species considered have been characterized at one time or another by number of ligulate or tubular flowers or both.

TABLE 9. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF NUMBER OF TUBULAR FLOWERS IN ONE HEAD

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	s	$\sqrt{x}$
<i>G. sarothrae</i>	Temecula, Calif.	2758	50	5.3	5	4	7	3	.77	.108
	Chula Vista, Calif.	2766	50	4.6	5	0	6	6	1.09	.154
	Rancho Santa Fe, Calif.	2769	50	5.9	6	4	7	3	.70	.099
	Payson, Arizona	2794	50	3.6	4	0	4	4	1.30	.183
	Ash Fork, Arizona <sup>1</sup>	2801	50	3.8	4	2	6	4	.90	.127
	Hyde Park, Arizona	2805	50	3.5	4	3	4	1	.50	.070
	Hansen, Idaho	2911	5	5.6	6	6	7	1	*	*
<i>G. bracteata</i>	Patterson, Calif.	2743	50	9.0	9	6	11	5	1.09	.154
	Pond Ranch, Calif.	2748	50	8.9	9	8	11	3	.75	.106
	Temblor Range, Calif.	2755	50	4.3	4	2	6	4	.86	.121
<i>G. microcephala</i>	Hyde Park, Arizona	2804	50	—	1	0	2	2	.42	.059
<i>G. serotina</i>	Tucson, Arizona	2777	50	7.7	8	5	10	5	1.25	.176
<i>G. californica</i>	Angel Island, Calif.	2428	16	10.2	10	8	12	4	*	*
	Oakland, Calif.	2154	25	11.1	10	8	15	7	5.71	1.142

\* Data insufficient.

<sup>1</sup> Sample taken from two plants.

TABLE 10. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF NUMBER OF LIGULATE FLOWERS IN ONE HEAD

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	s	$\sqrt{x}$
<i>G. sarothrae</i>	Temecula, Calif.	2758	50	5.5	5	4	7	3	.65	.091
	Chula Vista, Calif.	2766	50	5.5	5	4	7	3	1.47	.207
	Rancho Santa Fe, Calif.	2769	50	5.8	6	4	8	4	.84	.118
	Payson, Arizona	2794	50	4.6	5	4	5	1	.50	.070
	Ash Fork, Arizona <sup>1</sup>	2801	50	4.4	4	3	5	2	.60	.084
	Hyde Park, Arizona	2805	50	4.6	5	4	5	1	.50	.070
	Hansen, Idaho	2911	5	6.2	*	5	7	2	*	*
<i>G. bracteata</i>	Patterson, Calif.	2743	50	7.6	8	5	9	4	.93	.131
	Pond Ranch, Calif.	2748	50	6.5	6	5	8	3	.73	.103
	Temblor Range, Calif.	2755	50	4.9	5	3	6	3	.74	.104
<i>G. microcephala</i>	Hyde Park, Arizona	2804	50	—	1	0	1	1	.49	.069
<i>G. serotina</i>	Tucson, Arizona	2777	50	6.5	7	3	8	5	1.23	.173
<i>G. californica</i>	Angel Island, Calif.	2428	16	7.3	*	*	*	*	*	*
	Oakland, Calif.	2154	25	7.2	7	5	10	5	6.34	1.268

\* Data insufficient.

<sup>1</sup> Sample taken from two plants.

Neither in range nor in mean is there any absolute difference between species. A general trend is nevertheless present. *Gutierrezia californica* has from 8 to 15 tubular flowers,



with a mode of 10, which is more than in any other species. Ligulate flowers vary from 5 to 8 with modes of 7 and 8. The populations of *G. bracteata* have a range of from 6 to 11 tubular flowers, and 5 to 9 ligulate flowers in two popula-

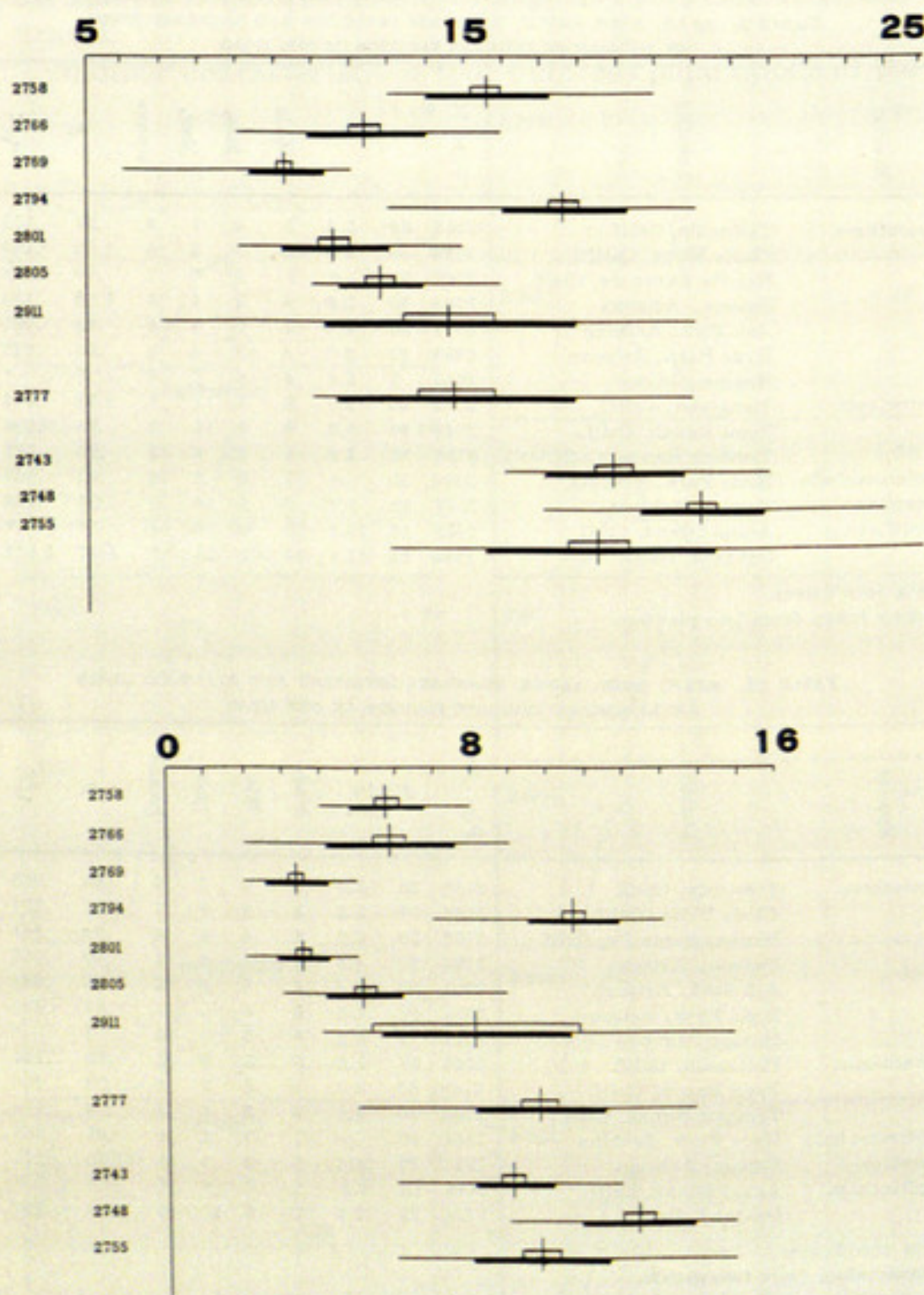


FIG. 9. Mean (vertical line), range (middle horizontal line), standard deviation (dark lower bar) and standard error (light upper bar) of length of pappus of tubular flowers. FIG. 10. Id. of pappus of ligulate flowers. For further explanations see text.



tions, with modal classes of 9-6 and 8, respectively. However, a third population (Solbrig 2755) has only 2 to 6 tubular and 3 to 6 ligulate flowers and modes of 4 and 5. This last population thus follows the pattern of *G. sarothrae* rather than that of *G. bracteata*. This feature shows up in other characteristics too, as will be seen. At this stage of our investigations, however, there is insufficient information to give an explanation for this behavior.

*Gutierrezia serotina* has 5 to 10 tubular and 3 to 8 ligulate flowers per capitulum in the population studied. The modal classes are 8 and 7, respectively.

TABLE 11. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF LENGTH OF PAPPUS OF TUBULAR FLOWERS

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	s	$\sqrt{x}$
<i>G. sarothrae</i>	Temecula, Calif.	2758	50	14.6	15	12	19	7	1.60	.220
	Chula Vista, Calif.	2766	50	11.4	12	8	15	7	1.56	.220
	Rancho Santa Fe, Calif.	2769	50	9.3	10	5	11	6	1.04	.147
	Payson, Arizona	2794	50	16.6	16	12	20	8	1.57	.222
	Ash Fork, Arizona	2801	50	10.6	10	8	14	6	1.38	.195
	Hyde Park, Arizona	2805	50	11.8	12	10	15	5	1.05	.148
	Hansen, Idaho	2911	28	13.6	15	6	20	14	3.30	.634
<i>G. bracteata</i>	Patterson, Calif.	2743	50	17.9	19	15	22	7	1.77	.250
	Pond Ranch, Calif.	2748	50	20.2	20	16	25	9	1.55	.219
	Temblor Range, Calif.	2755	50	17.5	18	12	26	12	2.98	.421
<i>G. serotina</i>	Tucson, Arizona	2777	50	13.8	12	10	20	10	3.22	.455

All measurements expressed in mm.  $\times 10$ .

TABLE 12. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF LENGTH OF PAPPUS OF LIGULATE FLOWERS

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	s	$\sqrt{x}$
<i>G. sarothrae</i>	Temecula, Calif.	2758	50	5.8	5-6	4	8	4	1.01	.142
	Chula Vista, Calif.	2766	50	5.9	5	2	9	7	1.67	.236
	Rancho Santa Fe, Calif.	2769	50	3.4	3	2	5	3	.76	.107
	Payson, Arizona	2794	50	10.7	10	7	13	6	1.17	.165
	Ash Fork, Arizona	2801	50	3.6	3	2	5	3	.67	.094
	Hyde Park, Arizona	2805	50	5.2	5	3	9	6	.95	.134
	Hansen, Idaho	2911	31	8.1	7	4	15	11	2.48	1.433
<i>G. bracteata</i>	Patterson, Calif.	2743	50	9.1	9	6	12	6	.99	.140
	Pond Ranch, Calif.	2748	50	12.4	12	9	15	6	1.46	.206
	Temblor Range, Calif.	2755	50	9.8	10-11	6	15	9	1.73	.244
<i>G. serotina</i>	Tucson, Arizona	2777	50	9.8	10	5	14	9	1.70	.240

All measurements expressed in mm.  $\times 10$ .



The number of tubular flowers varies from 3 to 7 in *G. sarothrae* (one head had no tubular flowers) with modes of 4 or 5. The polyploid population No. 2769 had a mode of 6,

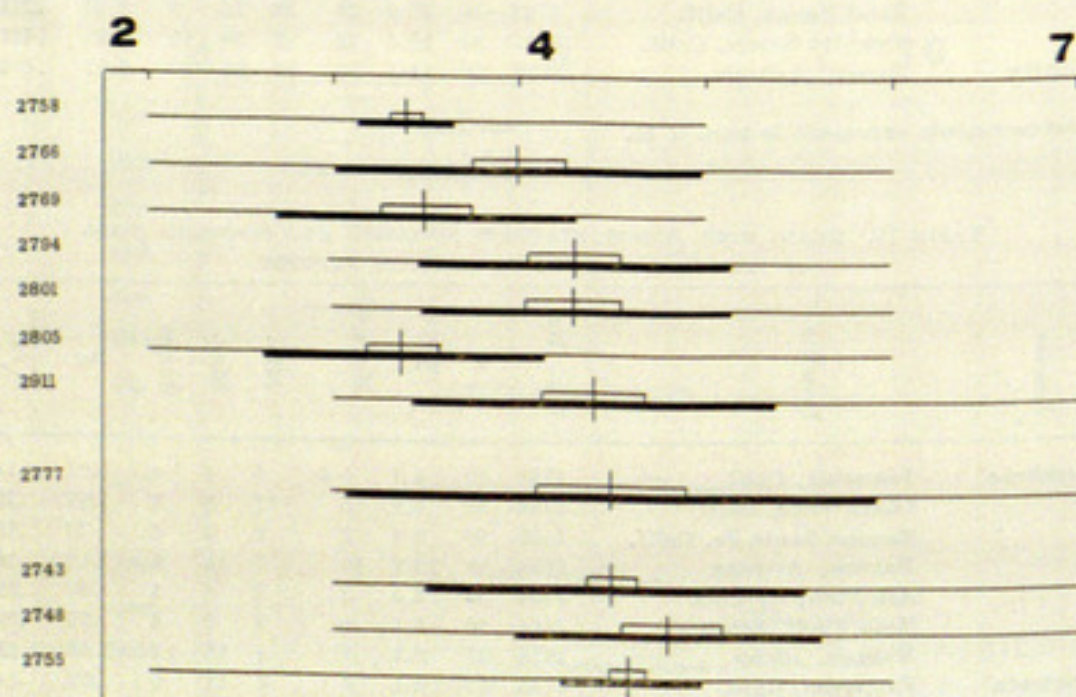
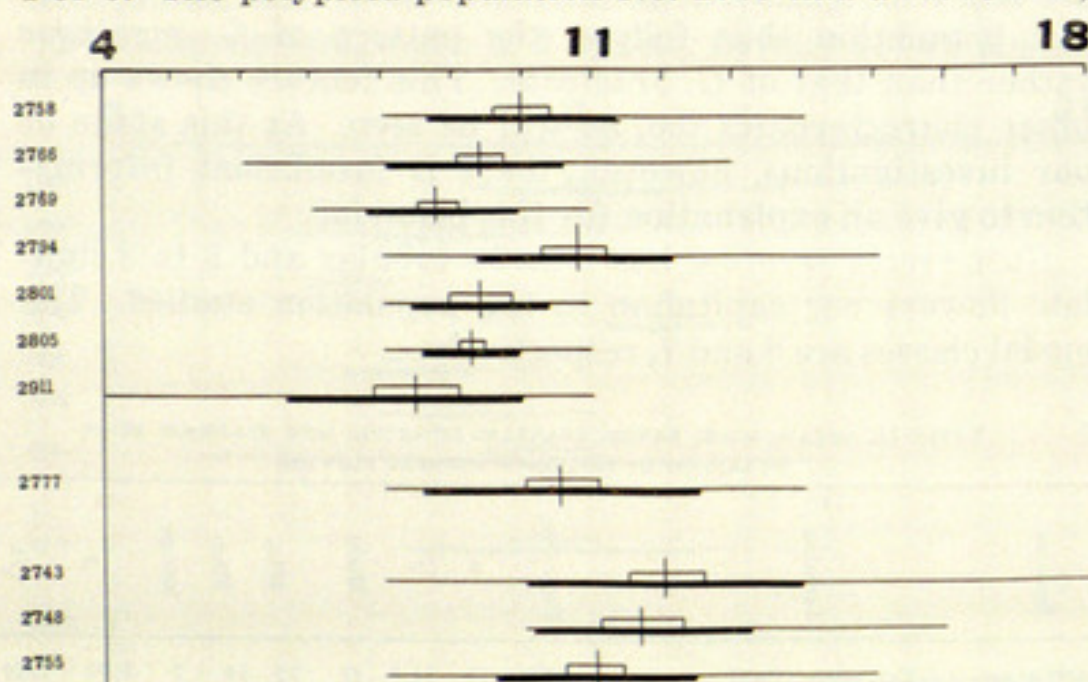


FIG. 11. Mean (vertical line), range (middle horizontal line), standard deviation (dark lower bar) and standard error (light upper bar) of length of achene of tubular flowers. FIG. 12. Id. of width of achene of tubular flowers. For further explanations see text.



as did population No. 2911. Only five heads could be counted in this last population so that these data cannot be taken into consideration. The number of ligulate flowers varied from 4 to 8, while the most frequent modal classes were 5 and 6 if we disregard population No. 2911.

*Gutierrezia microcephala* showed 0 to 1 tubular and ligulate flowers. One head had 2 tubular flowers, while 1 was the mode for both ligulate and tubular flowers.

TABLE 13. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF LENGTH OF ACHENE OF TUBULAR FLOWER

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	s	$\sqrt{x}$
<i>G. sarothrae</i>	Temecula, Calif.	2758	50	10.0	10	8	14	6	1.37	.193
	Chula Vista, Calif.	2766	50	9.3	9	6	13	7	1.27	.179
	Rancho Santa Fe, Calif.	2769	50	8.8	9	7	11	4	.94	.132
	Payson, Arizona	2794	50	10.8	10	8	15	7	1.43	.202
	Ash Fork, Arizona	2801	50	9.4	10	8	11	3	.97	.137
	Hyde Park, Arizona	2805	50	9.2	9	8	11	3	.65	.091
	Hansen, Idaho	2911	28	8.5	9	4	11	6	1.88	.360
	Patterson, Calif.	2743	50	12.0	11	8	18	8	1.93	.272
<i>G. bracteata</i>	Pond Ranch, Calif.	2748	50	11.7	11	10	16	6	1.61	.227
	Tembler Range, Calif.	2755	50	10.7	10	8	15	7	1.47	.207
	Tucson, Arizona	2777	50	10.5	10	8	14	6	1.97	.278

All measurements expressed in mm.  $\times 10$ .

TABLE 14. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF WIDTH OF ACHENE OF TUBULAR FLOWER

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	s	$\sqrt{x}$
<i>G. sarothrae</i>	Temecula, Calif.	2758	50	3.4	3	2	5	3	.21	.029
	Chula Vista, Calif.	2766	50	4.0	4	2	6	4	.97	.137
	Rancho Santa Fe, Calif.	2769	50	3.5	3	2	5	3	.79	.111
	Payson, Arizona	2794	50	4.3	4	3	6	3	.82	.115
	Ash Fork, Arizona	2801	50	4.3	5	3	6	3	.83	.117
	Hyde Park, Arizona	2805	50	3.4	3	2	6	4	.75	.106
	Hansen, Idaho	2911	28	4.4	5	3	7	4	.96	.181
	Patterson, Calif.	2743	50	4.5	5	3	7	4	.99	.140
<i>G. bracteata</i>	Pond Ranch, Calif.	2748	50	4.8	5	3	7	4	.83	.117
	Tembler Range, Calif.	2755	50	4.6	5	3	6	3	.36	.050
	Tucson, Arizona	2777	50	4.5	5	3	7	4	1.40	.198

All measurements expressed in mm.  $\times 10$ .

The information presented above may be summed up in the following tabulation:

	californica		bracteata		serotina		sarothrae		microcephala	
	range	mode	range	mode	range	mode	range	mode	range	mode
ligulate	5-8	7-8	3-9	3-5	3-8	7	4-8	5-6	0-1	1
tubular	8-15	10	2-11	4-9	5-10	8	3-7	4-6	0-2	1
total	13-23	17-18	5-20	7-14	8-18	15	7-15	9-12	0-3	2



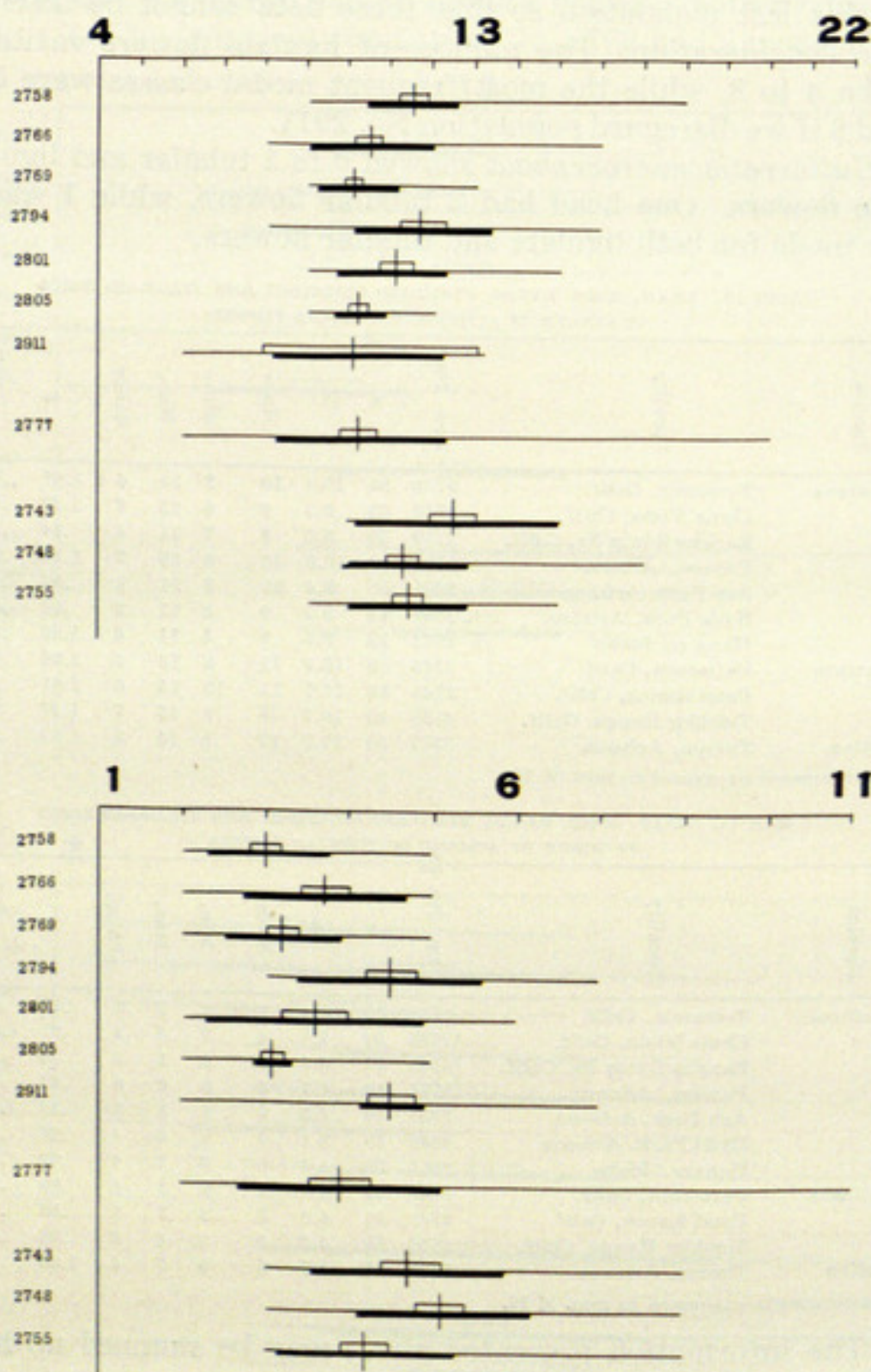


FIG. 13. Mean vertical line), range (middle horizontal line), standard deviation (dark lower bar) and standard error (light upper bar) of length of achene of ligulate flowers. Fig. 14. Id. of width of achene of ligulate flowers. For further explanations see text.



Thus, *G. microcephala*, and to a certain extent *G. californica*, may be characterized by the number of flowers in a head. The other species cannot be identified on this character alone. However, if the flowers of a sufficiently large number of heads are counted, some clue may be obtained as to their identity, and in some cases a preliminary determination can be made.

PAPPUS. The pappus of the ligulate flowers is shorter than that of the tubular ones. Nevertheless, there is considerable similarity in the relative distribution of the means. The mean of pappus length of *G. bracteata* is significantly larger than that of *G. sarothrae*, with the exception of the poly-

TABLE 15. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF LENGTH OF ACHENE OF LIGULATE FLOWER

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	s	$\sqrt{x}$
<i>G. sarothrae</i>	Temecula, Calif.	2758	50	11.5	11	9	18	9	1.11	.157
	Chula Vista, Calif.	2766	50	10.5	10	8	16	8	1.46	.206
	Rancho Santa Fe, Calif.	2769	50	10.1	10	9	13	4	.67	.094
	Payson, Arizona	2794	50	11.7	11	8	16	8	1.59	.224
	Ash Fork, Arizona	2801	50	11.1	10	9	15	6	1.31	.185
	Hyde Park, Arizona	2805	50	10.2	10	9	12	3	.61	.086
	Hansen, Idaho	2911	31	10.1	10	6	15	9	1.986	1.444
<i>G. bracteata</i>	Patterson, Calif.	2743	50	12.5	12	10	22	12	2.38	.336
	Pond Ranch, Calif.	2758	50	11.3	11	10	17	7	1.52	.214
	Tembler Range, Calif.	2755	50	11.4	11	9	15	6	1.31	.185
<i>G. serotina</i>	Tucson, Arizona	2777	50	10.2	10	6	20	14	2.02	.285

All measurements expressed in mm.  $\times 10$ .

TABLE 16. MEAN, MODE, RANGE, STANDARD DEVIATION AND STANDARD ERROR OF WIDTH OF ACHENE OF LIGULATE FLOWER

Species	Locality	Pop. No.	n	$\bar{x}$	Mode	Min.	Max.	Range	s	$\sqrt{x}$
<i>G. sarothrae</i>	Temecula, Calif.	2758	50	3.0	3	2	5	3	.700	.099
	Chula Vista, Calif.	2766	50	3.7	3	2	5	3	.980	.139
	Rancho Santa Fe, Calif.	2769	50	3.2	3	2	5	3	.690	.097
	Payson, Arizona	2794	50	4.5	5	3	7	4	1.110	.157
	Ash Fork, Arizona	2801	50	3.6	3	2	6	4	1.310	.185
	Hyde Park, Arizona	2805	50	3.1	3	2	5	3	.130	.018
	Hansen, Idaho	2911	50	4.5	5	2	7	5	.330	.190
<i>G. bracteata</i>	Patterson, Calif.	2743	50	4.7	4	3	8	5	1.170	.165
	Pond Ranch, Calif.	2748	50	5.1	5	3	8	5	.930	.131
	Tembler Range, Calif.	2755	50	4.4	4	3	8	5	1.050	.148
<i>G. serotina</i>	Tucson, Arizona	2777	50	3.9	4	2	10	8	1.270	.179

All measurements expressed in mm.  $\times 10$ .



ploid population of this last species (see page 31). The length of pappus of *G. serotina* is somewhat intermediate.

ACHENE. No significant differences in length or width of achene could be detected. *Gutierrezia bracteata* had the largest achenes and some populations of *G. sarothrae* the smallest; however, the differences are believed to have no taxonomic significance.

CONCLUSION. A certain amount of variability in the characters of the populations of an outbreeding species can be predicted on theoretical grounds. The variability encountered in species of *Gutierrezia* is therefore not surprising. Nevertheless, unbiased estimates of the amount of variability in higher plants are few and usually deal with woody plants (Critchfield, 1958). Statistical methods are of common use in genetics and related fields but are used only occasionally in taxonomic studies. The novelty in this study lies in the sampling method, which is a variation of the "completely randomized" method, applied to observational, rather than experimental studies.

As for the results themselves, "key" characters and their variability are expressed in terms of frequencies and ranges and can be dealt with in a more objective fashion as a consequence. The most important aspect is that in most cases we have a continuous range of variability for most characters throughout the range of the genus. Species therefore become meaningful only when they are expressed in terms of series of populations with "frequency peaks" for more than one character, rather than in terms of presence or absence of a fixed frequency of a character (such as an  $x$  number of flowers per capitulum).

## EVOLUTION

### GENERAL CONSIDERATIONS

Several groups of plants in which polyploidy has played an important role in speciation are known today (Goodspeed, 1954; Clausen, Keck and Hiesey, 1945, etc. For a review see Stebbins, 1950). In most cases polyploid species can be separated morphologically from their diploid ancestors and relatives. Nevertheless, some instances are known in which the polyploid plants cannot be separated from the diploids in any other way than by counting their chromosomes (Bell, 1954; Thompson, 1951; Cave and Constance, 1950; Heckard,



1960). Some of the species of *Gutierrezia* have polyploids which cannot be separated either morphologically or ecologically from plants with a lower level of ploidy. Tetraploids of *Gutierrezia sarothrae* with  $n = 8$  are apparently insufficiently distinct from diploids with  $n = 4$  to permit their identification on gross morphology. One tetraploid population from Payson, Arizona (Solbrig 2794) was studied in some detail: the mean of several but not all characters measured was slightly larger in the tetraploids than the mean of the same characters in the diploids. There nevertheless was an overlap in the range, which seems to justify not giving a separate designation to the polyploid in spite of the probable barrier that exists to crossing. Pollen grain and stomata diameter measurements did not reveal any significant differences. Neither could any substantial difference be detected between the diploids and the known polyploid plants of *G. microcephala* and *G. bracteata*.

Stebbins (1950), after surveying the corresponding literature, has indicated that the production of a "gigas" effect as a result of autopolyploidy is correlated with the existence of a strongly heterozygous diploid. Assuming that the polyploids encountered are autopolyploids, this might indicate that the diploids are rather homozygous. Nevertheless, it is the author's opinion that the polyploids are the result of segmental allopolyploidy (Stebbins, 1950). The author has no direct or indirect evidence to support this assumption other than the indirect evidence of work done with other plants (Goodspeed and Clausen, 1928; Sears, 1948; Schnack and Solbrig, 1952, etc.) and the more direct, but still insufficient, proof of the perfect or nearly perfect pairing at meiosis observed in all instances in the polyploids.

Most species of *Gutierrezia* grow in small to moderately large populations. Exceptions to this are, to a certain extent, the annual species, *G. texana* and *G. glutinosa*, the perennial *G. microcephala* and populations of *G. sarothrae* in the southwestern United States. All the other species observed grew in an over-dispersed fashion, the populations containing approximately 20 to 500 plants. The area occupied varied from a few hundred square meters to some hectares. Each population studied showed greater uniformity within than between populations. This pointed out that there was some kind of isolation mechanism which prevented the free flow



of genes from one population to the other. Consequently an investigation of the breeding mechanism was undertaken which it was felt might shed some light on this problem.

As has been indicated before, the flowers are mechanically adapted for outbreeding, even though tests performed showed that there apparently is no genetical mechanism to prevent selfing. In outbreeding plants one usually expects a greater amount of heterozygosity than in self-pollinating plants; the *Astereae*, so far as known, are insect pollinated and *Gutierrezia* is no exception.

All plants of *Gutierrezia* observed are visited by insects; the amount of visitation varied from very heavy to light. These variations are somewhat correlated with time of day and the number of other plants in bloom in the surrounding vegetation. As a rule, in the months of August to October, when *Gutierrezia* blooms, there are few or no other plants flowering in the surrounding area with the exception of shrubby *Compositae* (usually *Astereae*!). The sporadic collections of insects made were not very meaningful, since no systematic studies and observations of pollinators were attempted. Nevertheless, some observations may be recorded. In several instances populations of *Gutierrezia bracteata* and *G. sarothrae* in California were heavily infested with beetles of the genus *Epicauta*. These beetles are gregarious, feed on pollen, and crawl over the plants in large numbers. Undoubtedly by doing so they achieve at least some pollination. But since, unlike bees, they tend to remain on one plant, visiting one flower after another until the food source is depleted and only then moving to another plant, they necessarily pollinate mostly flowers with pollen from the same plant.

Beetles of the genus *Crossidius* also were collected on *Gutierrezia sarothrae*. This genus of beetles is largely confined to arid regions of western North America. Its larvae are all root borers, chiefly in roots of *Chrysothamnus*, *Haplopappus*, *Artemisia* and *Gutierrezia* (Linsley, 1957). The adults feed on pollen of the same species and also use the heads as mating places; in doing so they contribute to the pollination of the flowers. They are better fliers than *Epicauta* and it is believed that they contribute to outbreeding. Several species have been recorded by Linsley (1957) on *Gutierrezia sarothrae*, *G. bracteata*, and *G. microcephala*.



In some cases species of *Crossidius* seem to be specific on *Gutierrezia*.

In addition to beetles, bees were also collected. Honeybees were observed in several instances gathering nectar and pollen. But since this species (*Apis mellifera*) is of relatively recent introduction in the United States, it is not considered to be as important as native bees which also were observed. It is of interest to note here that no large bees, aside from the domestic bee, were found, while some small ones were. In a recent monograph of *Perdita*, a genus of oligolectic bees (Timberlake, 1954, 1958), several species are indicated as feeding on *Gutierrezia bracteata*, *G. sarothae*, and *G. microcephala*. In some instances the *Perdita* species seem to be monolectic in relation to species of *Gutierrezia*, but the collections are far too few to allow an absolute statement. According to MacSwain (personal communication), it is most likely that other genera of oligolectic bees feed on *Gutierrezia*. Nothing is known about oligotropic and monotropic bees in relation to the genus.

The species of *Perdita* are small and their flights probably do not cover a large area. They would therefore contribute to cross pollination of plants within a single population, but they would not be very effective in carrying pollen between populations separated by as much as a few miles. It may be said that, in general, bees contribute to reinforce the geographical isolation of populations (Grant, 1949).

The preliminary picture that emerges from these observations is as follows: The species of *Gutierrezia* are mechanically adapted to outbreeding, although there seem to be no barriers to selfing (see section of Cytology and Genetics). The flowers are pollinated by insects, mainly beetles and small bees. These insects are generally poor fliers, which, due to their habits or constitution, tend to remain within a population and its surrounding area. They produce outbreeding between plants of the same population, hence the intrapopulation variability, but they contribute also to some extent to the selfing of plants. On the other hand, their limited range of movement reinforces the geographical barriers between populations.

Several papers dealing with evolutionary relationships of flowers and bees have appeared recently (Grant, 1950 b; Leppik, 1957, etc.). Others have investigated the relation-



ships between oligolectic bees and flower constancy (Linsley, 1958; Linsley and MacSwain, 1957, 1958, etc.). Oligolectic bees can be defined "as those in which the individual members of the population, through its range and in the presence of other pollen sources, consistently and regularly collect pollen from a single plant species or a group of related plant species, turning to other sources, if at all, only in the face of a local pollen shortage" (Linsley and MacSwain, 1957). The ability to recognize the pollen source is apparently transmitted to the larva when it is fed with pollen of the host plant and is most likely related to olfactory and gustatory characteristics in the pollen. Morphological and physiological adaptations exist in both the bee, to permit a better synchronization with the host, and in the plant, to attract the insect. In the presence of a shortage of the pollen source the oligolectic bee can change to other sources (Linsley and MacSwain, 1957, 1958). It is possible, therefore, that in each population of *Gutierrezia* pollinated by oligolectic bees, as for example *Perdita*, the insects are adapted to a certain pollen or flower type and favor it over other types. This could be in response to a mutation especially favorable to the bee (Grant, 1950a) or as a result of chance, as will be seen.

New populations of *Gutierrezia* are established when new favorable sites are open. As has been seen (under Ecology and Distribution) this may be due to such causes as over grazing or soil disturbance. These new populations are probably initiated by a few seeds (and hence there is an advantage to the species of being capable of self-pollination), since the seeds are not especially adapted to dispersal. Under favorable conditions the population might in time expand to a few hundred plants. The genotypes of the first members of the colony will be determined strictly by chance between the genotypes present in the neighboring populations, provided not one genotype in the sum-total of those present in neighboring populations has a comparatively very high frequency. This process is part of what is known as random genetic drift (Wright, 1949; Dobzhansky, 1953). A combination of random genetic drift and selection by oligolectic bees could explain the uniformity within populations of *Gutierrezia* and the differences between populations (which often are statistically significant, see Variation Studies). This is to



be viewed as a possible although not necessarily a probable explanation, and it does not necessarily rule out environmental or edaphic selection even if no such differences could be detected (see Ecology and Distribution).

#### SPECIATION

The basic chromosome number for *Gutierrezia* is  $x = 4$ . This number was found in *Gutierrezia texana*, *G. glutinosa*, *G. serotina*, and in the great majority of the populations of *G. sarothrae* investigated. The tetraploid populations of *G. sarothrae* and the diploid populations of *G. bracteata* and *G. microcephala* have  $n = 8$ . Twelve is found in several polyploid populations of *G. bracteata* and in *G. californica*. Finally, one population of *G. microcephala* had 16 pairs of chromosomes.

Four is a rather uncommon number in Compositae-Astereae, while nine seems to be the basic number of the tribe (Raven, Solbrig, Kyhos and Snow, 1960). Apparently a process of chromosomal reduction has taken place in those genera which show less than nine chromosomes (cf. also Stebbins, Jenkins and Walters, 1951). In *Gutierrezia* an increase in chromosome number through polyploidy has taken place secondarily.

*Gutierrezia sarothrae* is envisioned as the North American species most directly related to the basic stock. All other perennial species in North America are considered to be derived from it or from one of its direct ancestors, either by adaptive radiation or by polyploidy or both. This assumption is based on cytological, distributional and morphological data.

As has been stated, *Gutierrezia sarothrae* has four pairs of chromosomes in most of the populations investigated, which is considered to be the basic chromosome number in the genus. It is the most widely distributed of all the species and its range overlaps that of all the others. It also shows the widest ecological as well as morphological diversity. In short, it seems to have all the characteristics necessary to be considered the most primitive living North American species of the genus.

Polyploid populations of *G. sarothrae* show what might possibly have been the first stages in the speciation and differentiation of *G. bracteata* and *G. microcephala*. The polyploid populations of *G. sarothrae*, in addition to having a



double number of chromosomes, show slight deviations in the mean of certain characters. Some of these same deviations are so pronounced in *G. bracteata* and *G. microcephala* that they can be identified readily, which is not true of the 8-chromosome population of *G. sarothrae*. The inconclusive evidence supporting the view that the polyploid populations arose as a result of hybridization between two populations of a lower chromosomal level has been stated above. The same process occurring between populations of *G. microcephala* and *G. bracteata* could account for the polyploids of those two species, or these might be the result of backcrossing with polyploid or diploid *G. sarothrae*. An attempt to investigate this possibility through the study of herbarium specimens of 12- and 8-chromosome *G. bracteata* and 4-chromosome *G. sarothrae* failed to yield any conclusive answer. Nevertheless, there were indications that the 12-chromosome *G. bracteata* might be an allopolyploid between 8-chromosome *G. bracteata* and 4-chromosome *G. sarothrae*. The morphological characters of the 12-chromosome *G. bracteata* seem to be intermediate between the characters of the two other groups. More work, especially of an experimental nature, is needed in this area.

*Gutierrezia serotina* seems to be an extreme morphological variant of *G. sarothrae*. It would be interesting to know whether it is also isolated from it genetically. Cytological information is lacking in the case of *G. grandis*, and no ideas as to its evolution can be advanced.

*Gutierrezia californica* seems to be related to *G. bracteata* and might have been derived from it. On the other hand, *G. californica* is very similar morphologically to the Chilean *G. paniculata*. The fact that *G. californica* grows in such a specialized habitat as serpentine would seem to speak against the idea that *G. californica* was derived directly from *G. paniculata* through long-range dispersal. Also, the fact that a hybrid between *G. californica* and *G. bracteata* was obtained seems to rule out this hypothesis. Nevertheless, more information is needed, especially with regard to *G. paniculata*.

No suggestions on their evolution can be advanced in respect to the annual species. The pappus of *G. glutinosa* is more like that of the other species of the genus, while *G. texana*, in spite of its reduced pappus, has an involucre more



in accordance with the generic type. Xerophytic annuals seem to be specialized life forms within the tribe, which consists mostly of shrubs (Raven, Solbrig, Kyhos, and Snow, 1960). If this is so, it would reaffirm the advanced nature of the genus. It also suggests that section *Hemiachyris* has been derived from section *Gutierrezia*.

In concluding this discussion, it is appropriate to emphasize the importance that the type of distribution has played in the evolution of the genus. In a group like *Gutierrezia*, where we are dealing with a series of populations more or less isolated from each other, the role of the population as the recombination unit is greatly increased. If we consider also the fact that most species are distributed over a wide territory, in which profound environmental differences undoubtedly occur, we can easily understand the range of morphological diversity encountered.

In addition to the influential micro-environmental differences which might account for part of the differences between populations, random genetic drift is thought to be largely responsible for the morphological diversity between populations. This is inferred from the following circumstances: (1) We are dealing with a series of populations separated by relatively large distances. (2) The populations are generally small. (3) The seed-dispersal mechanism is rather inefficient for the family. (4) Once the populations are established, there seems to be little chance for interchange of genetic material. On the other hand, the populations are rather stable in the sense that being composed of perennial plants they do not show the yearly fluctuations in number characteristic of populations of annuals. Nevertheless, field observations indicate that they respond strongly to yearly environmental fluctuations, as measured by the number of seedlings found. Since the ability to produce offspring is in the last analysis the crucial point where selection pressures are expressed, these annual fluctuations in production of seedlings may be as vital to the species and perhaps of the same or a greater degree of importance for the operation of such a process as random genetic drift, as the more impressive fluctuations of populations of spring annuals in the California deserts (Epling, Lewis and Ball, 1960).



## RELATIONSHIPS WITH OTHER GENERA

The phylogenetic relationship of *Gutierrezia* with other genera is still an open question. An exhaustive investigation of most genera of *Astereae* is needed before any conclusive answers can be given. However, it may be appropriate to record some suggestions that have occurred to the author in the course of the present investigation.

*Gutierrezia* was placed by Hoffmann (1897) in subtribe *Solidagineae* because of the homochromous character of the capitula, i.e., both tubular and ligulate flowers are of the same color, usually yellow. In the light of work done in other genera of *Compositae* (Babcock and Cave, 1938) it would seem that such a characteristic may not be of much importance. Nevertheless, the *Solidagineae* have been accepted by most authors, even though relationships with other subtribes, particularly the *Asterineae* are obvious.

The chromosome numbers for at least some species are known in about half of the genera of the subtribe. Nine is the most common number encountered in some of the large genera such as *Solidago*, and sections of *Haplopappus*, as well as in *Acamptopappus*, *Amphipappus*, *Chrysopsis*, and *Heterotheca* (Raven, Solbrig, Kyhos, and Snow, 1960, and literature in same; Solbrig, 1960).

The pappus characteristic of the tribe is one comprising well developed hairs, as in *Haplopappus*. *Gutierrezia* and a few other genera differ in having a scaly or reduced pappus; these genera are *Grindelia*, *Gymnosperma*, and *Xanthocephalum*. *Amphipappus* and *Amphiachyris* are somewhat intermediate, while *Hysterionica* has a pappus with a row of hairs and a row of minute scales. All but *Amphipappus*, *Hysterionica*, and *Grindelia* are closely related (Shinners, 1950; Solbrig, 1960). While *Amphipappus* and *Hysterionica* are not closely allied to the rest of the genera cited above, there are certain characteristics in *Grindelia* (such as chromosome number, type of pappus, and shape of involucre) which seem to indicate affinity with these genera. However, probably no linear relationship exists between any of them, and the striking similarities between some species belonging to different genera are probably due to convergent evolution.

Finally, the heterochromous genus *Greenella* should be mentioned. The morphological similarity of one of its species, *Greenella arizonica* A. Gray, to *Gutierrezia glutinosa*



is unquestionable and some authors have doubted the distinctness of the genus (A. Gray, 1884; Shinnars, 1950). The other two species of *Greenella*, *G. discoidea* and *G. ramulosa*, are sufficiently distinct to establish the validity of the genus. Until more information is available, it is believed that *Greenella arizonica* should be maintained in its present status, since it has enough characters in addition to its heterochromous character to separate it from *Gutierrezia*.

#### TAXONOMIC TREATMENT

***Gutierrezia* Lag. Nov. Gen. et Spec. 30, 1816**

*Brachyris* Nutt. Gen. 2: 163, 1818.

*Brachyachyris* Spreng. Syst. 3: 574, 1825.

*Hemiachyris* DC. Prodr. 5: 313, 1836.

*Odontocarpa* DC. Prodr. 5: 71, 1836.

Suffruticose, erect, glabrous to tomentose, perennials or stout annuals. Leaves petiolate, alternate, subcoriaceous, linear-lanceolate, entire, narrow. Heads in corymbose or paniculate inflorescences, in clusters or solitary at the end of branchlets or solitary in the axils of leaves, on long to very short peduncles. Heads turbinate to campanulate, the involucre bracts in two to many rows, imbricated, with green and swollen tips. Flowers yellow, the ligules not more than  $1\frac{1}{2}$  times the involucre; tubular flowers campanulate with very short tube and a narrow throat with 5 small triangular lobes; stamens 5; styles of tubular flowers with long branches very much exerted at maturity and long stigmatic hairs in the upper part and stigmatic papillae in the lower part of the stigmatic branches; styles of the ligulate flowers only papillate; pappus of short to medium-long squamellae, shorter or absent in the ligulate flowers; achenes turbinate, slightly flattened, tomentose, with hairs arranged in loose rows.

Type-species, *Gutierrezia linearifolia* Lag. (No specimens identified by Lagasca have been found)

#### KEY TO THE SPECIES

- A. Plants perennial; involucre turbinate except in No. 1; flowers 20 or fewer per head ..... Section *Gutierrezia*.
- B. Heads about 10 mm. long, solitary or in small clusters at ends of branches; leaves broad, 5-6 mm. wide ..... 6. *G. grandis*.
- B. Heads less than 10 mm. long, or if longer the leaves not more than 3-4 mm. wide
- C. Involucre campanulate; heads numerous, 3-6 mm. high, 3-5 mm. broad, solitary at the ends of branchlets; plants not more than 50 cm. high ..... 5. *G. serotina*.
- C. Involucre turbinate; heads in clusters at ends of branchlets or, if solitary, more than 6 mm. high.
- D. Heads with only 2 or 3 flowers; involucre very narrow; achenes of disk flowers aborted ..... 4. *G. microcephala*.



- D. Heads with more than 4 flowers; involucre turbinate; achenes of disk flowers fertile.
- E. Heads clustered at ends of branchlets; flowers 5 to 10; involucre narrow, less than 5 mm. wide .... 3. *G. sarothrae*.
- E. Heads mostly solitary at ends of branchlets; flowers usually more than 10; involucre more than 5 mm. wide.
- F. Inflorescence loosely corymbose; heads 6-10 mm. high, 4-6 mm. wide; open, little-branched shrub ..... 1. *G. californica*.
- F. Inflorescence paniculate; heads 4-7 mm. high 2-5 mm. wide; globose, much-branched shrub .... 2. *G. bracteata*.
- A. Plants annual; involucre turbinate-campanulate to campanulate; flowers more than 20 per head ..... Section *Hemiachyris*.
- G. Involucre turbinate-campanulate; heads long-pedunculate along length of branches; pappus of ligulate flowers absent or reduced; tubular flowers 10-20 ..... 7. *G. texana*.
- G. Involucre campanulate; heads at ends of branches; pappus present in both ligulate and tubular flowers; tubular flowers 20-40 ..... 8. *G. glutinosa*.

1. *Gutierrezia californica* (DC.) T. & G. Fl. N. Amer. 2: 193, 1842

*Brachyris californica* DC. Prodr. 5: 313, 1836.

Perennial shrubs or bushes. Stems semi-woody, glabrous or sparsely tomentulose, rugose or irregularly striate, mostly simple or few-branched, arising from a short, woody base. Leaves arranged singly along the branches, linear, 5 to 35 mm. long, 1-3 mm. broad, the surface punctate, hairy, entire with ciliate margins. Heads solitary or sometimes in groups of 2-3 at ends of branches, arranged in loose-corymbose inflorescences. Peduncles 5 mm. or more long. The involucre 6 to 10 mm. high, 4-6 mm. broad, turbinate to campanulate, the bracts ca. 20, arranged in three overlapping series, lanceolate to ovate, acute or obtuse, some somewhat carinate, the outer shorter and narrower than the inner, coriaceous or sub-coriaceous, usually with a green, somewhat swollen tip, the inner bracts with a membranaceous border, glabrous. Receptacle flat or somewhat convex, alveolate. Ligulate flowers about 9, the ligules narrowly lanceolate, 3-4 mm. long, ca. 1 mm. broad; tubular flowers about 11, 3-4 mm. high, glabrous, the throat oblong, slightly larger than the tube. Pappus of 6 to 10 narrow scales, as long as the achene in tubular flowers, only a third in the ligulate ones. Styles of tubular flowers with well developed stigmatic hairs and a short border of stigmatic papillae at the base of the stigmatic branch on each side; the ligulate flowers with only a border of stigmatic papillae along the whole stigmatic branch. Achenes terete, tapering at base, tomentulose, the hairs slightly larger in achenes of ligulate flowers.

TYPE-LOCALITY. "In California", Douglas.

DISTRIBUTION. Known only from three populations in the area of San Francisco Bay, California, growing on serpentine soil (fig. 3).

REPRESENTATIVE SPECIMENS. California. Angel Island, 1957, Solbrig 2428 (UC); Oakland, Redwood Park, 1956 Solbrig 2154 (UC); Marin County, Point Bonita, 19-VI-1892, Michener and Bioletti 1096 (UC);



Alameda County, Oakland Hills, beyond Paroltas, 10-XI-1869, A. Kellogg and W. G. W. Harford 387 (US, MO); Hills near Oakland, 1-VII-1889, E. R. Drew (UC); Alameda County, dry summit of Redwood Ridge, 21-IX-1931, Constance 382 (UC); Oakland Hills, VII-1888, E. L.

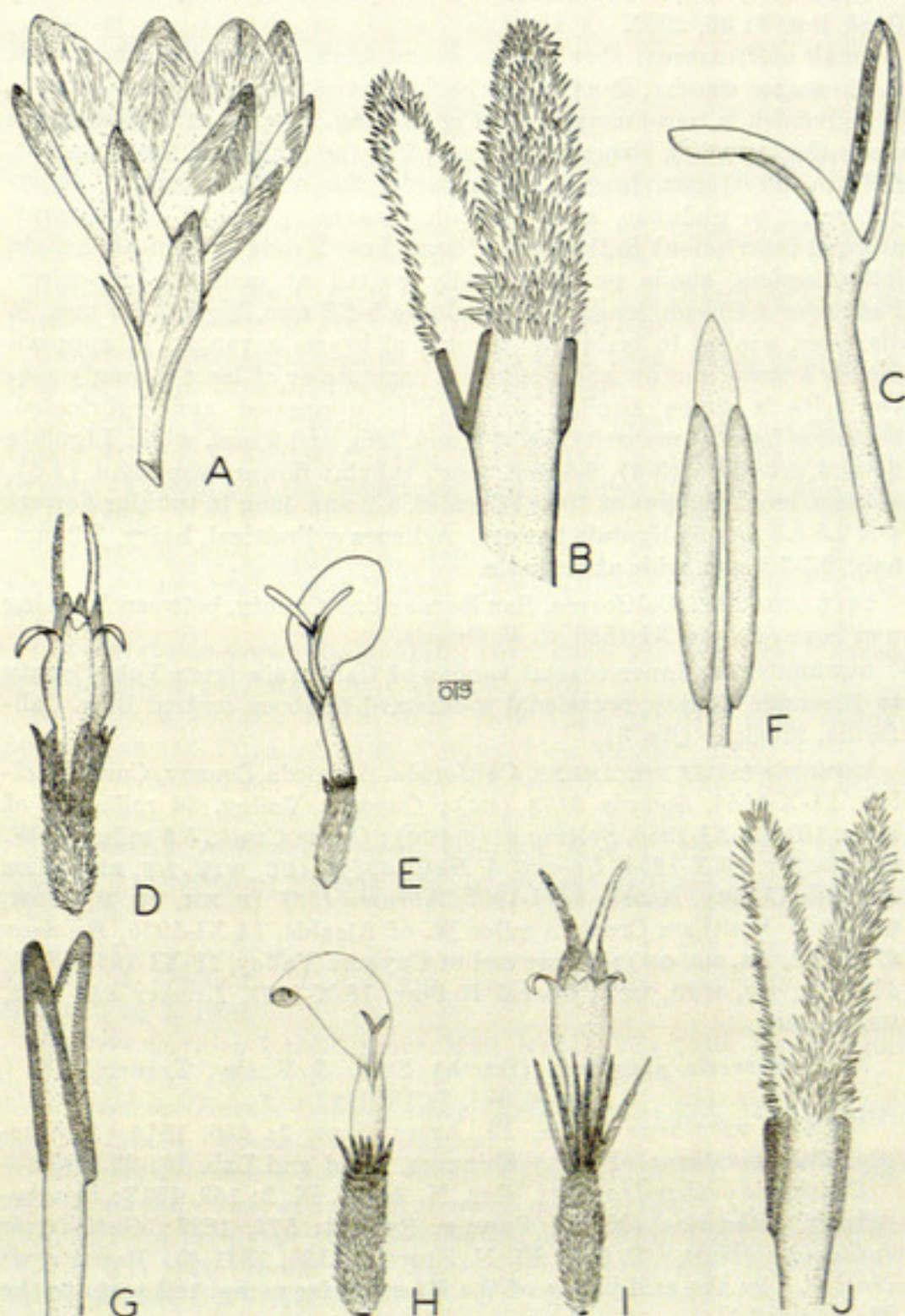


FIG. 15. *Gutierrezia californica* A. Involucre  $\times 6$ ; B. Style of tubular flower  $\times 20$ ; Style of ligulate flower  $\times 20$ ; D. Tubular flower  $\times 6$ ; E. Ligulate flower  $\times 6$ ; F. Stamen  $\times 20$ ; *Gutierrezia bracteata* G. Style of ligulate flower  $\times 20$ ; H. Ligulate flower  $\times 6$ ; I. Tubular flower  $\times 10$ ; J. Style of tubular flower  $\times 20$ .



*Greene* (US); San Francisco, *Wilkes* (US); Near Oakland, *H. G. Bloomer* (NY).

2. *Gutierrezia bracteata* Abrams, Bull. Torr. Club 34: 265, 1907

*Gutierrezia californica* var. *bracteata* (Abrams) Hall, Univ. Calif. Publ. Bot. 3: 36, 1907.

Small suffrutescent shrub up to 50 cm. high, paniculately branched, the branches slender, flexible, the bark light to dark gray, the branchlets greenish, a root-crown present or lacking. Leaves arranged singly along the branches, somewhat clustered at the middle of the branches, filiform, 30-50 mm. long 1-2 mm. wide, the surface smooth, short-pubescent to glabrous, entire, smaller leaves ("bracts" in Abrams' original description) in the axils of branches. Heads in open-paniculate inflorescences, single or occasionally paired at ends of branchlets. Peduncles 5-50 mm. long. The involucre 5-6.5 mm. high, 2-3.5 mm. in diameter, conical to turbinate, involucre bracts arranged in approximately 3 rows, narrow and elongated, carinate or at least strongly convex with a green swollen tip, tightly appressed and imbricated, becoming loose at maturity, up to 4 mm. long and 2 mm. wide. Ligulate flowers usually 5 (3-6), 6-8 mm. long; tubular flowers usually 4 (2-6), 4-6 mm. long. Pappus of 10 to 12 scales, 1-2 mm. long in tubular flowers and 0.5-1.5 mm. in ligulate flowers. Achenes cylindrical, hairy, 1-2 mm. long, 0.5-1.0 mm. wide at anthesis.

TYPE LOCALITY. California, San Bernardino County, between Banning and Seven Palms, XI-1889, *C. R. Orcutt*.

DISTRIBUTION. Inner coastal ranges of California from Yolo County to Riverside County, occasional southward to about central Baja California, Mexico. (fig. 3)

REPRESENTATIVE SPECIMENS. **California.** Alameda County, Corral Hollow, 21-X-1956, *Solbrig 2159* (UC); Cuyama Valley, 54 miles E. of Hwy. 101, 22-XI-1956, *Solbrig 2166* (UC); Cache Creek, 5.8 miles N. W. of Rumsey, 19-X-1954, *Everett & Balls 20366* (UC, WTU, NY, RM); Los Angeles County, Azusa, 5-VI-1902, *Abrams 1577* (F, RM, UC, MO, POM, GH, NY); Waltham Creek, 5 miles W. of Alcalde, 14-XI-1936, *Belshaw 2735* (UC, WS, MO, GH); Upper end of Cuyama Valley, 18-XI-1932, *Wolf 4417* (A, WS, WTU, UC); Corral Hollow, 18-X-1861, *Brewer 848* (WS, US, UC, MO).

3. *Gutierrezia sarothrae* (Pursh) Britt. & Rusby, Trans. N. Y. Acad. Sci. 7: 10, 1887

*Solidago sarothrae* Pursh, Fl. Amer. Sept. 2: 540, 1814; *Xanthocephalum sarothrae* (Pursh) Shinnars, Field and Lab. 18: 29, 1950.

*Brachyris euthamiae* Nutt. Gen. N. Amer. Pl. 2: 163, 1818; *Brachyachyris euthamiae* (Nutt.) Spreng. Syst. 3: 574, 1825; *Gutierrezia euthamiae* (Nutt.) T. & G. Fl. N. Amer. 2: 193, 1841-43. Based upon Nuttall, "On the arid plains of the Missouri from the Arikarees to the Mountains".

*Brachyris divaricata* Nutt. Trans. Amer. Phil. Soc. 7: 313, 1841; *Gutierrezia divaricata* (Nutt.) T. & G. Fl. N. Amer. 2: 194, 1841-43. Based upon Nuttall, "On the Platte near the Rocky Mountains".



*Gutierrezia Haenkei* Sch. Bip. Flora 38: 115, 1855. Based upon Haenke, "Mexico, Acapulco".

*Gutierrezia juncea* Greene, Pittonia 4: 56, 1899. Based upon Skehan, "near Gray, New Mexico", VIII-1898.

*Gutierrezia diversifolia* Greene, Pittonia 4: 53, 1899. Based upon Watson 551, "Laramie, Wyoming".

*Gutierrezia divergens* Greene, Pittonia 4: 58, 1899. Based upon Parish, "San Bernardino Mesas" [California].

*Gutierrezia lepidota* Greene, Pittonia 4: 57, 1899. Based upon Greene, "Plains about Grand Junction, Colorado", 27-VIII-1899.

*Gutierrezia fasciculata* Greene, Pittonia 4: 56, 1899. Based upon Greene, "Grand Junction, Colorado", 26-VIII-1896.

*Gutierrezia filifolia* Greene, Pittonia 4: 55, 1899. Based upon E. O. Wooton, "White Mts. of New Mexico", 24-VIII-1897.

*Gutierrezia longifolia* Greene, Pittonia 4: 54, 1899. Based upon E. O. Wooton, "White Mts. of New Mexico", VIII-1897.

*Gutierrezia tenuis* Greene, Pittonia 4: 55, 1899; *Xanthocephalum tenuis* (Greene) Shinnars, Field & Lab. 18: 29, 1950. Based upon Greene, "Foothills of the mountains back of Silver City, New Mexico", 30-IX-1880.

*Gutierrezia myriocephala* A. Nels. Bot. Gaz. 37: 264, 1904. Based upon A. Nelson 8645, "near Badger, Laramie County, Wyoming", 3-IX-1901.

*Gutierrezia scoparia* Rydb. Bull. Torr. Club 31: 647, 1904. Based upon Clements 16, "Manitou, Colorado", 1901.

*Gutierrezia linearis* Rydb. Bull. Torr. Club 31: 647, 1904. Based upon Earle 474, "Gray, Lincoln County, New Mexico", 1900.

*Gutierrezia laricina* Greene, Rep. Sp. Nov. 7: 195, 1909. Based upon C. R. Orcutt, "Colorado Desert in California", X-1889.

*Gutierrezia Goldmanii* Greene, Rep. Sp. Nov. 7: 195, 1909. Based upon E. A. Goldman, "Florida Mts., in extreme southern New Mexico", 8-IX-1908.

*Gutierrezia furfuracea* Greene, Rep. Sp. Nov. 7: 195, 1909. Based upon E. A. Goldman, "Cactus flat, upper Rio Gila, southeastern New Mexico", 13-X-1908.

*Gutierrezia fulva* Lunell, Amer. Midl. Nat. 1: 235, 1910. Based upon J. Lunell, "Des Lacs, Ward County" [North Dakota].

*Gutierrezia Greenei* Lunell, Amer. Midl. Nat. 1: 233, 1910. Based upon J. Lunell, "Leeds, North Dakota".

*Gutierrezia ionensis* Lunell, Amer. Midl. Nat. 2: 194, 1911. Based upon J. Lunell, "east of Ione, Morrow County, Oregon", 16-VII-1903.

*Gutierrezia sarothrae* var. *pauciflora* Eastw. Proc. Calif. Acad. Sci. IV, 18: 480, 1929. Based upon Mason 1971, "Turtle Bay, Lower California, Mexico", 2-VI-1925.

*Gutierrezia globosa* A. Nels. Amer. Jour. Bot. 23: 265, 1936. Based upon A. Nelson 11,739, "Between San Ysidro and Bernalillo, New Mexico", 29-VIII-1931.

*Gutierrezia corymbosa* A. Nels. Amer. Jour. Bot. 23: 265, 1936. Based



upon A. Nelson, "Ten miles east of Santa Fe, New Mexico", 30-VIII-1931.

Shrubs, 15-90 cm. high, profusely branched prevalently from the base, the secondary branching variable, usually slight and concentrated in the upper part, from shallow, fasciculate roots, or one central taproot. Root-crown woody, up to 7.5 cm. thick. Leaves of two types, the primary scattered along the stems, 2-7 cm. long, up to 3 mm. wide, the secondary fascicled in axils of primary leaves or branchlets, up to 2 cm. long and 1-2 mm. wide, linear-lanceolate, entire, glabrous to tomentulose, often with regular amounts of resin on both surfaces. Heads in corymbose inflorescences, usually in fascicles of 3-10 at the ends of branchlets, sometimes single. Involucre 3-10 mm. long, 2-5 mm. wide, turbinate, involucre bracts narrow, acute, with a green and swollen tip, imbricated, usually appressed, forming a compact capitulum, in several rows and often covered with resin. Ligulate flowers usually 4 or 5 (3-7), 2-5 mm. long; tubular flowers 3 or 4 (2-6), 2-3 mm. long; pappus about as long as achene, of 8-10 scales, in ligulate flowers 1/2 - 1/3 shorter. Achenes terete, 1-2 mm. long, hairy.

TYPE-LOCALITY. "On the plains of the Missouri", *Lewis*.

DISTRIBUTION. Between the Cascades-Sierra Nevada and the Rocky Mountains from southern Canada to northern and central Mexico, eastern foothills of the Rocky Mountains and infrequent on the Great Plains. Also in southern California, and Baja California, Mexico (fig. 2).

REPRESENTATIVE SPECIMENS. **Canada.** Along Highway from Calgary to Waterton Lakes, near Pincho, 31-VIII-1938, *Nelson & Nelson 3122* (RM, MO, UC). **Mexico. Chihuahua.** Rocky hills near Chihuahua, 26-IX-1885, *Pringle 337* (PH, GH, US, WTU). **Baja California.** Between Ojos Negros and Neji Rancho, 16-IX-1929, *Wiggins & Gillespie 4155* (F, MO, NY, A, GH, US). **United States. Arizona.** 12.6 miles E. of Ash Fork, 26-VIII-1958, *Solbrig 2801* (UC). 5 miles N. of Payson, 26-VIII-1958, *Solbrig 2794* (UC). **California.** Dry Ridges, Bear Valley, 7-VIII-1902, *Abrams 2916* (LA, UC, NY, WTU, PH, US, F). Ramona, X-1903, *Brandegge* (GH, US, MO, RM, NY). 2 miles W. of Temecula, 18-VIII-1958, *Solbrig 2758* (UC). **Colorado.** Denver, 4-IX-1920, *Clokey 3880* (US, GH, NY, UC, WTU, MO, F, RM). Greenhorn, 2-IX-1921, *Clokey 4320* (WS, MO, WTU, RM, UC, US). Buena Vista, 1-2-VIII-1919, *Eggleston 15348* (GH, NY, MO, F). **Idaho.** Hansen, 23-VI-1958, *Solbrig 2911* (UC). McCammon, 4-VIII-1911, *Nelson & Macbride 1583* (US, RM, GH, NY, F, UC). **Kansas.** 2 miles E. Meade, 7-X-1936, *Horr 574* (SMU, UC, RM, US, WS). **Nevada.** Kyle Canyon, Charleston Mountains, 9-VIII-1937, *Clokey 7737* (MO, SMU, UC, NY, RM, WTU, WS). Kyle Canyon Fan, Charleston Mountains, 9-VIII-1938, *Clokey 8155* (MO, NY, F, UC, RM, WTU, WS). **New Mexico.** Sierra Blanca, 18-VIII-1904, *Metcalf 1230* (UNM, MO, NY, UC). Pyramid Peak, 16-VIII-1930, *Fosberg S3775* (PH, MO, UC, US). **Oklahoma.** Altus, 24-X-1936, *Hopkins & Van Valkenburgh 695* (SMU, UC, US, RM, MO, WTU, WS). **Texas.** Randall County, Palo Duro State Park, 20-X-1945, *Cory 50407* (UC, SMU, US). Culberson County, north of Van Horn, 10-X-1944, *Waterfall 5780* (GH, MO, SMU). **Utah.** Western Bear's Ear, Elk Moun-



tains, 2-VIII-1911, *Rydberg & Garrett 9370* (RM, US, UC, NY). Washington. Asotin County, north of Rogersburg, 7-IX-1936, *Constance 1813* (GH, MO, US, WTU, WS). Wyoming. Laramie, 12-IX-1899, *Nelson & Nelson 6858* (RM, NY, GH, MO).

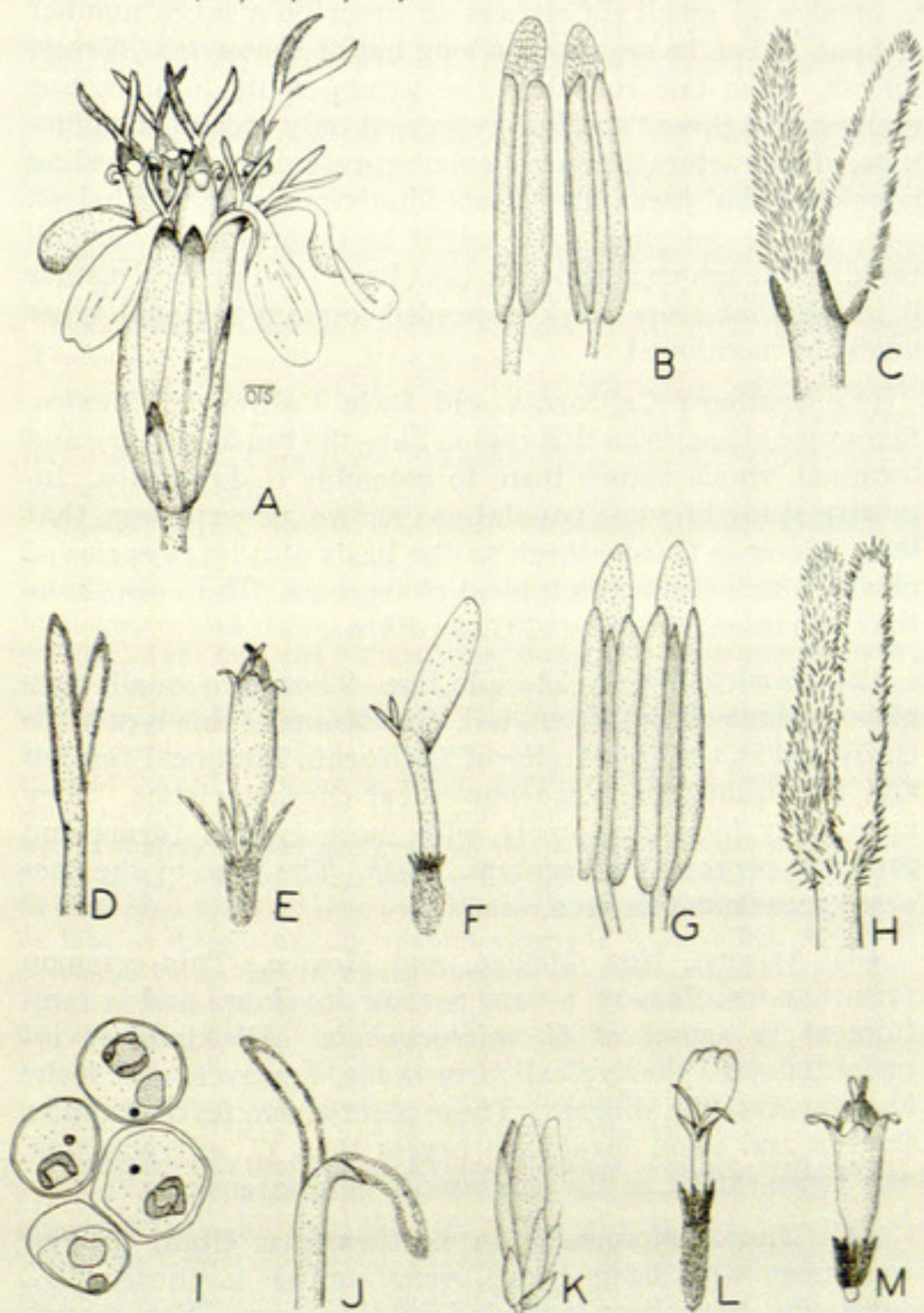


FIG. 16. *Gutierrezia sarothrae* A. Flowering head  $\times 16$ ; B. Stamens  $\times 20$ ; C. Style of tubular flower  $\times 20$ ; D. Style of ligulate flower  $\times 20$ ; E. Tubular flower  $\times 6$ ; F. Ligulate flower  $\times 6$ ; *Gutierrezia microcephala*. G. Stamens  $\times 20$ ; H. Style of tubular flower  $\times 20$ ; I. Aborted pollen grains  $\times 1000$ ; J. Style of ligulate flower  $\times 20$ ; K. Involucre  $\times 10$ ; L. Ligulate flower  $\times 10$ ; M. Tubular flower  $\times 10$ .



This species is the most abundant, the most widespread, and the most variable. This variability, associated with a disjunct type of distribution, has led those botanists prone to emphasize small differences to describe a large number of taxa, as can be seen by the long list of synonyms. Nevertheless, when one considers the group in its totality, one realizes that these "species" represent only special combinations of characters, often not even representing one breeding population, but just a few isolated individuals. Nevertheless, some of the described taxa might be deserving of varietal rank. Although no subspecific taxa have been proposed since it is felt that more work is needed, certain regional types might be mentioned.

(1) Southern California and Baja California, Mexico. Some specimens from this region have the heads solitary and terminal, which causes them to resemble *G. bracteata*. Intensive study of some populations shows, nevertheless, that they belong to *G. sarothrae* on the basis of a large series of plants which show the typical characters. They also have the chromosome number of *G. sarothrae*.

(2) North of Utah-Colorado line. These are small, very globose plants, some 20 cm. tall. Specimens of this type were cultivated at the University of California Botanical Garden and maintained their morphological characteristics. They apparently hybridize freely with more typical forms and probably represent an ecotypic form. The type of the species comes from this area.

(3) Arizona, New Mexico, and Mexico. This common form has few flowers, a very narrow involucre and is reminiscent in aspect of *G. microcephala*. All kinds of intermediates to the typical form occur, however, and make an interpretation difficult. These plants have fertile tubular flowers and more involucre bracts than *G. microcephala*, and hence can be easily separated from that species.

(4) Uintah Mountains in northeastern Utah. A few specimens with large heads, very similar to those of *G. bracteata*, have been collected in this area. Not enough information is available on this material, and since there are also intermediates, a decision will have to be made when more is known about the *Gutierrezias* in this area.



4. *Gutierrezia microcephala* (DC.) A. Gray, Pl. Fendl. 74, footnote 18, 1849

*Brachyris microcephala* DC. Prodr. 5: 313, 1836; *Gutierrezia euthamiae* T. & G. var. *microcephala* (DC.) A. Gray, Syn. Fl. N. Amer. 1 (2): 115, 1884; *G. sarothrae* var. *microcephala* (DC.) Benson, Amer. Jour. Bot. 30: 631, 1943; *Xanthocephalum microcephalum* (DC.) Shinnery, Field & Lab. 18: 29, 1950.

*Xanthocephalum lucidum* Greene, Pittonia 2: 282, 1892; *Gutierrezia lucida* (Greene) Greene, Fl. Francis. pt. 4: 361, 1897. Based upon a specimen from "the region of the Mohave Desert and southward" [California], no collector indicated.

*Gutierrezia linoides* Greene, Leaf. Bot. Obs. 2: 22, 1909. Based upon J. C. Blumer, "Limestone of the Chiricahui Mts." [Arizona], 1907.

*Gutierrezia glomerella* Greene, Pittonia 4: 54, 1916. Based upon Wootton 449 "Organ Mts., New Mexico".

*Gutierrezia digyna* Blake, Contr. U. S. Nat. Herb. 22: 591, 1924; *Xanthocephalum digynum* (Blake) Shinnery, Field & Lab. 18: 29, 1950. Based upon V. L. Cory 26,335, "12 miles east of Marfa, Presidio County, Texas", 19-X-1937.

Globose shrub, 30-100 cm. high. Branches slender, grayish to yellowish-green, about 1 mm. in diameter, glabrous, slightly fistulate, arising from a well developed root-crown or short stem, up to 1-2 cm. in diameter, bark rugose, gray. Leaves narrow-lanceolate of two types, cauline 2-5 cm. long and 2-4 mm. wide, axillary leaves shorter and much narrower, often borne in fascicles, lanceolate, entire, often resinous, or either type absent, the axillary in young plants and the cauline in older specimens or under special environmental conditions. Heads in glomerules at the end of branches, sessile. Involucre 3-4 mm. long, 1-1.5 mm. wide, narrowly turbinate, involucral bracts less than 10, lanceolate, with a slightly thicker and greenish tip. Ligulate flowers usually 1 or 2 (up to 4), 3-4 mm. long; tubular flowers 1-3, 2-3 mm. long. Pappus of few scales up to 2-3 mm. long, shorter in the ligulate flowers. Styles of tubular flowers usually without stigmatic papillae but with well developed hairs, that of ligulate flowers only with stigmatic papillae. Achenes of tubular flowers aborted, those of the ligulate flowers fertile, 2-3 mm. long, hairy.

TYPE-LOCALITY. "In Mexico prope locum dictum Saltillo", Berlandier.

DISTRIBUTION. Southwestern United States from western Texas to California, and northern and central Mexico (fig. 5).

REPRESENTATIVE SPECIMENS. Mexico. Coahuila. Saltillo, 1898, Palmer 143 (UC, F, MO). United States. Arizona. Douglas, 23-VIII-1958, Solbrig 2789 (UC). 3.5 miles S. of St. David, 23-VIII-1958, Solbrig 2790 (UC). Ft. Lowell, 20-X-1903, Thornber 93 (US, UC). California. San Bernardino and Riverside County line, road from Yucca Valley to San Bernardino, 27-VIII-1958, Solbrig 2807 (UC). Wyman Canyon, White Mountains, 29-VI-1931, Duran 3151 (UC, F, MO, US, GH). Colorado. Naturita, 11-VIII-1914, Payson 595 (GH, MO, WS, F). Deer Ann, 25-VIII-1901, Baker 915 (MO, US, UC, GH). Nevada. Kyle Canyon, Charleston Mountains, 27-VI-1936, Clokey 7413 (GH, UC, PH, SMU, US, MO, WS,



WTU, F). Texas. Vicinity of El Paso, 8-X-1913, *Rose & Fitch 17847* (US, MO). Utah. Armstrong and White Canyons, near the Natural Bridges, 4-6-VIII-1911, *Rydberg & Garrett 9425* (US, UC, NY).

5. *Gutierrezia serotina* Greene, *Pittonia* 4: 57, 1899

*Gutierrezia polyantha* A. Nels. Amer. Jour. Bot. 25: 117, 1938. Based upon *Nelson & Nelson 1638*, "a few miles north of Tucson, Arizona", 26-IV-1935.

Small hemispheric shrub, 10-40 cm. high. Branches leafy to the top, green or lightly gray, slightly striate, glabrous or nearly so, with very few or no side branches, abundant from root-crown, 2-4 cm. in diameter. Root a slender taproot with abundant secondary roots. Leaves single along the branches or in fascicles at axils of single leaves in lower third of branches, linear, 1-2 cm. long and up to 1 mm. wide, glabrous. Heads solitary or in loose glomerules at the tip of branches, arranged in corymbose inflorescences, sessile or short-pedunculate. Involucre 2-4 mm. high, 2-3 mm. wide, hemispheric to turbinate-campanulate, involucre bracts broad, almost as wide as long, obtuse, glabrous, margin membranaceous, with a slightly thickened, greenish or brown tip, arranged in 2 or 3 loose series. Ligulate flowers about 7 (4-8), 4-5 mm. long; tubular flowers about 8 (5-10), 3-4 mm. long, salverform. Pappus of 10-12 lanceolate scales, 1.4 mm. (1-2) long in the tubular flowers, 1 mm. (0.5-1.5) long in the ligulate ones. Achenes of ligulate and tubular flowers approximately the same size, 1.5 mm. long; 0.5 mm. wide, hairy, with the trichomes arranged in parallel rows.

TYPE-LOCALITY. "Plains about Tucson in southern Arizona", 3-III-1892, *Toumey*.

DISTRIBUTION. Plains about Tucson, occasional southward into Mexico. (fig. 4)

REPRESENTATIVE SPECIMENS. Arizona. Tanque Verde Ranch, 17 miles E. of Tucson, 22-VIII-1958, *Solbrig 2777* (UC). 7.9 miles E. of Oracle Junction, 23-VIII-1958, *Solbrig 2791* (UC). Oracle, Spring 1941, *H. S. Gentry 6111* (UC). Martinez's Ranch, 16 miles E. of Tucson, 8-IV-1940, *L. J. Brass 14305* (GH, NY, UC). Redington Pass, Pima County, 28-IV-1938, *R. C. Foster 617* (GH, UC). Near Willcox, 25-V-1928, *R. H. Peebles 5436* (US). Pima County, Tucson to Redington, 27-V-1935, *R. H. Peebles 11315* (US). Mesas near Camp Lowell, 13-IV-1881, *C. G. Pringle* (F, PH).

6. *Gutierrezia grandis* Blake, Contr. U. S. Nat. Herb. 22:591, 1924  
*Xanthocephalum grande* (Blake) Shinnars, Field & Lab. 18: 28, 1950.

Large shrub, 30-60 cm. high. Branches few, not more than 2-4 mm. wide, greenish, striate, arising from a root-crown or stem a few cm. above ground, stem short, slender, grayish, glabrous. Root a strong taproot. Leaves linear-lanceolate, large and wide, 2-6 cm. long, 2-6 mm. wide, margin entire, surface smooth, glabrous or somewhat hairy, multinerved, the central nerve and to a certain extent the lateral ones prominent. Heads few, solitary at the ends of branchlets or in glomerules of 3-5, arranged in loose corymbose inflorescences, sessile or pedunculate, peduncle 1-10 mm. long. Involucre 5-6 mm. high, 3-4 mm.



wide, turbinate, appressed, involucre bracts elliptical, obtuse, in several series, with a thickened green tip and thicker median region. Ligulate flowers 5-9, 4-6 mm. long; tubular flowers 3-7, about 4-5 mm. high. Pappus of about 10 scales up to 1 mm. in length in the tubular flowers, somewhat shorter in the ligulate ones. Achenes about 1-2 mm. long, hairy.

TYPE-LOCALITY. "Head of Cañon de las Baretas, in the Sierra Madre, near Icamole, Nuevo León, Mexico", 3-II-1907, *W. E. Safford 1257*.

DISTRIBUTION. This species is known only from a few localities in central Mexico. (fig. 4).

REPRESENTATIVE SPECIMENS. Mexico. Nuevo León. Icamole, Head of Cañon de las Barretas, 3-II-1907, *W. E. Safford 1257* (US). Coahuila. Sierra de Parras, X-1910, *C. A. Purpus* (MO, NY, F, US, UC, GH). San Luis Potosí. Sierra de Catorce, no date, *F. Rodriguez* (F). Monte Real de Catorce, 1827, *Berlandier 1360* (GH). Potrero, 8-IX-1939, *F. Shreve* (UC, GH).

**7. *Gutierrezia texana* (DC.) T. & G. Fl. N. Amer. 2: 194, 1842**

*Hemiachyris texana* DC. Prodr. 5: 314, 1836.

Robust annual, 20-80 cm. high. Stems one to several, subdivided or not, 2-4 mm. diameter, grayish-green, slightly ribbed, glabrous, branchlets grayish-green, fissured, glabrous or very slightly pubescent, not more than 1 mm. in thickness, arising from base. Root a slender taproot not more than 10 cm. long. Leaves lanceolate, up to 5 cm. long and 5 mm. wide, acute, glabrous, entire, surface rugose or smooth, multinerved with the middle vein prominent on both surfaces, the lateral longitudinal ones less so. Heads at the ends of branchlets and axils of leaves and branchlets. Peduncles 2-3 mm. long. Involucres 3-4 mm. high, 3-6 mm. broad, turbinate-campanulate, involucre bracts numerous, about 3 mm. long and 1.5-2 mm. wide, in about three irregular series, elliptical, margins membranaceous, tips green, midrib region darker-colored. Ligulate flowers 10-15, tube 1-2 mm. long and ligule 2-3 mm. long and 2 mm. wide; tubular flowers about 12-18, corolla campanulate, throat very short, about 0.5 mm. long, tube 1.5 mm. long. Pappus of about 10-12 scales, in the tubular flowers not longer than 1.2 mm., in the ligulate ones reduced to a crown of minute setae about 0.1 mm. long. Styles elongated with well developed hairs and papillae, stigma branches long, up to 1 mm. in the tubular flowers, with papillae only and the stigma branches shorter in the ligulate flowers. Achenes of both ligulate and tubular flowers developed, 1 mm. long, 0.5 mm. wide at anthesis, growing to twice that size at maturity in some cases.

TYPE-LOCALITY. "Mexici prov. Texas", *Berlandier 1763, 1765*.

DISTRIBUTION. From southern Oklahoma to San Luis Potosí, Mexico, chiefly in central and western Texas (fig. 5).

REPRESENTATIVE SPECIMENS. Illinois. East St. Louis, 1897, *Letterman* (MO, PH, NY, US). Texas. Near Dallas, VII-VIII, *Reverchon 1297* (NY, MO, US, F, GH). Comanche Springs, 1849-1851, *Lindheimer 921* (MO, F, US, UC). Dallas, 27-X-1900, *Bush 1624* (NY, GH). Fort Worth, 30-IX-1902, *Tracy 8159* (GH, F, NY, MO). Austin, 20-X-1937, *Tharp 283* (PH, WS, UC).



8. *Gutierrezia glutinosa* (Schauer) Sch. Bip. Flora 38: 115, 1855

*Hemiachyris glutinosa* Schauer, Linnaea 19: 724, 1847.

*Gutierrezia sphaerocephala* A. Gray, Pl. Fendl. 73, 1849; *Xanthocephalum sphaerocephalum* (A. Gray) Shinnars, Field & Lab. 18: 29, 1950. Based upon Fendler 527, "Low prairie, from the upper to the middle Spring of the Cimarron, VIII."

*Gutierrezia eriocarpa* A. Gray, Pl. Wright. 1: 94, 1852; *Xanthocephalum sphaerocephalum* var. *eriocarpum* (A. Gray) Shinnars, Field and Lab. 18: 29, 1950. Based upon Wright 280, "Prairies along the Rio Grande, Texas".

*Gutierrezia Coulteri* Hemsl. Diagn. Pl. Nov. 33, 1879. Based upon Coulter 315, "Mexico, Zimapan".

*Gutierrezia Berlandieri* A. Gray, Proc. Amer. Acad. Arts & Sci. 15: 31, 1880. Based upon Berlandier 1298, "Near San Luis Potosí" [Mexico].

Stout annual 2-60 cm. high. Stem branching from the base or at about 1/3 its height from the ground, gray or greenish-gray, 2-3 mm. in diameter, branchlets slender, light green, fistulose. Root a short taproot. Leaves lanceolate, 2-3 cm. long, 2-3 mm. wide, entire, surface smooth to rugose, glabrous. Heads at the end of branchlets, not numerous, sometimes less than 10, pedicellate. Involucre campanulate, 3-5 mm. high, 4-8 mm. wide, involucre bracts elliptical, arranged in 2 poorly defined series, acute, with membranaceous margins, tip and mid-rib section slightly darker and thicker. Ligulate flowers 10-20, corollas 3-4 mm. long; tubular flowers 20-40, corollas slightly campanulate 2-3 mm. long. Pappus variable in length, less than 1/2 mm. to as long as the achene, shorter in the ligulate flowers. Achenes about 1.5 mm. at anthesis, up to 2.5 mm. at maturity, turbinate, hairy, with the hairs in rows.

TYPE-LOCALITY. "Crescit in terris mexicanis", Aschenbach 291.

DISTRIBUTION. Central and northwestern Mexico to southwestern Texas and southern New Mexico (fig. 4).

REPRESENTATIVE SPECIMENS. Mexico. Coahuila. 2 miles NW of Frontera, 24-26-VIII-1938, Johnston 7182 (GH, US). Chihuahua. Plains near Chihuahua, 11-X-1885, Pringle 622 (WTU, F, NY). United States. New Mexico. 20 miles S. of Roswell, 8-IX-1900, Earle & Earle 533 (NY). Near Las Cruces, 11-VI-1897, Wootton 130 (NY, GH, MO). Texas. Ft. Quitman levee road, 18-VI-1943, Waterfall 4596 (MO, GH). Chisos Mountains, 15-18-VII-1921, Ferris & Duncan 2748 (NY).

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