

CHROMOSOME COUNTS OF COMPOSITAE FROM THE UNITED STATES, MEXICO, AND GUATEMALA¹

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Chromosome numbers can be extremely useful in systematic studies, particularly for helping to reveal evolutionary relationships. For the past fifteen years numerous chromosome reports from plants have been published, especially in the Compositae, and these counts have been compiled in several major sources (Darlington & Wylie, 1955; Cave, 1958-65; Ornduff, 1967-69; Fedorov, 1969; Moore, 1970-72). However, a rapid glance through these references indicates not only that many species never have been counted, but also that many taxa are known only from a single plant in one population. In view of the common occurrence of euploid and aneuploid races in plants as illustrated by several detailed investigations (e.g., Lewis, 1962, 1970; Stuessy, 1971a), it is desirable to have several to many counts from each species before accurate judgments can be made regarding evolutionary relationships (Stuessy, 1971b; Kovanda, 1972; Strother, 1972). The present paper helps to remedy these deficiencies in the Compositae by: (1) reporting first chromosome counts for several genera, species, and varieties; and (2) reporting additional populational chromosome counts for taxa documented previously.

MATERIALS AND PROCEDURES

The meiotic chromosomal material for this study was collected during the past several years by the senior and junior authors on various field excursions. Immature capitula were killed and fixed in modified Carnoy's fluid (4 chloroform: 3 absolute alcohol: 1 glacial acetic acid) and refrigerated in the laboratory until later prepared by con-

¹Publication No. 843 from the Department of Botany, The Ohio State University, Columbus.

ventional acetocarmine squash techniques. Voucher specimens collected by Keil and assistants are on deposit in the herbarium of The Ohio State University (OS); vouchers collected by Stuessy are in the herbarium of the University of Texas at Austin (TEX).

RESULTS

The chromosome counts obtained in the present study are listed in Table 1. First counts are reported for two genera, 16 additional species, and one variety; 112 additional counts are for taxa counted previously, seven of which are new numbers. The first counts for genera are from *Epaltes* Cass. ($n = 10$) and *Tricarpha* Longpre ($n = 8$), and first counts for species are in *Bidens* L., *Calea* L., *Guardiola* Cerv. ex H. & B., *Machaeranthera* Nees, *Melampodium* L., *Otopappus* Benth., *Sclerocarpus* Jacq., *Senecio* L., *Sigesbeckia* L., *Simsia* Pers., *Spilanthes* Jacq., *Tridax* L., and *Zaluzania* Pers.

DISCUSSION

Because many of the counts presented here corroborate previous chromosomal reports, the discussions are restricted either to first counts or to new reports for genera, species, or varieties. The order of commentary will follow the sequence of tribes in the classification of Hoffmann (1890-94), which is the same as that used in Table 1. References for statements regarding the range of chromosomal variation within genera will not be given; documentation for these counts comes from the several major sources cited in the introduction to this paper.

EUPATORIEAE. Counts for three herbaceous species of *Stevia* Cav. represent new reports. *Stevia elatior* H.B.K. is cited here as $n = 12_{II}$ & 12_I (Fig. 1), whereas the two previously recorded numbers have been $n = 34_I$ (Powell & Turner, 1963) and $n = 33_I$ (Grashoff, Bierner, & Northington, 1972). Our count for *Stevia organoides* H.B.K.,

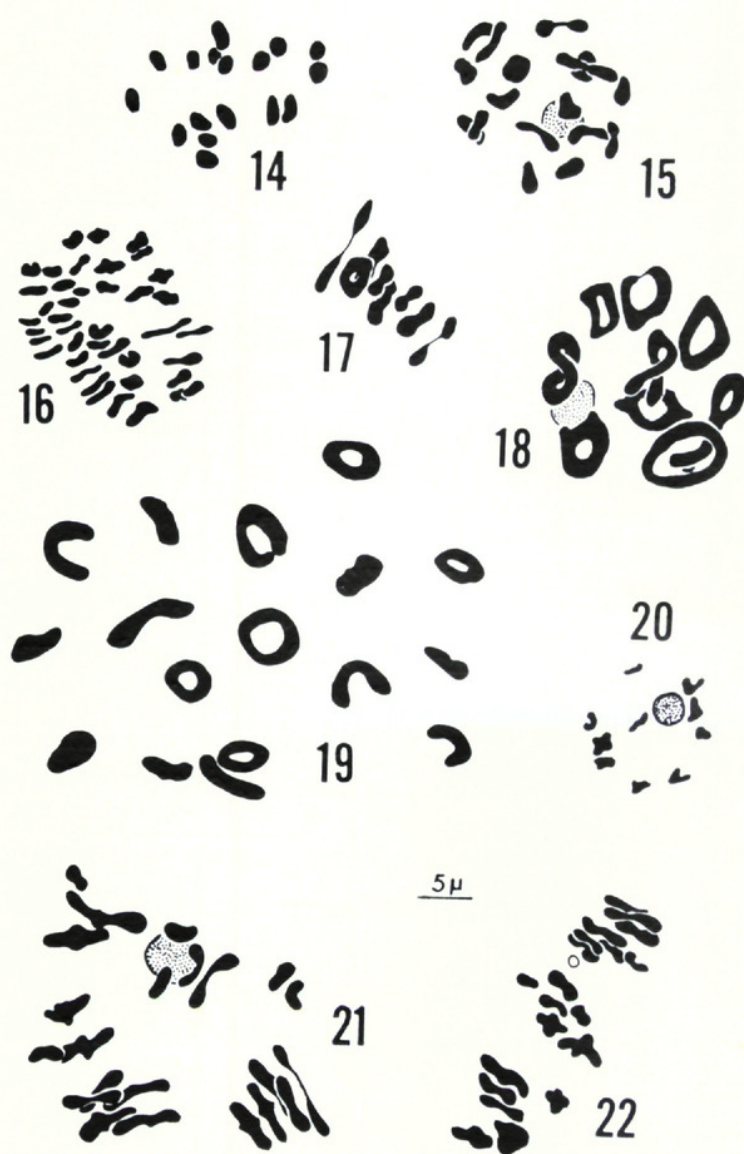
reported here as $n = 11$ (Fig. 2), is the first for this taxon at what appears to be the diploid level; the previous counts were $n = 34_I$ and $n = \text{ca. } 43 \pm 1_I$ (Grashoff *et al.*, 1972). *Stevia plummerae* A. Gray var. *durangensis* Robins. has been reported before only once by Grashoff *et al.* (1972) as $n = \text{ca. } 17$, but our count is $n = 44_I$ (Fig. 3). As pointed out by Grashoff *et al.* (1972), it is common to find varying meiotic chromosomal associations and numbers in species that have apomictic races, as are present in these three taxa. It is not surprising, therefore, that our reported counts add to this chromosomal diversity.

ASTEREAE. Several previous counts have been reported for *Erigeron karwinskianus* DC.: $2n = 32$ (Carano, 1924; Battaglia, 1950); $2n = 36$ (Fagerlind, 1947; Larsen, 1953, 1954; Kliphuis & Wieffering, 1972); $n = 9$ and $n = 27_I$ (Turner, Ellison, & King, 1961); and $n = \text{ca. } 27$ (Turner, Powell, & King, 1962). Considering the variation in chromosome number that has been documented previously in this species, as well as our new report of $n = 5_{II}$ & 17_I (Fig. 4), it is likely that *E. karwinskianus* is apomictic through at least part of its range from Mexico to northern South America (Solbrig, 1962). It is interesting that our count comes from a population very near the locality cited by Turner *et al.* (1961) for their counts of $n = 9$ and $n = 27_I$.

Machaeranthera coulteri (A. Gray) Turner & Horne (as *Psilactis coulteri* A. Gray) was reported as $n = 5$ by Solbrig, Anderson, Kyhos, Raven, and Rüdénberg (1964). However, based on the recent revision of sect. *Psilactis* of *Machaeranthera* by Turner and Horne (1964), the geographic location of the voucher for the count seems more appropriate for *M. arida* Turner & Horne than for *M. coulteri*. The latter species, as recently interpreted, is known only from the vicinity of Guaymas, Sonora, where our voucher was collected. Our first count of $n = 5$ (Fig. 5) for *Machaeranthera coulteri* is particularly interesting because in the previously mentioned revision of sect. *Psilactis* of the genus (Turner & Horne, 1964; cf. their



Figs. 1-22. Camera lucida drawings of meiotic chromosomes of species of Compositae. Diplotene, Fig. 18; diakinesis, Figs. 5, 7-10, 12, 15, 19-21; metaphase I, Figs. 1, 3, 4, 6, 11, 14, 16, 17; metaphase II, Figs. 2 (one half of cell shown), 13. All figures same scale. Bivalents black, univalents white. KC = Keil & Canne, KM = Keil & McGill, K = Keil. Fig. 1, *Stevia elatior*, K 9396, $n = 12_{II}$ & 12_I ; Fig. 2, *Stevia origanoides*, KC 8884, $n = 11$; Fig. 3, *Stevia plummerae* var. *durangensis*, KC 8927-1, $n = 44_I$; Fig. 4, *Erigeron karwinskianus*, KC 9178, $n = 5_{II}$ & 17_I ; Fig. 5, *Machaeranthera coulteri*, KC 8637, $n = 5$; Fig. 6, *Epiltes mexicana*, KC 9211, $n = 10$; Fig. 7, *Bidens*



riparia var. *refracta*, KC 8710, $n = 12$; Fig. 8, *Guardiola platyphylla*, KM 8558, $n = 12$; Fig. 9, *Melampodium appendiculatum*, KC 8706A, $n = 10$; Fig. 10, *Otopappus imbricatus*, KC 9112, $n = 16$; Fig. 11, *Parthenium incanum*, KM 7765A, $n = 18_{II}$ & 18_I ; Fig. 12, *Sclerocarpus spatulatus*, KC 8671A, $n = 11$; Fig. 13, *Sigesbeckia jorullensis*, KC 8902, $n = 30$; Fig. 14, *Simsia eurylepis*, KC 9231, $n = 17$; Fig. 15, *Simsia grayi*, KC 9081, $n = 17$; Fig. 16, *Spilanthes phaneractis*, KC 9035, $n = 41$; Fig. 17, *Tricarpha durangensis*, KC 8860A, $n = 8$; Fig. 18, *Tridax tenuifolia* var. *microcephala*, KC 8808, $n = 9$; Fig. 19, *Zaluzania grayana*, KM 8379A, $n = 17$; Fig. 20, *Schkuhria pinnata* var. *guatemalensis*, K 9402A, $n = 10$; Fig. 21, *Senecio runcinatus*, KC 9192, $n = 22$; Fig. 22, *Pinaropappus roseus*, KC 9177, $n = 20_{II}$ & 1_I .

Fig. 3), *M. coulteri* on morphological grounds was placed in the $x = 5$ cytophyletic group along with *M. arida* and *M. crispa* (Brandg.) Turner & Horne, both known chromosomally as $n = 5$. More recently *M. arizonica* Jackson & R. R. Johnson and *M. parviflora* A. Gray have been added to this group and both species have been counted as $n = 5$ (Jackson & Johnson, 1967). This first chromosomal report for *M. coulteri* substantiates its phyletic association with these other species. All other taxa in sect. *Psilactis* are known chromosomally as either $n = 4$ or $n = 9$ (Turner & Horne, 1964).

INULEAE. The first report for *Epaltes* (*E. mexicana*), $n = 10$ (Fig. 6), is in keeping with its present subtribal disposition in the Plucheinae. Of the related genera of the same subtribe (Hoffmann, 1890-94) that are known chromosomally (*Blumea* DC., *Pluchea* Cass., *Pterigeron* (DC.) Benth., *Pterocaulon* Ell., *Sphaeranthus* L., and *Tessaria* Ruiz & Pav.), all are based on $x = 10$ except *Blumea* which appears multibasic with $x = 9, 10$, and 11 . On morphological and geographical grounds, in our opinion, *Epaltes mexicana* Less. is quite similar to some species of *Pluchea*, the former differing mainly in its smaller heads and flowers and in its epappose achenes. As emphasized by Bentham (1873) and Godfrey (1952), the generic boundaries in the Plucheinae are not well defined and perhaps should be re-evaluated.

HELIANTHEAE. *Bidens riparia* is reported for the first time as $n = 12$ (Fig. 7) in a genus that has most frequently counted numbers of $n = 12, 24$, and 36 (clearly based on $x = 12$).

The first count for *Calea zacatechichi* Schlecht., $n = \text{ca. } 19$, is in keeping with previous reports for other species of the genus ($n = 9, 16, 18, 19, 24, 32$). According to the most recent revision of the Mexican and Central American taxa (Robinson & Greenman, 1896), *C. zacatechichi* is most closely related to *C. nelsonii* Robins. & Greenm. which has been counted as $n = \text{ca. } 18$ (Turner *et al.*, 1962). The

morphological and chromosomal heterogeneity within *Calea* and the absence of a recent revision of the entire genus suggest that a thorough modern study is much needed.

Guardiola, a genus of about ten species, has been placed traditionally in the subtribe Melampodiinae (Hoffmann, 1890-94). However, recent studies by the junior author suggest that on morphological and cytological evidence it belongs more properly in the Coreopsidinae (Stuessy, 1973). Our first count of $n = 12$ (Fig. 8) for *G. platyphylla* A. Gray is consistent with the recent reports of $n = 12$ for both *G. tulocarpus* A. Gray (Grashoff *et al.*, 1972) and *G. mexicana* H. & B. (Solbrig, Kyhos, Powell, & Raven, 1972),² and with the base number of $x = 12$ for several other members of this subtribe.³

The count of $n = 10$ (Fig. 9) is a first report for *Melampodium appendiculatum* Robins. In a recent revision of the genus (Stuessy, 1972) this species is placed in series *Cupulata* of sect. *Melampodium*; three other related species (*M. cupulatum* A. Gray, *M. rosei* Robins., and *M. tenellum* Hook. & Arn.) also are known chromosomally as $n = 10$ (Stuessy, 1971b). The addition of this new count increases the number of species surveyed within the genus to 27 out of 37.

The first generic report for *Otopappus* (*O. scaber* S. F. Blake) has been published recently by Solbrig *et al.* (1972) as $n = 16$. Our first report for *O. imbricatus* (Sch.-Bip.) S. F. Blake of $n = 16$ (Fig. 10) confirms this chromosomal level for the genus. The related genera *Salmea* DC. and *Notoptera* Urb. (Blake, 1915) are known respectively as $n = 18 + 2$ frag. (Turner *et al.*, 1962) and $n = \text{ca. } 15 \text{ \& } 16$ (Turner *et al.*, 1962; Turner & King, 1964), although very few taxa have been examined from each.

²The count published by Solbrig *et al.* was listed for *G. atriplicifolia* A. Gray, but in the most recent published revision of the genus (Robinson, 1899) this epithet is regarded as synonymous with *G. mexicana*.

³(e.g., *Bidens* L., *Coreopsis* L., *Cosmos* Cav., *Glossocardia* Cass., *Thelesperma* Less.)

Parthenium L., and particularly *P. argentatum* A. Gray, has been studied extensively for many years (cf. Hammond & Polhamus, 1965), including a comprehensive revision by Rollins (1950). *Parthenium incanum* H.B.K. has been reported previously as having a polyploid series of $n = 18$, 27, 36, and 45, but our new count is $n = 18_{II}$ & 18_I (Fig. 11). This interploid number could represent the product of hybridization between *P. incanum* and other species of the genus that grow in the vicinity, such as *P. argentatum*, but our voucher specimens show no morphological indication of such intergradation. Alternatively, the meiotic configuration could indicate a hybrid between $n = 18$ and $n = 36$ cytotypes of the same species. The plants under consideration also could be apomictic, a condition that is known to occur in populations in the northern range of *P. incanum* (Rollins, 1950) where our material was collected.

The count of $n = 11$ (Fig. 12) for *Sclerocarpus spatulatus* Rose is consistent with previously reported numbers of $n = 11$, 12, 14, and 18 in the genus as recently defined by Feddema (1971). The closely related genus, *Aldama* LaLlave & Lex., is known chromosomally as $n = 17$ (Turner *et al.*, 1962; Powell & Cuatrecasas, 1970; Feddema, 1971).

Sigesbeckia L. of the subtribe Helianthinae is a small genus of less than ten species. It is worthwhile to mention that a close morphological resemblance exists with *Trigonospermum* Less. (McVaugh & Anderson, 1972; Stuessy, 1973) and perhaps also with *Rumfordia* DC., the former of the subtribe Melampodiinae and the latter of the Helianthinae. Our count of $n = 15$ is a first report for *S. agrestis* Poepp. & Endl. All but two other reports in the genus [$n = 12$ (Subramanyam & Kamble, 1967) and $2n = 20$ (Hsu, 1967) for *S. orientalis* L.] have been either $n = 15$ or $n = 30$. Intraspecific euploidy is known to occur in *S. orientalis* (Mehra, Gill, Mehta, & Sidhu, 1965) and it is now documented for *S. jorullensis* H.B.K. by our counts of $n = 15$ and 30 (Fig. 13). Only one count of $n = 15$ (Solbrig *et al.*, 1972) has been recorded previously for this species.

Of the approximately 35 species of *Simsia* recognized by various authors (Blake, 1913, 1917, 1928; Cuatrecasas, 1954; Robinson & Brettell, 1972), ten have been counted from morphologically diverse parts of the genus, and all counts have been $n = 17$. Our first counts of $n = 17$ (Figs. 14 & 15) for *S. eurylepis* S. F. Blake and *S. grayi* Sch.-Bip. ex S. F. Blake emphasize the chromosomal uniformity within the genus.

Spilanthes with approximately 60 species (Moore, 1907) is a taxonomically complex genus much in need of revisionary attention. It appears to belong in the subtribe Galinsoginae rather than in the Helianthinae as traditionally placed (Hoffmann, 1890-94). Chromosomally the situation also is complex. Even though only six species have been counted, four base numbers, $x = 7, 12, 13$, and 16 , are present. Our first report of $n = \text{ca. } 45$ for *S. ocymifolia* (Lam.) A. H. Moore adds another chromosomal level to the already chromosomally diverse sect. "Salivaria" (= sect. *Spilanthes*) known with $n = 7, 12, 16$, and 26 . All previous reports for sect. *Acmella* (Rich.) DC. have been clearly based on $x = 13$ (only $n = 13$ and $n = 26$ counts reported). Our new report of $n = 41$ (Fig. 16) for *S. phaneractis* (Greenm.) A. H. Moore increases the chromosomal diversity of this section as well.

Tricarpha is a genus of two species recently described by Longpre (1970). Our first count for the genus (from *T. durangensis* Longpre) of $n = 8$ (Fig. 17) substantiates its presumptive close relationship to *Sabazia* Cass. ($n = 4, 8$, and 16) and *Selloa* Kunth ($n = 8$) as mentioned by Longpre (1970). The problem of generic delimitation in the subtribe Galinsoginae, involving *Tricarpha*, *Sabazia* and *Selloa* as well as *Galinsoga* Ruiz & Pavon, *Stenocarpha* S. F. Blake, *Tridax* and *Jaegeria* Kunth, is much in need of further study, despite the appearance in recent years of several excellent revisions (Powell, 1965; Turner, 1965; Torres, 1968; Longpre, 1970). Part of the difficulty in sorting out the proper affinities of all the taxa in the Galinsoginae is that previous workers have been working from the

perspective primarily of a single genus and not from a perspicacious overview of many of the genera within the subtribe. An added difficulty is the absence of a recent revision of *Galinsoga* (most recent treatment that of Robinson, 1894), the understanding of which clearly is central to sorting out these generic relationships.

Our first report for *Tridax tenuifolia* Rose, $n = 9$ (Fig. 18), fits well with the established base number of $x = 9$ for sect. *Tridax* to which *T. tenuifolia* belongs (Powell, 1965).

Of the 14 species of *Zaluzania* recognized by Sharp (1935), six have been counted with definite numbers of $n = 16$ and 18. Our first report, $n = 17$ (Fig. 19), for *Z. grayana* Robins. & Greenm. firmly establishes this as a new chromosomal level for the genus (a previous count of $n = 17 \pm 1$ for *Z. montagnaeifolia* Sch.-Bip. was reported by Powell and Turner, 1963).

HELENIEAE. *Schkuhria pinnata* (Lam.) Cabrera has been counted before as $2n = 20$ (Covas and Schnack, 1946), and var. *virgata* (LaLlave) Heiser of the same species has been reported as $n = \text{ca. } 20$ (Turner *et al.*, 1962). Recently McVaugh (1972) transferred *S. anthemoidea* (DC.) Coult. var. *guatemalensis* (Rydb.) Heiser to *S. pinnata*, and our counts of $n = 10$ (Fig. 20) for this taxon are the first reports. A count of $n = 11$ (Table 1) was obtained from material tentatively identified as *S. anthemoidea*. However, our voucher specimen differs from the characters of this species as delimited by Heiser (1945) in having more numerous disc florets and large ray florets, as in *S. schkuhrioides* (Link & Otto) Thellung in Fedde. In pappus structure, though, our plants are much more similar to *S. anthemoidea* than to *S. schkuhrioides*. This collection may represent a previously undescribed taxon.

SENECIONEAE. Our first reports of $n = \text{ca. } 30$ for *Senecio hartwegii* Benth. and $n = 22$ (Fig. 21) for *S. runcinatus* Less. are consistent with counts reported previously for other taxa of the genus. Thirty-three species of *Senecio*

have been reported as $n = 30$ and six are known with $n = 22$. Although the genus is based either on $x = 5$ (Barkley, 1962) or $x = 10$ (Ornduff, Raven, Kyhos, & Kruckeberg, 1963; Ornduff, Mosquin, Kyhos, & Raven, 1967), the diversity of haploid numbers is great, representing 30 different chromosomal levels from $n = 5$ to $n = \text{ca. } 92$.

CICHORIEAE. The small genus *Pinaropappus* Less. has been counted from only one species, *P. roseus* Less., and the reported counts are $n = 9$ and 18 (Darlington & Wylie, 1955; Turner *et al.*, 1961; Powell & Turner, 1963; Powell & Sikes, 1970). Our present count of $n = 20_{II} \text{ \& } 1_I$ (Fig. 22) is a new report for this taxon. The meiotic configurations of cells in our preparation were irregular with bridges, lagging chromosomes, and varying numbers of univalents.

ACKNOWLEDGMENTS

Field work for this investigation was completed largely with support from NSF grant GB-30240; publication costs were defrayed partially by funds from NSF grant GB-37678. Thanks are extended to Judith M. Canne and Lyle A. McGill for assistance on collecting trips.

Table 1. Chromosome counts of Compositae from the United States, Mexico, and Guatemala.

Taxon	Locality and voucher	Chromosome number (n) ^a
EUPATORIEAE		
<i>Ageratum corymbosum</i> Zuccag.	MEXICO: Sinaloa: 16.4 mi. NE. of Santa Lucia, KC 8859. ^b	10
<i>Brickellia coulteri</i> A. Gray	MEXICO: Durango: 8.8 mi. S. of Nazareno, KM 8025. ^c	9
<i>Stevia anadenotricha</i> (Robins.) Grashoff	MEXICO: Durango: 12.7 mi. SW. of La Ciudad, KC 8883.	12
† <i>Stevia elatior</i> H.B.K.	GUATEMALA: Guatemala: 12.8 km. E. of Cd. Guatemala, K 9396. ^d	12 _{II} & 12 _I (Fig. 1)
† <i>Stevia origanoides</i> H.B.K.	MEXICO: Durango: 12.7 mi. SW. of La Ciudad, KC 8884.	11 (Fig. 2)
† <i>Stevia plummerae</i> A. Gray var. <i>durangensis</i> Robins.	MEXICO: Durango: 9.7 mi. NE. of La Ciudad, KC 8927-1.	44 _I (Fig. 3)
<i>Stevia salicifolia</i> Cav. var. <i>salicifolia</i>	MEXICO: Chihuahua: 9.5 mi. W. of General Triás, KM 8288.	12
ASTEREAE		
<i>Aphanostephus arizonicus</i> A. Gray	MEXICO: Chihuahua: 10.4 mi. S. of Cd. Chihuahua, KM 8263A.	4
<i>Aphanostephus ramosissimus</i> DC.	MEXICO: Chihuahua: 24 mi. N. of Cd. Chihuahua, S 1097. ^e	4
<i>Aster exilis</i> Ell.	MEXICO: Sinaloa: 11 mi. NE. of Santa Lucia, KC 8850A.	5

<i>Aster spinosus</i> Benth.	MEXICO: Coahuila: 5.5 mi. E. of Nazareno, KM 8010.	9
<i>Baccharis glutinosa</i> Pers.	MEXICO: Sonora: Arroyo Cuchujaqui on Álamos-Guircoba rd., KC 8675.	9
<i>Conyza sophiaefolia</i> H.B.K.	MEXICO: Sinaloa: 11 mi. NE. of Santa Lucia, KC 8848.	9
<i>Erigeron divergens</i> Torr. & A. Gray	MEXICO: Chihuahua: 39 mi. W. of Cd. Chihuahua, S 1025.	9
† <i>Erigeron karwinskianus</i> DC.	MEXICO: Veracruz: 11.1 mi. E. of Puebla-Veracruz boundary on Rte. 150-D, KC 9178.	5 _{II} & 17 _I (Fig. 4)
<i>Grindelia</i> sp. nov.f	MEXICO: Chihuahua: 2 mi. S. of Cuauhtémoc, S 1041.	6
** <i>Machaeranthera coulteri</i> (A. Gray) Turner & Horne	MEXICO: Sonora: ca. 15 mi. E. of Guaymas, KC 8637.	5 (Fig. 5)
<i>Machaeranthera pinnatifida</i> (Hook.) Shinnery	MEXICO: Chihuahua: ca. 2 mi. W. of Parral, S 993.	4
<i>Machaeranthera scabrella</i> (Greene) Shinnery	MEXICO: Coahuila: 110 mi. S. of Piedras Negras, KM 7855; 14.9 mi. N. of Rancho Acatita, KM 8079A. UNITED STATES: Texas: PRESIDIO CO.: 15.2 mi. W. of Lajitas, KM 7787.	4
<i>Xanthocephalum sericocarpum</i> A. Gray	MEXICO: Chihuahua: 2 mi. S. of Cuauhtémoc, S 1044.	4
INULEAE		
*** <i>Epaltes mexicana</i> Less.	MEXICO: Veracruz: 33.5 mi. E. of Poza Rica, KC 9211.	10 (Fig. 6)

HELIANTHEAE

- Ambrosia artemisiifolia* L. UNITED STATES: Illinois: LAKE CO.: Lake Forest College campus, S 1132. 18
- Ambrosia psilostachya* DC. MEXICO: Tamaulipas: ca. 2 mi. SE. of Reynosa, S 774 (ca. 18). UNITED STATES: Texas: KINNEY CO.: 42 mi. NW. of Eagle Pass, S 877a, b. 18
- Ambrosia psilostachya* DC. MEXICO: Chihuahua: 7 mi. NW. of Cuauhtémoc, S 1062a. ca. 36
- Ambrosia psilostachya* DC. UNITED STATES: Texas: BRAZORIA CO.: 12 mi. NE. of Freeport, Turner 5747 (ca. 54); GALVESTON CO.: 60 S. Theresa, Galveston, Miller s.n. 54
- Baltimore recta* L. GUATEMALA: Santa Rosa: 3.5 km. NW. of Culapa, K 9403. 15
- Bidens pilosa* L. var. *minor* (Blume) Sherff f. *minor* MEXICO: Guerrero: 10 mi. S. of Chilpancingo, KC 9126. 12
- Bidens pilosa* L. var. *radiata* Sch.-Bip. in Webb & Berth. f. *dondiaefolia* (Less.) Sherff MEXICO: Distrito Federal: 17.7 mi. W. of D.F.-Puebla boundary on Rte. 190-D, KC 9164. 12
- Bidens pilosa* L. var. *radiata* Sch.-Bip. in Webb & Berth. f. *radiata* MEXICO: Chihuahua: 15.5 mi. W. of Santa Lucia, KM 8304. 12
- ***Bidens riparia* H.B.K. var. *refracta* (Brandg.) O.E. Schulz MEXICO: Sonora: 5.5 mi. E. of Arroyo Cuchujaqui on Alamos-Milpillas rd., KC 8710. 12 (Fig. 7)
- Calea urticifolia* (Mill.) DC. GUATEMALA: Guatemala: 6.8 km. NE. of Amatita, K 9430. 19
- ***Calea zacatechichi* Schlecht. MEXICO: Jalisco: 1.2 mi. NW. of Magdalena airport, KC 9008. ca. 19

<i>Chrysanthellum mexicanum</i> Greenm.	MEXICO: Nayarit: ca. 18 mi. SE. of Tepic, <i>KC</i> 8965.	8
<i>Cosmos linearifolius</i> (Sch.-Bip.) Hemsl. var. <i>linearifolius</i>	MEXICO: Durango: 10.5 mi. SW. of La Ciudad, <i>KC</i> 8892.	23
<i>Cosmos parviflorus</i> (Jacq.) Pers.	MEXICO: Sinaloa: 16.4 mi. NE. of Santa Lucia, <i>KC</i> 8858.	12
<i>Dicranocarpus parviflorus</i> A. Gray	MEXICO: Coahuila: jctn. Rte. 40 & rd. to San Pedro, <i>KM</i> 7991.	10
<i>Eclipta alba</i> (L.) Hassk.	MEXICO: Sinaloa: 14.5 mi. S. of Sinaloa-Sonora boundary on Rte. 15, <i>KC</i> 8736.	11
<i>Flaveria trinervia</i> (Spreng.) C. Mohr.	MEXICO: Jalisco: Ocotlán, <i>KC</i> 9036.	18
<i>Guardiola mexicana</i> H. & B.	MEXICO: Guerrero: 7 mi. NE. of Taxco, <i>KC</i> 9107.	12 _{II} & frag.
** <i>Guardiola platyphylla</i> A. Gray	UNITED STATES: Arizona: COCHISE CO.: ca. 10.5 mi. W. of Coronado Natl. Mem. headqtrs., <i>KM</i> 8558.	12 (Fig. 8)
<i>Helianthus laciniatus</i> A. Gray	MEXICO: Durango: 2 mi. NW. of Bermejillo, <i>S</i> 940.	17
<i>Heterosperma pinnatum</i> Cav.	MEXICO: Sinaloa: 3.8 mi. SW. of Santa Lucia, <i>KC</i> 8833.	25
<i>Jaegeria hirta</i> (Lag.) Less.	GUATEMALA: Alta Verapaz: 4 mi. NE. of San Pedro Carchá, <i>S</i> 596. MEXICO: Durango: 8.3 mi. SW. of La Ciudad, <i>KC</i> 8903C, 8909; 4.8 mi. SW. of La Ciudad, <i>KC</i> 8916; 15.6 mi. NE. of La Ciudad. <i>KC</i> 8929. Michoacán: 54 mi. E. of Zamora, <i>KC</i> 9060. Puebla: Teteles, <i>S</i> 498. Sinaloa: 3.8 mi. SW. of Santa Lucia, <i>KC</i> 8832A.	18

- Jaegeria macrocephala* Less. 18
 MEXICO: Michoacán: 26 mi. S. of Pátzcuaro, S 686. Veracruz: 8 mi. N. of Jalapa, S 491, 492.
 ***Melampodium appendiculatum* 10 (Fig. 9)
 Robins. MEXICO: Sonora: 0.3 mi. N. of Arroyo Cuchujaqui on Álamos-Guerocho rd., KC 8672A; 4.7 mi. E. of Arroyo Cuchujaqui on Álamos-Milpillas rd., KC 8706A.
Melampodium cupulatum A. Gray 10
 MEXICO: Sinaloa: 27.3 mi. S. of Sinaloa-Sonora boundary on Rte. 15, KC 8742A.
Melampodium divaricatum (Rich. MEXICO: Sinaloa: 7.7 mi. SE. of Escuinapa, KC 8950. 12
 in Pers.) DC. MEXICO: Jalisco: Ocotlán, KC 9034. 11
Melampodium perfoliatum (Cav.) H.B.K. 15
 GUATEMALA: Suchitepequez: 4.5 km. E. of puente Madre Vieja, K 9436A. 15
Melastoma aspera (Jacq.) Small MEXICO: Nayarit: ca. 18 mi. SE. of Tepic, KC 8960-1. Sinaloa: 0.4 mi. SW. of Santa Lucia, KC 8835. Sonora: 4.7 mi. E. of Arroyo Cuchujaqui on Álamos-Milpillas rd., KC 8708. 16 (Fig. 10)
 MEXICO: Guerrero: 2.6 mi. S. of Taxco, KC 9112.
 ***Otopappus imbricatus* (Sch.-Bip.) S. F. Blake 36
 UNITED STATES: Texas: PRESIDIO CO.: 10 mi. S. of Shafter, KM 7764.
 var. *lyratum* (A. Gray) Rollins 18II & 18I (Fig. 11)
 †*Parthenium incanum* H.B.K. 28
 UNITED STATES: Texas: PRESIDIO CO.: 10 mi. S. of Shafter, KM 7765A, B.
Philactis nelsonii (Greenm.) MEXICO: Chiapas: 11 mi. N. of Arriaga, S 630. 8
 S. F. Blake
Sanvitalia procumbens Lam. MEXICO: México: 1.1 mi. N. of Ixtapán de la Sal, KC 9093A.

** <i>Sclerocarpus spatulatus</i> Rose	MEXICO: Sonora: 2.4 mi. S. of Álamos, KC 8671A.	11 (Fig. 12)
<i>Sclerocarpus sessilifolius</i> Greenm.	MEXICO: Nayarit: ca. 18 mi. SE. of Tepic, KC 8963-1.	14
** <i>Sigesbeckia agrestis</i> Poepp. & Endl.	GUATEMALA: Alta Verapaz: 4 mi. NE. of San Pedro Carchá, S 595.	15
<i>Sigesbeckia jorullensis</i> H.B.K.	MEXICO: México: 2 mi. E. of Cuajimalpa, S 672, 673.	15
† <i>Sigesbeckia jorullensis</i> H.B.K.	MEXICO: Durango: 9.7 mi. SW. of La Ciudad, KC 8902.	30 (Fig. 13)
** <i>Simsia eurylepis</i> S. F. Blake	MEXICO: Veracruz: 10.8 mi. SW. of Panuco, KC 9231.	17 (Fig. 14)
** <i>Simsia grayi</i> Sch.-Bip. ex S. F. Blake	MEXICO: Michoacán: 1.8 mi. S. of Tuxpan, KC 9081.	17 (Fig. 15)
<i>Spilanthes americana</i> (Mut.) Hieron. var. <i>parvula</i> (Robins.) A. H. Moore	MEXICO: Veracruz: 5 mi. N. of Jalapa, KC 9188.	ca. 24
** <i>Spilanthes ocymifolia</i> (Lam.) A. H. Moore	GUATEMALA: Guatemala: 6.8 km. NE. of Amatitla, K 9429A.	ca. 45
** <i>Spilanthes phaneractis</i> (Greenm.) A. H. Moore	MEXICO: Jalisco: Ocotlán, KC 9035.	41 (Fig. 16)
<i>Tithonia calva</i> Sch.-Bip.	MEXICO: Sinaloa: 6.8 mi. NE. of Santa Lucia, KC 8845.	17
<i>Tragoceros americanus</i> (Mill.) S. F. Blake	MEXICO: Jalisco: 2 mi. NW. of Tequila, S 739.	11
*** <i>Tricarpha durangensis</i> Longpre	MEXICO: Sinaloa: 21.9 mi. NE. of Santa Lucia, KC 8860A.	8 (Fig. 17)
<i>Tridax coronopifolia</i> (Kunth) Hemsl.	MEXICO: Michoacán: 2.8 mi. S. of La Barca, KC 9039A.	9

- Tridax mexicana* A. M. Powell
MEXICO: Jalisco: 6.1 mi. E. of Jalisco-Nayarit boundary on Rte. 15, *KC* 8992. 9
- Tridax procumbens* L.^g
MEXICO: Sinaloa: 44 mi. SE. of Culiacán, *KC* 8804. 18
- ***Tridax tenuifolia* Rose**
var. *microcephala* Rose
MEXICO: Sinaloa: ca. 40 mi. NW. of Mazatlán, *KC* 8808. 9 (Fig. 18)
- Viguiera stenoloba* S. F. Blake
MEXICO: Coahuila: 5 mi. W. of Saltillo, *S* 927. ca. 34
- ***Zaluzania grayana***
Robins. & Greenm.
MEXICO: Chihuahua: 36 mi. E. of Cd. Guerrero, *KM* 8379A. 17 (Fig. 19)
- Zinnia angustifolia* H.B.K.
MEXICO: Nayarit: ca. 18 mi. SE. of Tepic, *KC* 8966. 11

HELENIEAE

- Bahia absinthifolia* Benth. var.
dealbata (A. Gray) A. Gray
MEXICO: Coahuila: 0.2 mi. E. of El Numbre, *KM* 7963 (ca. 24); 8.9 mi. N. of Rancho Acatita, *KM* 8073A. 24
- Bahia pedata* A. Gray
MEXICO: Chihuahua: 29.9 mi. S. of Cd. Jiménez, *KM* 8221A. UNITED STATES: Texas: CULBERTSON CO.: 3.7 mi. W. of Van Horn, *KM* 7688. 12
- Dyssodia aurea* (A. Gray) Nels.
var. *polychaeta* (A. Gray)
M. C. Johnst.
UNITED STATES: Texas: BREWSTER CO.: Big Bend Natl. Pk., 8.7 mi. N. of headqtrs., *KM* 7821A. 8
- Dyssodia papposa* (Vent.) Hitchc.
Dyssodia pentachaeta (DC.)
Robins. subsp. *pentachaeta* var.
belenidium (DC.) Strother
MEXICO: Puebla: 8 mi. E. of Puebla, *KC* 9172. 13
- MEXICO: Coahuila: 2.1 mi. N. of Rancho Acatita, *KM* 8066. 16

<i>Florestina tripteris</i> DC.	MEXICO: Coahuila: 63 mi. S. of Piedras Negras, KM 7847A. Durango: 16 mi. S. of Nazareno, KM 8030A.	10
<i>Gaillardia pulchella</i> Foug.	UNITED STATES: New Mexico: GRANT CO.: 0.3 mi. S. of jctn. Rtes. US 180 & NM 61, KM 8460A.	17
<i>Gaillardia pinnatifida</i> Torr.	UNITED STATES: New Mexico: HIDALGO CO.: 14 mi. NE. of Lordsburg, KM 8491A.	17
<i>Gaillardia pinnatifida</i> Torr. var. <i>linearis</i> (Rydb.) Bidd.f	MEXICO: Chihuahua: 2 mi. S. of Cuauhtémoc, S 1051.	17
<i>Galeana pratensis</i> (H.B.K.) Rydb.	GUATEMALA: Jutiapa: 7.3 mi. W. of jctn. Rtes. 3 & CA-1, K 9410. MEXICO: Nayarit: ca. 8 mi. SE. of Tepic, KC 8954-1.	9
<i>Hymenoxys richardsonii</i> (Hook.) Cockerell var. <i>floribunda</i> (A. Gray) K. F. Parker	UNITED STATES: New Mexico: HIDALGO CO.: 14 mi. NE. of Lordsburg, KM 8492A.	15
<i>Nicolletia edwardsii</i> A. Gray	MEXICO: Coahuila: La Rosa, KM 7922.	10
<i>Palafoxia rosea</i> (Bush) Cory var. <i>robusta</i> (Rydb.) Cory	MEXICO: Veracruz: 4 mi. NE. of Nautla, KC 9207.	11
<i>Palafoxia sphacelata</i> (Nutt. ex Torr.) Cory	MEXICO: Chihuahua: 43 mi. N. of Villa Ahumada, S 1115.	12
<i>Palafoxia texana</i> DC. var. <i>texana</i>	MEXICO: Coahuila: 0.8 mi. W. of San Raphael, KM 7966.	11
<i>Pectis papposa</i> Harv. & A. Gray var. <i>grandis</i> Keil	MEXICO: Chihuahua: 28 mi. W. of jctn. Rtes. 45 & rd. to Casas Grandes, S 1109.	12
<i>Porophyllum coloratum</i> (H.B.K.) DC.	MEXICO: Jalisco: 6.1 mi. E. of Jalisco-Nayarit boundary on Rte. 15, KC 8996.	12

<i>Porophyllum punctatum</i> (Mill.) S. F. Blake	MEXICO: Veracruz: 4 mi. NE. of Nautla, <i>KC</i> 9203.	12
<i>Porophyllum ruderale</i> (Jacq.) Cass. subsp. <i>macrocephalum</i> (DC.) R. R. Johnson	UNITED STATES: Arizona: SANTA CRUZ CO.: Peña Blanca Lake, <i>KC</i> 8585.	11
<i>Schkuhria</i> cf. <i>anthemoidea</i> (DC.) Coult.	MEXICO: Jalisco: 2.1 mi. NW. of Magdalena airport, <i>KC</i> 8998.	11
* <i>Schkuhria pinnata</i> (Lam.) Cabrera var. <i>guatemalensis</i> (Rydb.) McVaugh	GUATEMALA: Santa Rosa: 3.5 km. NW. of Culitapa, <i>K</i> 9402A. MEXICO: Nayarit: ca. 8 mi. SE. of Tepic, <i>KC</i> 8956-1.	10 (Fig. 20)
<i>Tagetes filifolia</i> Lag.	MEXICO: Sinaloa: 3.8 mi. SW. of Santa Lucia, <i>KC</i> 8834A.	12
<i>Tagetes lucida</i> Cav.	MEXICO: Nayarit: ca. 18 mi. SE. of Tepic, <i>KC</i> 8968-1.	11
<i>Tagetes micrantha</i> Cav.	MEXICO: Chihuahua: 2 mi. S. of Cd. Guerrero, <i>KM</i> 8320A.	12
<i>Tagetes subulata</i> Cerv.	MEXICO: México: 1 mi. N. of Guerrero-México boundary on Rte. 55, <i>KC</i> 9101.	12
ANTHEMIDEAE		
<i>Artemisia ludoviciana</i> Nutt. subsp. <i>mexicana</i> (Willd.) Keck	MEXICO: Durango: 14 mi. SW. of La Ciudad, <i>KC</i> 8941.	18
SENECIONEAE		
<i>Odontotrichum sinuatum</i> (Cerv.) Rydb.	MEXICO: Jalisco: 1.2 mi. NW. of Magdalena airport, <i>KC</i> 9011.	30
<i>Schistocarpha oppositifolia</i> (Kuntze) Rydb. ^h	MEXICO: Veracruz: 11.8 mi. W. of Tuxpán, <i>KC</i> 9222.	8

** <i>Senecio hartwegii</i> Benth.	MEXICO: Durango: 8.3 mi. SW. of La Ciudad, KC 8906.	ca. 30
** <i>Senecio runcinatus</i> Less.	MEXICO: Veracruz: ca. 6 mi. E. of Las Vigas, KC 9192.	22 (Fig. 21)
MUTISIEAE		
<i>Trixis californica</i> Kellogg	UNITED STATES: Texas: BREWSTER CO.: 12.5 mi. N. of Castolón, KM 7814.	27
CICHORIEAE		
† <i>Pinaropappus roseus</i> Less.	MEXICO: Veracruz: 11.1 mi. E. of Puebla-Veracruz boundary on Rte. 150-D, KC 9177.	20 _{II} & 1 _I (Fig. 22)

^aUnless indicated otherwise, the reported meiotic chromosome numbers represent bivalents.

^bKC = *Keil & Canne*; ^cKM = *Keil & McGill*; ^dK = Keil; ^eS = *Stuessy*.

^tVoucher determined by B. L. Turner, ^gA. M. Powell, ^hR. McVaugh.

*First report for variety, **species, ***genus.

†New reported number for taxon.

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