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CHROMOSOME NUMBERS FOR NORTH AMERICAN EUPHORBIACEAE[1]

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ABSTRACT

Chromosome number determinations are reported for 101 collections distributed among 54 species of the North American Euphorbiaceae. First counts are presented for 44 species. When appropriate, systematic discussions regarding chromosomal information are included. Camera lucida drawings are published for previously undocumented chromosome reports.

OUR KNOWLEDGE of chromosome numbers in the Euphorbiaceae is limited. To date only about six percent of the more than 7,000 species have been counted, and many of these counts are based on the study of only one population per species. Pioneering work in this area was initiated by Perry (1943) with the publication of chromosome numbers for species from various parts of the world. Recently, substantial contributions were made to our knowledge of the karyology of the family by Hans (1973), to that of the subfamilies Phyllanthoideae and Crotonoideae by Webster and Ellis (1962) and Miller and Webster (1966), and to that of the genera *Monadenium* and *Synadenium* by Jones and Smith (1969). With the exception of the aforementioned articles, chromosome numbers have been scattered here and there in the literature and limited to one or a few species.

The purpose of our study of North American members of the Euphorbiaceae is threefold: (1) to provide chromosome number determinations for species previously unknown karyologically; (2) to supplement the knowledge for taxa which have been reported previously in the literature; and (3) to note variation, if any, in the chromosome number of wide ranging species.

MATERIALS AND METHODS—All chromosome counts were determined from acetocarmine squashes of pollen mother cells by standard procedures. Camera lucida drawings were made from cells of most preparations, but only those which are new records or differ from previous reports are illustrated (Fig. 1–38). Individuals contributing material to this study are indicated by the collection number and the initial of their last name (Table 1, Fig. 1–38). All voucher specimens are deposited in TEX.

RESULTS AND DISCUSSION—The 101 chromosome number determinations, representing 54 species, resulting from this study are presented in Table 1. The collection numbers which are marked with an asterisk are those for which chromosomes have been illustrated. Only those counts which represent first reports for a species or which differ from any previous determination are included in the discussion.

Acalypha—The count for *A. lindheimeri* ($n =$ ca. 20) is the first for this species and suggests a tetraploid origin of this taxon based on $x = 10$, which is one of two basic numbers suggested for this genus by Hans (1973).

Argythamnia—Apparently *A. brandegei*, $2n = 26$, a member of the subgenus *Ditaxis*, is the only taxon of this genus for which a count has previously appeared (Chisaki & Ingram, 1956). This, along with our counts for *A. humilis* var. *laevis*, $n = 13$, and *A. serrata*, $n =$ ca. 13, suggests a basic number of $x = 13$ for the genus. Our experience in working with taxa of this genus suggests that some of its species may be apomictic since meiosis appears to be very irregular. Chromosome numbers, although difficult to count accurately, vary greatly even in different microsporocytes from the same bud.

Croton—Our counts represent five of the 10 sections recognized by Mueller (1866). Five species of miscellaneous tropical affinity belong to Mueller's sect. *Croton* subsect. *Eutropia* (subsect. *Medea* [Kl.] Baill. as treated by Pax and Hoffmann, 1931): *C. pottsii* ($n = 9$); *C. humilis*, *C. magdalenae*, and *C. torreyanus* ($n = 10$); and *C. fruticulosus* ($n =$ ca. 24). This diversity in numbers is a little surprising in view of the fact that

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Fig. 1–16. Camera lucida drawings of meiotic chromosome configurations. The chromosomes in Fig. 13 ca. 2.1 μm long; all others are the same relative size. **1.** *Croton dioicus, B, H 1438* (MI; $2n = 28$). **2.** *C. dioicus, B, H 1358* (Diak; $2n = 56$). **3.** *C. humilis, U 1026* (MI; $2n = 20$). **4.** *C. magdalenae, U, H 1198* (MI; $2n = 20$). **5.** *C. monanthogynus, U 990* (MII; $2n = 20$). **6.** *C. pottsii, B, H 1425* (MI; $2n = 18$). **7.** *C. texensis, H, T 3438* (Diak; $2n = 28$). **8.** *C. torreyanus, U 1004* (PII; $2n = 20$). **9.** *Euphorbia acuta, B, H 1306* (MI; $2n = 28$). **10.** *E. acuta, B, H 1403* (MI; $2n = 56$, arrows indicate quadrivalents). **11.** *E. albomarginata, U 1033* (MII; $2n = 24$). **12.** *E. astyla, U 1020* (AI; $2n = 28$). **13.** *E. capitellata, H, S 3265* (MI; $2n = 14$). **14.** *E. carunculata, B, H 1400* (MI; $2n = 12$). **15.** *E. cinerascens, B, H 1294* (MI; $2n = 32$). **16.** *E. eriantha, B, H 1426* (MI; $2n = 28$).

previous counts in sect. *Croton* suggest $x = 10$, with the exception of the South American *C. ruizianus* ($n = 32$, 64, perhaps based on $x = 8$) (Diers, 1961).

The other sections of *Croton* represented among our counts include *C. capitatus* ($n = 10$) in sect. *Heptallon*; *C. monanthogynus* ($n = 10$) in sect. *Angelandra*; and *C. californicus* ($n = 14$), *C. dioicus* ($n = 14$, 28), and *C. texensis* ($n = 14$, 28) in sect. *Drepadenium*. Our report for *C. monanthogynus* differs from that of Perry (1943), who reported $2n = 16$. Reports for additional

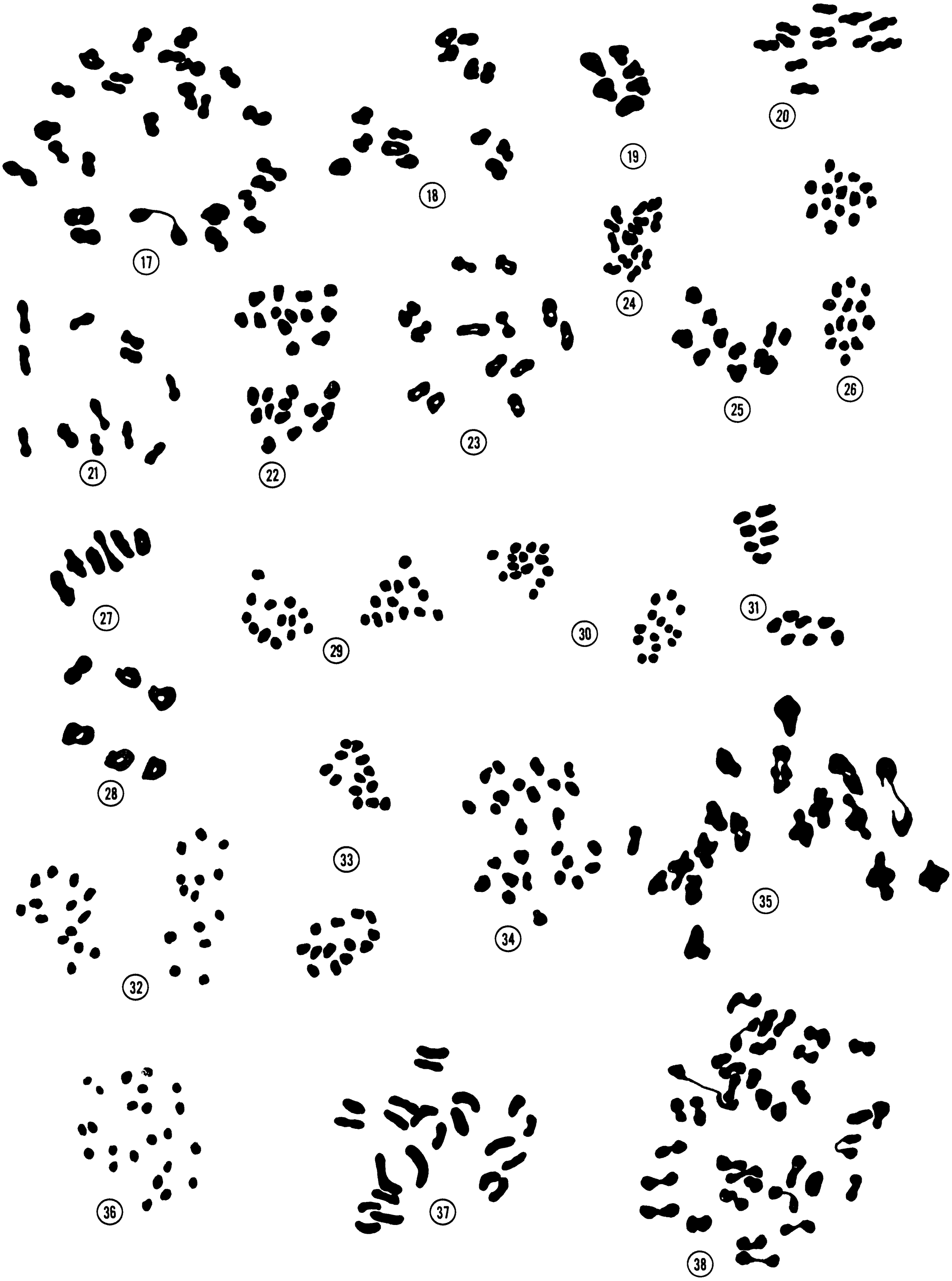

Fig. 17–38. Camera lucida drawings of meiotic chromosome configurations. The scale is the same as on the previous plate. **17.** *Euphorbia fendleri* var. *chaetocalyx*, *B*, *H 1385* (MI; $2n = 56$). **18.** *E. exstipulata*, *H*, *T 3415* (MI; $2n = 28$). **19.** *E. geyeri* var. *wheeleriana*, B, H *1408* (MI; $2n = 12$). **20.** *E. micromera*, *B*, *H 1410* (MI;

North American species include *C. palmeri* ($2n = 16$; Perry, 1943), *C. cortesianus* ($n = 10$), and *C. xalapensis* ($n =$ ca. 60) (Miller and Webster, 1966), all in sect. *Croton*; and *C. alabamensis* ($n = 16, 32$; Farmer and Thomas, 1970) in sect. *Eluteria.*

The occurrence of $n = 10$ in several different sections of *Croton* supports Hans' (1973) suggestion that this is, in fact, the basic number for the genus, while $x = 7, 8, 9$ are secondarily derived by aneuploid loss. In sect. *Drepadenium* the numbers $n = 14, 28$ may have been derived by polyploidy from $x = 7$, a number yet unknown in *Croton.* Our data suggest that *C. dioicus* and *C. texensis* both have chromosomal races. Fewer than 25 of about 1,000 species of *Croton* have been counted. A cytogenetical study might well give valuable insight into the evolution of the genus.

Euphorbia—We report counts for 37 taxa, only three of which have been published previously. Subgenera *Esula*, *Agaloma*, and *Poinsettia* are each represented by only a few counted taxa, while 27 of the taxa belong to subg. *Chamaesyce.* In subg. *Esula*, one species (*E. spathulata*, $n = 6$) belongs to sect. *Tithymalus*, while the other two are in sect. *Esula*: *E. brachycera* ($n = 14$) and *E. tetrapora* ($n = 13$). The haploid number of $n = 14$ in *E. brachycera* has not been previously recorded in sect. *Esula*, but numbers of 7 and 14 have been recorded frequently in sect. *Tithymalus.* The complement of $n = 13$ found in *E. tetrapora* is a very unusual number for *Euphorbia*, but it has been reported in *E. exigua* of sect. *Esula*, and this European species is probably fairly closely related to *E. tetrapora.*

In subg. *Agaloma*, the count for *E. exstipulata* ($n = 14$) is the first for any species in the small North American sect. *Zygophyllidium.* Our report for *E. wrightii* ($n = 14$) agrees with the reports of Perry (1943) for *E. corollata and E. ipecacuanhae*, two other species in sect. *Tithymalopsis.* Our count for *E. marginata* ($n = 28$) in sect. *Petaloma* agrees with Perry's report on the same species. The count for *E. californica* ($n = 14$) agrees with the count made by Perry on another species in sect. *Tricherostigma*, *E. fulgens.* These new reports along with three previous ones strengthen the evidence for $x = 14$ as the prevailing basic number in subg. *Agaloma.*

Our reports in subgen. *Chamaesyce* include the first counts for the species comprising subsect. *Acutae*: *E. acuta*, $n = 14, 28$; *E. angusta*, $n = 14$; *E. lata*, $n =$ ca. 28. These counts are especially significant because this section appears to be primitive within *Chamaesyce* and possesses a basic number of $x = 14$, thus strengthening the hypothesis of the origin of *Chamaesyce* from ancestors within subgen. *Agaloma* (Webster, 1967).

Two species, *Euphorbia capitellata* and *E. tomentulosa*, prove to have a number ($n = 7$) heretofore unreported in subsect. *Hypericifoliae.* However, $n = 14$ has been reported in *E. hypericifolia* and *E. parviflora* (Hans, 1973), which suggests that these species are tetraploids from a base of $x = 7$ as in *E. capitellata* and *E. tomentulosa.* It seems possible that the prevailing number of $n = 14$ in both subgen. *Agaloma* and subgen. *Chamaesyce* is of tetraploid origin from an original $x = 7$.

The remainder of the taxa counted in subgen. *Chamaesyce* fall into subsect. *Chamaesyce*, which includes the majority of species of the subgenus. Most of the numbers observed have been previously counted in other species, viz. 14 (*E. astyla*, *E. simulans*, *E. theriaca*); 12 (*E. micromera*, *E. serpens*); and 6 (*E. caruncolata*, *E. geyeri*, and *E. stictospora*).

Two reports exist in the literature for *Euphorbia prostrata*, $2n = 20$ (Murin and Chaudhri, 1970) and $n = 9$ (Datta, 1967), but it appears that the name was misapplied in that the aforementioned, presumably, should be referred to as *E. chamaesyce* while *E. prostrata* should refer only to a New World species as discussed by Correll and Johnston (1970). In any event, our report of $n = 6$ disagrees with all previous reports.

Polyploidy has been important in subgen. *Chamaesyce* in that apparent tetraploid races were discovered in *E. acuta.* Individuals of *E. acuta* having translocations also occur, as evidenced by ring formation. Our reports for *E. fendleri* var. *fendleri*, $n = 14$, and *E. f.* var. *chaetocalyx*, $n = 26$, suggest that the latter be reinstated at the specific level as treated by Tidestrom (1935). This contention is further reinforced by the fairly extensive overlap in the ranges of these varieties (Wheeler, 1941). A formal systematic treatment for this complex will not be forthcoming, however, until a third variety, *E. f.* var. *triligulata*, has been examined. Derived aneuploid varieties or

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$2n = 24$). **21.** *E. missurica, H, T 3441* (MI; $2n = 24$). **22.** *E. missurica, W 851* (AI; $2n = 26$). **23.** *E. polycarpa* var. *hirtella, H, S 3222* (MI; $2n = 26$). **24.** *E. polycarpa* var. *intermixta, H, S 3290* (MI; $2n = 28$). **25.** *E. serpyllifolia, H, T 3416* (Diak; $2n = 22$). **26.** *E. simulans, U 950* (MII; $2n = 28$). **27.** *E. spathulata, U 926* (MI; $2n = 12$). **28.** *E. stictospora, B, H 1289* (MI; $2n = 12$). **29.** *E. tetrapora, U 981* (AI; $2n = 26$). **30.** *E. theriaca, B, H 1424* (MII; $2n = 28$). **31.** *E. tomentulosa, U, H 1227* (MII; $2n = 14$). **32.** *E. wrightii, W 842* (AI; $2n = 28$). **33.** *E. sp., H, S 3218* (MII; $2n = 26$). **34.** *E. chiangii, U 1017* (MII; $2n = 26$). **35.** *Pedilanthus macrocarpus, H, S 3273* (MI; $2n = 36$). **36.** *Phyllanthus abnormis* var. *abnormis, H, T 3439* (MI; $2n =$ ca. 48). **37.** *Stillingia linearifolia, H, S 3256* (AI; $2n = 22$). **38.** *S. texana, U 1485* (MI; $2n = 72$).

TABLE 1. *Chromosome numbers of North American Euphorbiaceae*

Genus and Species	*n* =	Locality and Collector
Acalypha lindheimeri Muell. Arg.[a]	ca. 20 II	TX: Travis Co., *U 987.*
Argythamnia humilis var. *laevis* (Torr.) Shinners[a]	13 II	TX: Pecos Co., *B, H 1361.*
A. serrata (Torr.) Muell. Arg.[a]	ca. 13 II	MEX: BAJA CALIFORNIA: *H, S 3281.*
Croton californicus Muell. Arg.	ca. 14 II	MEX: BAJA CALIFORNIA: *H, S 3250.*
C. californicus Muell. Arg.	14 II	MEX: BAJA CALIFORNIA: *H, S 3274*; *U, H 1222*; *U, H 1266*; SONORA: *U, H 1137*; CA: Riverside Co., *H, S 3232.*
C. capitatus Michx. var. *capitatus*	10 II	TX: Johnston Co., *U 1034.*
C. dioicus Cav.[a]	14 II	MEX: COAHUILA: *U 1000*; *U 1005*; *U 1008*; NUEVO LEON: *U 1019*; TX: Brewster Co., *B, H 1438**; Crockett Co., *U 966*; Pecos Co., *U 963a, 963b*; U *1272*; Tom Greene Co., *W 841.*
C. dioicus Cav.[a]	28 II	TX: El Paso Co., *B, H 1412*; Reeves Co., *B, H 1358*.*
C. fruticulosus Torr.[a]	ca. 24 II	TX: Travis Co., *U 973.*
C. humilis L.[a]	10 II	MEX: NUEVO LEON: *U 1026*.*
C. magdalenae Millsp.[a]	10 II	MEX: BAJA CALIFORNIA SUR: *U, H 1198*.*
C. monanthogynus Michx.[b]	10 II	TX: Travis Co., *U 990*.*
C. pottsii (Kl.) M.A.[a]	9 II	TX: Presidio Co., *B, H 1425*.*
C. texensis (Klotzsch) Muell. Arg.[a]	14 II	NM: Eddy Co., *H, T 3438*.*
C. texensis (Klotzsch) Muell. Arg.[a]	28 II	TX: Randall Co., *B, H 1378.*
C. torreyanus Muell. Arg.[a]	10 II	MEX: COAHUILA: *U 1004*.*
Euphorbia: Subgen. *Agaloma*		
E. californica Benth.[a]	ca. 14 II	MEX: BAJA CALIFORNIA SUR: *U, H 1181.*
E. exstipulata Engelm.[a]	14 II	AZ: Coconino Co., *H, T 3415**; TX: Culberson Co., *H, T 1415.*
E. marginata Pursh	28 II	TX: Blanco Co., *W 855*; Colorado Co., *W 860.*
E. wrightii T. & G.[a]	14 II	TX: Tom Green Co., *W 842*.*
Euphorbia: Subgen. *Esula*		
E. brachycera Engelm.[a]	14 II	NM: Otero Co., *B, H 1392.*
E. tetrapora Englem.[a]	13 II	OK: McCurtain Co., *U 981*.*
Euphorbia: Subgen. *Poinsettia*		
E. cyathophora Murr.	14 II	MEX: COAHUILA: *B, H 1313.*
E. eriantha Benth.[a]	14 II	TX: Presidio Co., *B, H 1426*.*
E. dentata Michx.	28 II	TX: Lubbock Co., *H, T 3380*; Hale Co., *B, H 1375.*
Euphorbia: Subgen. *Chamaesyce*		
E. acuta Engelm.[a]	14 II	MEX: COAHUILA: *B, H 1306*.*
E. acuta Engelm.[a]	28 II	NM: Lincoln Co., *B, H 1384.*
E. acuta Engelm.[a]	24 II + 2 IV to 28 II	TX: Winkler Co., *B, H 1403*.*
E. albomarginata T. & G.[a]	12 II	TX: Webb Co., *U 1033*.*
E. angusta Engelm.[a]	14 II	TX: Hays Co., *W 854*; *U 988*; Travis Co., *H 3302*; *W 817.*
E. astyla Boiss.[a]	14 II	MEX: COAHUILA: *U 1020**; *P, T 2273*; *P, T 2282.*
E. capitellata Engelm.[a]	7 II	MEX: BAJA CALIFORNIA: *H, S 3265*.*
E. carunculata Waterfall[a]	6 II	TX: Winkler Co., *B, H 1400*.*

Collector Abbreviations: B = Bacon, H = Hartman, P = A. M. Powell, S = Fred Seaman, T = B. L. Turner, U = Urbatsch, W = Watson.

[a] First report for a taxon.

[b] Count differs from any previous report for a species.

† New state collection record.

[c] New county collection record.

TABLE 1. *Continued*

Genus and Species	$n =$	Locality and Collector
E. cinerascens Engelm.[a]	16 II	MEX: COAHUILA: *B, H 1294**; NUEVO LEON: *P, T 2340.*
E. fendleri T. & G. var. *chaetocalyx* Boiss.[a]	26 II	NM: Lincoln Co., *B, H 1385**.
E. fendleri T. & G. var. *fendleri*[a]	14 II	TX: Travis Co., *H 3301*; W *356.*
E. geyeri Engelm. var. *wheeleriana* Warn. & Johnst.[a, c]	6 II	TX: Hudspeth Co., *B, H 1408**.
E. glyptosperma Engelm.[a]	ca. 12 II	TX: Nolan Co., *B, H 1366.*
E. glyptosperma Engelm.[a]	ca. 10 II	WY: Platte Co., *W 869.*
E. lata Engelm.[a]	ca. 28 II	MEX: COAHUILA: *B, H 1293.*
E. micromera Engelm.[a]	12 II	NM: Dona Ana Co., *B, H 1410**.
E. missurica Raf.[a]	12 II	NM: Eddy Co., *H, T 3441**.
E. missurica Raf.[a]	13 II	TX: Travis Co., *W 851**.
E. nutans Lag.[a]	6 II	TX: Jeff Davis Co., *B, H 1419*; Travis Co., *U, H 1035*; Williamson Co., *U, H 1038*; *H 3298.*
E. polycarpa Benth. var. *hirtella* Boiss.[a]	13 II	CA: Imperial Co., *H, S 3222*, 3224.*
E. polycarpa Benth. var. *intermixta* (Wats.) Wheeler[a]	14 II	MEX: BAJA CALIFORNIA SUR: *H, S 3290**.
E. prostrata Ait.[b]	6 II	MEX: NUEVO LEON: *P, T 2296.*
E. serpens H. B. K.[a]	12 II	TX: Hays Co., *W 853.*
E. serpyllifolia Persoon[a]	11 II	AZ: Coconino Co., *H, T 3416**.
E. serrula Engelm.[a]	ca. 20 II	TX: Presidio Co., *B, H 1420.*
E. simulans (Wheeler) Warn. & Johnst.[a]	14 II	TX: Presidio Co., *U 950**.
E. spathulata Lam.[a]	6 II	NM: Otero Co., *B, H 1393*; TX: Travis Co., *U 926**; *W 810*; Williamson Co., *H 3924.*
E. stictospora Engelm.[a]	6 II	MEX: COAHUILA: *B, H 1289**; TX: Lubbock Co., *H, T 3379.*
E. theriaca Wheeler[a]	14 II	TX: Presidio Co., *B, H 1424**
E. tomentulosa S. Wats.[a]	7 II	MEX: BAJA CALIFORNIA: *U, H 1227**.
E. sp.[a]	13 II	AZ: Pinal Co., *H, S 3218**.
E. chiangii M. C. Johnst.	13 II	MEX: COAHUILA: *U 1017**.
Pedilanthus macrocarpus Benth.[b]	18 II	MEX: BAJA CALIFORNIA: *H, S 3273**.
Phyllanthus abnormis Baillon var. *abnormis*[a†]	ca. 24 II	NM: Eddy Co., *H, T 3439**.
P. polygonoides Spreng.	8 II	NM: Lincoln Co., *B, H 1386*; TX: Brewster Co., *P 2352*; Travis Co., *W 808*; *W 992*; *W 852.*
Reverchonia arenaria Gray	8 II	NM: Eddy Co., *H, T 3440*; TX: Hudspeth Co., *B, H 1490.*
Stillingia linearifolia Wats.[a]	11 II	MEX: BAJA CALIFORNIA: *H, S 3256**; *H, S 3282*; CA: Riverside Co., *H, S 3230.*
S. texana I. M. Johnst.[a]	36 II	TX: Travis Co., *U 1485**.

populations are suggested by the counts for *E. polycarpa* and *E. missurica.*

Our reports in subgen. *Poinsettia* for *Euphorbia dentata* and *E. cyathophora* verify earlier counts for these taxa as reviewed by Dressler (1961). Aside from the $2n = 14$ reported from a plant of *E. dentata* from Virginia (Perry, 1943), all other taxa in this subgenus are $n = 14$, 28 which presumably are polyploids suggesting a basic number of $x = 7$. This same conclusion was reached by Ewart and Walker (1960), who observed multivalent association in cultivars of *Euphorbia pulcherrima* having $2n = 28$. That the subgen. *Agaloma* and *Poinsettia* have close affinities (Dressler, 1961) is reinforced by the cytological data.

In *Euphorbia dentata* the polyploid populations appear to be widely distributed with $n = 14$ being reported from Virginia, Missouri, and Oaxaca while $n = 28$ populations are known from Missouri, Texas, and Guanajuato, Mexico (Dressler, 1961). A biosystematic study of *E. dentata* is currently needed to help solve several taxonomic problems in this variable taxon.

Pedilanthus—One other report of $2n =$ ca. 34 for *P. macrocarpus* is known (Dressler, 1957), and our data suggest that the number for this species is, in fact, $n = 18$. Reports for other species in this genus are $n = 17$ (Datta, 1967) and $2n = 32$, 34, 36 (Dressler, 1957), which suggest cytogenetical diversity resulting from aneuploid changes within the genus.

Phyllanthus—The counts for *P. polygonoides* agree with reports by Webster and Ellis (1962), while that for *P. abnormis* ($n =$ ca. 24) represents a first report. The latter species was placed in subsect. *Swartziani*; however, Webster (1970) notes that it is taxonomically isolated from the native species of *Phyllanthus* and that its affinities are probably with the weedy, circumtropical *P. amarus* whose chromosome number is $2n = 52$.

Reverchonia—The counts of $n = 8$ substantiate the only previous report (Webster and Miller, 1963) for this monotypic genus endemic to the southwestern United States and northern Mexico.

Stillingia—The numbers for *S. linearifolia* and *S. texana* represent the first reports for these species. The chromosome numbers of *S. sylvatica* ($2n = 36$; Perry, 1943) and *S. sanguinolenta* ($n = 30$; Miller and Webster, 1966) are the only ones previously known cytologically. The latter two counts and that of *S. texana* represent the subgen. *Stillingia* (Rogers, 1951), while those for *S. linearifolia* are the only known reports for the subgen. *Gymnostillingia*. The counts reported here give additional evidence for different basic numbers within the genus as suggested by Miller and Webster (1966).

Stillingia texana and *S. sylvatica* are closely related (Rogers, 1951); the chromosome number of the former suggests that it had a polyploid origin. Additionally, Rogers suggests the existence of polyploid races in *S. sylvatica*.

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NOTE ADDED IN PROOF: *Hartman & Seaman 3265* is now determined as *E. tomentulosa* S. Wats. and not *E. capitellata* as reported above.