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David P. Gregory

William M. Klein

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# INVESTIGATIONS OF MEIOTIC CHROMOSOMES OF SIX GENERA IN THE ONAGRACEAE

DAVID P. GREGORY AND WILLIAM M. KLEIN

## INTRODUCTION

Numerous cytological studies have been made in the Onagraceae during the last few years (see Cleland, 1950; Lewis and Lewis, 1955, and Lewis et al., 1958). Some of these studies have provided valuable data in connection with detailed cytogenetic and taxonomic investigations. Other scattered observations have been reported in an effort to gain a more complete knowledge of the basic numbers in the family and of such phenomena as translocation heterozygosity, polyploidy and occurrence of diminutive chromosomes and supernumeraries. The observations reported here are the results of a two year investigation, some from a detailed study in one group (*Oenothera* subgenus *Anogra*), the others scattered through species of several genera to survey the family further.

All of the observations have been made using pollen mother cells so that the degree of translocation heterozygosity could be determined. Most of the material used was collected from wild populations, but some was obtained from plants grown at the Rancho Santa Ana Botanic Garden. Seed was gathered by the authors or supplied by botanists or Botanic Gardens as indicated in the table. The determinations have either been made by Dr. Philip A. Munz or are based on his revision of the group concerned. Voucher specimens have been deposited in the herbarium of the Rancho Santa Ana Botanic Garden.

The technique used for the meiotic squashes is that given by Lewis (Lewis and Lewis, 1955) with the use of Hoyer's medium to make the slides permanent (Beeks, 1955). Buds, fixed in 1:3 glacial acetic acid and ethyl alcohol and stored in the refrigerator, were hydrolysed in a mixture of equal parts of concentrated HCl and 95 per cent ethyl alcohol for a period of from ten to twenty minutes depending upon the material. The anthers were stained with aceto- or propriono-carmine. A phase contrast microscope was used for interpretation of all slides, and drawings were made with the aid of a camera lucida at the magnifications indicated on the plates. Chromosomes were sometimes moved in the drawings where they overlapped and could cause confusion, but not in cases of questionable interpretation. The degree of translocation heterozygosity is reported wherever it could be analyzed.

## DISCUSSION

*Gaura.* The chromosome number of thirteen of the currently recognized eighteen species has now been counted at least once, all having the basic number of seven. Most of the species are diploids, but polyploids have been found in three species. Translocation heterozygosity is present in the diploids as indicated by rings of from four to twelve chromosomes.

The two species with actinomorphic flowers, *G. mutabilis* and *G. macrocarpa,* are diploids with a small ring in one plant of *G. macrocarpa.* The group of related species, *G. gracilis, G. nealleyi, G. suffulta* and *G. brachycarpa,* consists of diploids with a maximum association of four chromosomes in a ring in addition to the bivalents. *Gaura villosa* and *G. sinuata* have more translocations in some plants with a maximum association in each

[1]The work on which this paper is based was financed in part by Grant 4316 from the National Science Foundation, to which grateful acknowledgment is made.

TABLE 1. NUMBER OF CHROMOSOMES AND MEIOTIC ASSOCIATION

| | *Gametic number* | *Meiotic associations*[1] | *Locality and collector* | *Investigator* |
|---|---|---|---|---|
| *Gaura:* Gauridium *mutabilis* Cav. | 7 | 7II | El Salto, Durango, Mexico (RSABG). *J. H. Maysilles 7792.* | G |
| *Gaura:* Eugaura *brachycarpa* Small. | 7 | 5II+r4 | 5 mi. s. of Seguin, Guadalupe Co., Texas. *Munz and Gregory 23442.* | G |
| *coccinea* Nutt. var. *coccinea.* | 14 +3s | (6II+1ch4 +3r4)[2] | 6.8 mi. w. of Crystal, Clark Co., Nevada. *Gregory 33.* | G |
| | 14 +3s | (6II+4r4) | 30 mi. se. of Carp, Clark Co., Nevada. *Gregory 50.* | G |
| | 14 +2s | (3II+1a6 +4a4) | 1 mi. n. of Jean, Clark Co., Nevada. *Gregory 56.* | G |
| | 21 | | 30 mi. s. of Mason, Gillespie Co., Texas. *Munz and Gregory 23434.* | G |
| *coccinea* var. *glabra* (Lehm.) Torr. and Gray. | 14 | | 1 mi. s. of The Forks, Highway 287, Larimer Co., Colorado. *H. and M. Lewis 1183.* | G |
| *coccinea* var. *epilobioides* (H. B. K.) Munz. | 14 +1s | | 49 mi. e. of Sanderson, Terrell Co., Texas. *Gregory 277.* | G |
| | 21 | | 11 mi. s. of Toyahvale, Jeff Davis Co., Texas. *Munz and Gregory 23377.* | G |
| | 21 | | 29 mi. ne. of Mexico City, Mexico, Mexico. *Ted Anderson 1083.* | G |
| *coccinea* var. *arizonica* Munz. | 21 | | Globe, Gila Co., Arizona. *Munz and Gregory 23322.* | G |
| *gracilis* Woot. and Standl. var. *gracilis.* | 7 | 5II+r4 | 6 mi. e. of Superior, Pima Co., Arizona. *Munz and Gregory 23321.* | G |
| *lindheimeri* Engelm. and Gray. | 7 | 1II+2r6 | 10 mi. e. of Beaumont, Orange Co., Texas. *Munz and Gregory 23460.* | G |
| *macrocarpa* Rothrock. | 7 | 7II | 13 mi. n. of Fort Davis, Jeff Davis Co., Texas. *Munz and Gregory 23380.* | G |
| | 7 | 5II+r4 | Same | G |
| *nealleyi* Coulter. | 7 | 7II | 27 mi. e. of Mayhill, Chaves Co., New Mexico. *Munz and Gregory 23345.* | G |
| | 7 | 7II | 5 mi. w. of Alpine, Brewster Co., Texas. *Munz and Gregory 23393.* | G |

[1]In this table r=ring, ch=chain, II=bivalent, I=univalent, a=association, s=supernumerary chromosome, RSABG=grown at the Rancho Santa Ana Botanic Garden from seed from the source indicated. If more than one plant of a collection was examined the number is given in parentheses. Meiotic associations that could not be determined exactly are also included in parentheses.

[2]The associations of chromosomes in polyploid species may be due either to translocation heterozygosity or to multivalent pairing, but they are indicated as in the diploids.

| | *Gametic number* | *Meiotic associations*[1] | *Locality and collector* | *Investigator* |
|---|---|---|---|---|
| *odorata* Sessé ex. Lag. | 14 | (?II+1a6 or 8+3a4) | 7 mi. s. of. Fredericksburg, Gillespie Co., Texas. *Munz and Gregory 23436.* | G |
| | 14 | (5II+1a6+ 3a4) | 20 mi. n. of Beeville, Bee Co., Texas. *Munz and Gregory 23445.* | G |
| *parviflora* var. *lachnocarpa* Weatherby. | 7 | 7II | 14 mi. e. of Alamogordo, Otero Co., New Mexico. *Munz and Gregory 23341.* | G |
| *sinuata* Nutt. ex Seringe. | 7 | 7II | 4.5 mi. se. of Brady, McCulloch Co., Texas. *Munz and Gregory 23430.* | G |
| | 7 | 5II+r4 | 2.5 mi. w. of Eden, Concho Co., Texas. *Munz and Gregory 23424.* | G |
| | 7 | 2II+r4+r6 | 3 mi. n. of Fort Davis, Jeff Davis Co., Texas. *Munz and Gregory 23383.* | G |
| | 14 | 4II+ch4+ 2r4+r8 | 7 mi. s. of Fredericksburg, Gillespie Co., Texas. *Munz and Gregory 23437.* | G |
| *suffulta* Engelm. ex Gray. var. *suffulta.* | 7 | | 3.5 mi. se. of Brady, McCulloch Co., Texas. *Munz and Gregory 23427.* | G |
| *suffulta* var. *terrellensis* Munz. | 7 | 7II | 5 mi. w. of Sanderson, Terrell Co., Texas. *Munz and Gregory 23403.* | G |
| *villosa* var. *arenicola* Munz. | 7 | 7II | Ward Co., Texas (RSABG). *Turner and Warnock 69.* | G |
| | 7 | 5II+r4 | 1 mi. e. of Monahans, Ward Co., Texas. *Munz and Gregory 23408.* | G |
| *villosa* Torrey var. *villosa.* | 7 | 2II+r4+r6 | 5 mi. e. of Midland, Midland Co., Texas. *Munz and Gregory 23415.* | G |
| *Jussiaea:* Myrtocarpus *caparosa* Camb. | 16 | 16II | (RSABG). *USDA 18946.* | G |
| *decurrens* (Walt.) D. C. | 8 | 8II | Just w. of Caryville, Washington Co., Florida (RSABG). *Godfrey and Kral 55164.* | G |
| *erecta* L. | 8 | 8II | Nw. of Toxahatchee, Palm Beach Co., Florida (RSABG). *Kral 5702.* | G |
| | 8 | 8II | 10 mi. se. of Naples, Collier Co., Florida. *Munz and Gregory 23474.* | G |
| *longifolia* D. C. var. *longifolia.* | 8 | 8II | (RSABG). *USDA 18756.* | G |
| *peruviana* L. | 48 | 48II | 1.5 mi. s. of Fort Meade, Polk Co., Florida. *Munz and Gregory 23470.* | G |
| *sericea* var. *genuina* Munz. | 16 | 16II | (RSABG). *USDA 18763.* | G |
| *Jussiaea:* Macrocarpon *suffruticosa* var. *ligustrifolia* (H. B. K.) Griseb. | 16 | 16II | 10 mi. se. of Naples, Collier Co., Florida (RSABG). *Munz and Gregory 23475.* | G |

| | *Gametic number* | *Meiotic associations*[1] | *Locality and collector* | *Investigator* |
|---|---|---|---|---|
| *Jussiaea:* Eujussiaea *leptocarpa* Nutt. | 16 | 16II | Boggy Bayou, Freeport, Walton Co., Florida (RSABG). *Godfrey 57651.* | G |
| *repens* var. *peploides* (H. K.B.) Griseb. | 8 | 8II | Cultivated in the pond at the Rancho Santa Ana Botanic Garden. | G |
| *repens* var. *glabrescens* O. Kuntze. | 8 | | 5.5 mi. se. of Presidio, Presidio Co., Texas. *Gregory 224.* | G |
| *Lopezia coronata* Andrews | 10 | 10II | (RSABG), seed from the Botanic Garden at Copenhagen. *Munz and Gregory 23316.* | G |
| | 10 | 10II | (RSABG), seed from Hortus Bergianus at Stockholm. *Munz and Gregory 23318.* | G |
| *mexicana* Jacq. | 10 | 10II | (RSABG), seed from the Botanic Garden at Lisbon. *Munz and Gregory 23319.* | G |
| *Ludwigia:* Dantia *palustris* var. *americana* (D.C.) Fern. and Griscom. | 8 | 8II | 10 mi. w. of Hot Springs, Garland Co., Arkansas. *Munz and Gregory 23502.* | G |
| *palustris* var. *nana* Fern. and Griscom. | 8 | 8II | 12 mi. w. of Beaumont, Jefferson Co., Texas. *Munz and Gregory 23459.* | G |
| *natans Ell.* var. *natans.* | 24 | 24II | 37 mi. se. of Perry, Dixie Co., Florida. *Munz and Gregory 23467.* | G |
| *Ludwigia:* Ludwigiantha *arcuata* Walt. | 16 | 16II | 2 mi. s. of Oakland, Orange Co., Florida (RSABG). *Godfrey 57332.* | G |
| *Ludwigia:* Ludwigiaria *alternifolia* var. *pubescens* Palmer and Steyermark. | 8 | 8II | Garland Co., Arkansas (RSABG). *Demaree 40523.* | G |
| *maritima* Harper. | | 8II | 14 mi. s. of Oakland, Orange Co., Florida (RSABG). *Godfrey 57354.* | G |
| *Ludwigia:* Microcarpium *curtissii* Chapman. | 24 | 24II | 10 mi. se. of Naples, Collier Co., Florida. *Munz and Gregory 23476.* | G |
| *glandulosa* Walt. var. *glandulosa.* | 16 | 16II | Leon Co., Florida (RSABG). Seed collected by *Godfrey.* | G |
| *linifolia* Poir. | 8 | 8II | 3 mi. e. of Ocean Springs, Jackson Co., Mississippi (RSABG). *Demaree 37879.* | G |
| *simpsonii* Chapman. | 24 | 24II | 6 mi. s. of Stuart, Martin Co., Florida (RSABG). *Munz and Gregory 23481.* | G |
| *sphaerocarpa* Elliot var. *sphaerocarpa.* | 16 | 16II | (RSABG). *Monoson 55.* | G |
| *Oenothera:* Anogra *californica* Wats. var. *californica.* (Great Basin) | 7 | 7II | 5 mi. s. Oasis, Inyo Co., California. *Klein 339.* | K |

| | *Gametic number* | *Meiotic associations*[1] | *Locality and collector* | *Investigator* |
|---|---|---|---|---|
| | 7 | 7II | Cedar Canyon, San Bernardino Co., California. *Klein 926.* | K |
| | 7 | 7II | 0.5 mi. ne. of Leeds, Washington Co., Utah. *Klein 1049.* | K |
| | 7 | 5II+r4 | Same. | K |
| | 7 | 7II | Pine Valley, Washington Co., Utah. *Klein 1052.* | K |
| | 7 | 5II+r4 | Same. *Klein 1054.* | K |
| | 7 | 7II | 23 mi. w. of Beaver, Beaver Co., Utah. *Klein 1060.* | K |
| | 7 | 7II (2) | 8.5 mi. w. of Milford, Beaver Co., Utah. *Klein 1064.* | K |
| | 7 | 5II+r4 | 2 mi. w. of Austin, Lander Co., Nevada. *Klein 1069.* | K |
| *californica* Wats. var. *californica.* (Coastal Ranges of Southern California) | 14 | 4II+2r4+ 2ch4+1ch3+ 1I | Morongo Valley, San Bernardino Co., California. *Klein 867.* | K |
| | 14 | | 23 mi. n. of Castaic, Los Angeles Co., California. *Klein 475.* | K |
| *deltoides* Torr. and Frem. var. *deltoides.* | 7 | 7II | 3.6 mi. s. of Kane Springs, Imperial Co., California. *Klein 61.* | K |
| | 7 | 7II | 4.5 mi. n. of Ripley, Riverside Co., California. *Klein 147.* | K |
| | 7 | 7II | 10 mi. e. of Yuma on Highway 95, Yuma Co., Arizona. *Munz, Gregory, and Klein 22965.* | K |
| | 7 | 7II (3) | Bermuda Dunes, Riverside Co., California. *Klein 797, 802, 805.* | K |
| | 7 | 5II+r4 | Bermuda Dunes, Riverside Co., California. *Klein 800.* | K |
| | 7 | 7II (2) | 3 mi. nw. of Bouse, Yuma Co., Arizona. *Klein 961, 962.* | K |
| | 7 | 5II+r4 | 2.5 mi. nw. of Bouse, Yuma Co., Arizona. *Klein 960.* | K |
| | 7 | | Highway 99, 20 mi. s. of the Riverside-Imperial Co. line, Imperial Co., California. *Klein 54.* | K |
| *deltoides* var. *ambigua* Munz. | 7 | 7II | Boulder City, Clark Co., Nevada. *Munz, Gregory, and Klein 22988.* | K |
| *deltoides* var. *arizonica* Munz. | 7 | 3II+r4+ ch4 | 18 mi. nw. of Hope, Yuma Co., Arizona. *Klein 955.* | K |
| | 7 | 7II | Same. *V. E. and A. Grant 10074.* | K |
| *deltoides* var. *cineracea* Munz. | 7 | 7II | Highway 80, 5 mi. e. of Holtville, Imperial Co., California. *Klein 75.* | K |
| | 7 | 7II | 3.5 mi. nw. of Indio City Limits, Riverside Co., California. *Munz, Gregory, and Klein 22962.* | K |
| *deltoides* var. *cognata* (Jeps.) Munz. | 7 | 7II | Highway 140, 20 mi. w. of Merced, Merced Co., California. *Kein 443.* | K |
| *deltoides* subsp. *eurekensis* Munz and Roos. | 7 | 7II | Eureka Valley, Inyo Co., California. *Klein 383.* | K |

| | *Gametic number* | *Meiotic associations*[1] | *Locality and collector* | *Investigator* |
|---|---|---|---|---|
| *deltoides* var. *howellii* Munz. | 7 | 5II+r4 | Antioch, Contra Costa Co., California. *Klein 440.* | K |
| *deltoides* var. *piperi* Munz. | 7 | 7II | 16 mi. ne. of Carson City, Lyon Co., Nevada. *Klein 425.* | K |
| | 7 | 5II+r4 | Same. *Klein 426.* | K |
| | 7 | 7II (5) | 5 mi. e. of Carson City, Lyon Co., Nevada. *Klein 1080, 1086, 1085, 1082, and 1079.* | K |
| | 7 | 5II+r4 | Same. *Klein 1081.* | K |
| *engelmanni* (Small) Munz. | 7 | 5II+r4 | 3 mi. w. of Big Spring, Howard Co., Texas. *Gregory 294.* | K |
| *nuttallii* Sweet. | 7 | 5II+r4 | Green Mountain Reservoir, Summit Co., Colorado. *H. and M. Lewis 1172.* | K |
| | 14 | 4II+2r4+ ch4+ch8 | 12 mi. n. of Livermore, Larimer Co., Colorado. *Klein 1136.* | K |
| | 14 | (3II+4r4+ ch6) | 12 mi. s. of Laramie, Albany Co., Wyoming. *H. and M. Lewis 1185.* | K |
| | 14 | | 19 mi. n. of Laramie, Albany Co., Wyoming. *Klein 1138.* | K |
| *pallida* Lindl. | 7 | 2II+r6+r4 | Highway 93, 6.5 mi. s. of the Idaho-Nevada state line, Elko Co., Nevada. *Klein 1153.* | K |
| | 7 | 3II+r8 | 11 mi. nw. of the south entrance to Zion National Park, Washington Co., Utah. *Klein 1094.* | K |
| *runcinata* (Engelm.) Munz. var. *runcinata.* | 7 | 7II | 14.6 mi. ne. of Horse Springs, Catron Co., New Mexico. *Gregory 323.* | K |
| *runcinata* var. *gypsophila* (Eastwood) Munz. | 7 | 5II+r4 | White Sands National Monument, Otero Co., New Mexico. *Gregory 309-313.* | K |
| *trichocalyx* Nutt. | 7 | 5II+r4 | Highway 6 and 50, 10 mi. e. of Wellington, Carbon Co., Utah. *Klein 1099.* | K |
| *Oenothera:* Calylophis *serrulata* var. *pinifolia* Engelm. | 7 | 5II+r4 | 5 mi. n. of Stockdale, Wilson Co., Texas. *Munz and Gregory 23443.* | G |
| | 7 | 3II+r8 | 6 mi. sw. of White City, Eddy Co., New Mexico. *Munz and Gregory 23359.* | G |
| *serrulata* var. *drummondii* f. *flava* Munz. | 7 | 2II+r4+r6 | 9 mi. se. of Brady, McCulloch Co., Texas. *Munz and Gregory 23431.* | G |
| *Oenothera:* Eulobus *crassifolia* Greene. | 7 | | 10 mi. s. of San Quintin, Baja California, Mexico. *Klein 13.* | G |
| *Oenothera:* Hartmannia *deserticola* (Loesener) Munz. | 7 | 7II | Near Rio Frio, Mexico City-Puebla Highway, Mexico, Mexico (RSABG). *Straw and Gregory 1120.* | G |
| | 7 | | Lagunas de Zempoala, Morelos, Mexico (RSABG). *Straw and Gregory 1068.* | G |

| | *Gametic number* | *Meiotic associations*[1] | *Locality and collector* | *Investigator* |
|---|---|---|---|---|
| *speciosa* Nutt. var. *speciosa.* | 7 | 7II | 10 mi. e. of Boerne, Kendall Co., Texas. *Munz and Gregory 23439.* | G |
| | 7 | 5II+r4 | 5 mi. w. of Garden City, Glasscock Co., Texas. *Munz and Gregory 23418.* | G |
| *speciosa* var. *childsii* (Bailey) Munz. | 14 | | 15 mi. w. of Beaumont, Jefferson Co., Texas. *Munz and Gregory 23456.* | G |
| | 21 | 7II+ch6+ 2ch4+r6+2r4 | 13 mi. sw. of West Columbia, Matagordo Co., Texas. *Munz and Gregory 23452.* | G |
| *Oenothera:* Kneiffia *linifolia* Nutt. var. *linifolia.* | 7 | 7II | 5 mi. w. of Mt. Ida, Montgomery Co., Arkansas (RSABG). *Munz and Gregory 23503.* | G |
| *spachiana* Torr. and Gray. | 7 | 7II | Kingston, Marshall Co., Oklahoma (RSABG). *Waterfall 11448.* | G |
| *fruticosa* var. *vera* f. *angustifolia* Lévl. | 14 | | 10 mi. n. of Charlotte, Mecklenburg Co., N. Carolina. *Munz and Gregory 23497.* | G |
| *tetragona* var. *brevistipata* (Pennell) Munz. | 14 | | 13 mi. w. of Savannah, Hardin Co., Tennessee. *Munz and Gregory 23500.* | G |
| *tetragona* Roth. var. *tetragona.* | 14 | | N. of Saluda, Saluda Co., S. Carolina. *Munz and Gregory 23496.* | G |
| | 21 | 5II+ch6+ ch4+r6+4r4 | 3 mi. n. of Hardeeville, Jasper Co., S. Carolina. *Munz and Gregory 23491.* | G |
| *Oenothera:* Lavauxia *taraxacoides* (Woot. and Standl.) Munz. | 7 | 2II+r4+r6 | 4 mi. e. of El Salto, Durango, Mexico (RSABG). *Waterfall 13711.* | G |
| *Oenothera:* Megapterium *brachycarpa* var. *wrightii* (A. Gray) Leveille. | 7 | 7II | 18.3 mi. s. of Toyahvale, Jeff Davis Co., Texas. *Gregory 170.* | G |
| | 7 | 5II+ch4 | 1 mi. e. of Emery Pass, Mimbres Mtns., Sierra Co., New Mexico. *Munz and Gregory 23331.* | G |
| | 7 | | 27 mi. e. of Mayhill, Chaves Co., New Mexico. *Munz and Gregory 23343.* | G |
| *Oenothera:* Pachylophis *caespitosa* var. *marginata* (Nutt.) Munz. | 7 | 5II+ch4 | 9.8 mi. n. of Coleville, Mono Co., California. *Klein 416.* | G |
| *xylocarpa* Coville. | 7 | | 4 mi. s. of Crestview, Mono Co., California. *Klein 401.* | G |
| *Oenothera:* Raimannia *albicaulis* Pursh. | 7 | 7II | 1.7 mi. w. of Mule Creek, Grant Co., New Mexico. *Munz and Gregory 23326.* | G |
| | 7 | 5II+r4 | 1.7 mi. w. of Mule Creek, Grant Co., New Mexico. *Munz and Gregory 23325.* | G |

| | *Gametic number* | *Meiotic associations*[1] | *Locality and collector* | *Investigator* |
|---|---|---|---|---|
| *coronopifolia* T. and G. | 7 | 5II+r4 | Twin Lakes, Lake Co., Colorado. *H. and M. Lewis 1168.* | K |
| | 14 | 2II+ch8+4r4 | 6 mi. e. of Flagstaff, Coconino Co., Arizona. *Munz and Gregory 23523.* | G |
| *drummodii* Hook. var. *drummondii.* | 7 | 4II+r6 | 8 mi. ne. of Tampico, Tamaulipas, Mexico (RSABG). *U. T. Waterfall 14644.* | G |
| | 7 | 4II+r6 | E. of Aransas Pass, San Patricio Co., Texas. *Munz and Gregory 23450.* | G |
| | 7 | 2II+r4+r6 | Same. | G |
| *humifusa* Nutt. | 7 | (r12 or 14) | Lake Park, Palm Beach Co., Florida. *Munz and Gregory 23480.* | G |
| *laciniata* Hill. var. *laciniata.* | 7 | | 10 mi. n. of Brunswick, Glynn Co., Georgia. *Munz and Gregory 23489.* | G |
| | 7 | | Pass Christian, Harrison Co., Mississippi. *Munz and Gregory 23461.* | G |
| *laciniata* var. *grandiflora* (Wats.) Robinson. | 7 | 7II | 3 mi. se. of Midland, Midland Co., Texas. *Munz and Gregory 23411.* | G |
| *laciniata* var. *pubescens* (Willd.) Munz. | 7 | r14 | Off the old highway between Mexico City and Cuernavaca, Morelos, Mexico (RSABG). *Straw and Gregory 1075.* | G |
| *rhombipetala* Nutt. ex T. and G. | 7 | 7II | 5 mi. w. of Elk City, Beckham Co., Oklahoma. *Munz and Gregory 23511.* | G |
| | 7 | 3II+2r4 | Waddell Ranch, Winkler Co., Texas. (RSABG). *H. Nessmith 124.* | G |
| *Oenothera:* Salpingia *tubicula* A. Gray. | 7 | 7II | 5 mi. n. of Marfa, Presidio Co., Texas. *Munz and Gregory 23389.* | G |
| | 7 | 5II+r4 | 4 mi. w. of Hope, Eddy Co., New Mexico. *Munz and Gregory 23350.* | G |
| | 7 | 5II+r4 | Carlsbad, Eddy Co., New Mexico. *Munz and Gregory 23353.* | G |
| *hartwegii* Benth. var. *hartwegii.* | 7 | 5II+r4 | Santa Rosa, Guadalupe Co., New Mexico. *Munz and Gregory 23516.* | G |
| | 7 | 2II+r4+r6 | 6 mi. sw. of White City, Eddy Co., New Mexico. *Munz and Gregory 23357.* | G |
| *hartwegii* var. *fendleri* Gray. | 7 | 5II+r4 | 6 mi. se. of Elk, Chaves Co., New Mexico. *Munz and Gregory 23346.* | G |
| *hartwegii* var. *filifolia* (Eastw.) Munz. | 7 | 3II+2r4 | White Sands National Monument, Otero Co., New Mexico. *Munz and Gregory 23335.* | G |
| *greggii* var. *lampasana* (Buckley) Munz. | 7 | 5II+r4 | 2.5 mi. w. of Eden, Concho Co., Texas. *Munz and Gregory 23425.* | G |

| | *Gametic number* | *Meiotic associations*[1] | *Locality and collector* | *Investigator* |
|---|---|---|---|---|
| | 7 | 4II+ch6 | 29 mi. sw. of White City, New Mexico, Culberson Co., Texas. *Munz and Gregory 23364.* | G |
| | 7 | 2II+r4+r6 | 4 mi. s. of Alpine, Brewster Co., Texas. *Munz and Gregory 23395.* | G |
| *Oenothera:* Sphaerostigma *dentata* var. *johnstonii* Munz. | 7 | 7II | Jawbone Canyon, Kern Co., California. *Munz and Gregory 23310.* | G |
| | 7 | 7II | 10 mi. n. of Red Rock Canyon, Kern Co., California. *Munz and Gregory 23313.* | G |
| *Stenosiphon linifolium* (Nutt.) Britton. | 7 | 3II+2r4 | 22 mi. w. of El Reno, Caddo Co., Oklahoma. *Munz and Gregory 23507.* | G |

species of one ring of four plus one of six. Bhaduri (1942) has reported a ring of twelve in *G. biennis* which is the largest ring known in the genus. He also reports (1941, 1942) a ring of six in one plant and two rings of four in another in *G. lindheimeri,* whereas the collection reported here has two rings of six. With more intensive sampling, complex translocation heterozygosity may prove to be extensive among this group of eastern species, four of which have not been studied cytologically.

Three collections of *G. sinuata* were diploid and a fourth strain of *G. sinuata* which was growing with *G. odorata* was tetraploid. Lewis et al. (1958) have also reported a tetraploid count for this species. Lewis recorded four associations of four chromosomes in the tetraploid, and in the tetraploid counted here there were three associations of four and one of eight. *Gaura odorata* is probably a tetraploid species (the collection reported as diploid in Lewis et al., 1958, is actually *G. suffulta*). There were seven associations of four in the plant counted by Lewis and he suggested it to be an autoploid. The two collections given in this paper could not be analyzed exactly, but one had one association of six or eight and at least two of four chromosomes. The other had one of six and probably three of four chromosomes. Though not as strong an indication of autoploidy as the previous one, these configurations would not be inconsistent with such an interpretation. *Gaura coccinea* includes plants with gametic numbers of 7 (Lewis et al., 1958), 14 and 21. There is much morphological variation in both the tetraploid and the hexaploid and these levels are not completely separated geographically, as one of the tetraploid plants is from west Texas, where all three levels occur. No morphological characteristics correlating with and differentiating the three chromosomal levels have been found as yet. The exact extent of chromosome association has been hard to determine in the preparations of *G. coccinea* polyploids. *Gaura coccinea* is a widespread and highly variable species and as presently constituted probably contains more than one species. Plants with one, two or three small supernumerary chromosomes were found in four of the tetraploid collections. In one, with two supernumeraries, the chromosomes seemed to form a diminutive pair at metaphase I.

*Jussiaea.* The nine species of the genus for which chromosome counts are reported here all have the basic number eight, and polyploidy seems common and is probably well advanced as indicated by the dodecaploid species, *J. peruviana.* Of the nine species counted four were diploid, four tetraploid and one dodecaploid. There are no hexaploids known in *Jussiaea* although three have been found in *Ludwigia.* There are chromosomal size differences between species of *Jussiaea* as well as *Ludwigia,* but these do not seem to be correlated

with polyploid level. There are roughly two size categories and both are found in each genus.

*Ludwigia.* As in *Jussiaea* the basic number is eight, evidence supporting the recent suggestion (Brenan, 1953; Hara, 1953) that the two genera be placed in one. Polyploidy is again evident, for of the ten species counted four were diploid, three tetraploid and three hexaploid. There was no indication of translocation heterozygosity in either *Ludwigia* or *Jussiaea.*

*Lopezia.* The two counts of ten pairs of chromosomes for *L. coronata,* when considered with the two identical counts for *L. mexicana* (the specimen reported in Lewis et al., 1958, as *L. lineata* is actually *L. mexicana*), suggest that Täckholm's (1914) report of eleven pairs for *L. coronata* might have been in error.

*Oenothera: Anogra.* In this subgenus chromosome studies at meiosis have been made for all but two of the nine species treated in the revision by Munz (1931). Five of these species are diploid, and for two others, *Oe. californica* and *Oe. nuttallii,* both diploid and tetraploid forms are known.

The tetraploids of *Oe. californica* which have been reported thus far (Lewis et al., 1958; Snow, 1959) were located in the coastal ranges of southern California. The diploid material which has been attributed to this same species centers in the Great Basin region. The maximum associations in the tetraploids reported here are four associations of four and a chain of three. Lewis et al. (1958) reported a maximum association of two rings or chains of eight and two of four chromosomes. Plants from the Great Basin region were commonly found to possess small rings, and individuals which were structurally homozygous, or heterozygous for a single translocation, were found in the same colony.

The diploid material of *Oe. nuttallii* was obtained from a single collection made in the Rocky Mountains of Colorado near the Green Mountain Dam. It was found to be heterozygous for a single translocation. The tetraploid material was from the plains and foothills just east of the Rocky Mountains near Laramie, Wyoming. The maximum meiotic association in the tetraploid was a chain of eight and three associations of four.

All of the entities presently included in the *Oe. deltoides* species complex have been counted at least once. Most of the material is structurally homozygous but where quite a number of individuals were examined it has usually been possible to find a few plants which are heterozygous for at least one translocation. The highest number of translocations encountered was in the variety *arizonica* which had two associations of four.

The other species of the subgenus so far observed are either seven paired or heterozygous for a single translocation, with one notable exception, *Oe. pallida.* In material from Zion Canyon National Park, an area in which three of the species in the subgenus are closely associated (*Oe. californica* [Great Basin], *Oe. runcinata* and *Oe. pallida*), chromosome associations of intermediate size have been found. Other material which has been collected from this region has been found to be somewhat intermediate morphologically and has been variously assigned to the three species mentioned above and also to a fourth, *Oe. trichocalyx.* A collection of *Oe. pallida* from northeastern Nevada had a ring of six and one of four.

In summary it can be said that this subgenus consists primarily of diploid individuals

PLATE 1. Camera lucida drawings of chromosomes during meiosis in species of *Gaura* and *Stenosiphon.* Figures 1, 2, 4, 6, 8, and 11, diakinesis; figures 3, 5, 7, 9, and 10, first metaphase. 1. *Gaura lindeheimeri,* one pair and two rings of six. 2. *Gaura brachycarpa,* five pairs and a ring of four. 3. *Gaura parviflora,* seven pairs. 4. *Gaura gracilis,* five pairs and a ring of four. 5. *Gaura suffulta* var. *terrellensis,* seven pairs. 6. *Gaura villosa* var. *arenicola,* five pairs and a ring of four. 7. *Gaura macrocarpa,* seven pairs. 8. *Gaura sinuata,* two pairs, a ring of six, and a ring of four. 9. *Gaura coccinea* var. *epilobioides,* 42 chromosomes, associations not determinable. 10. *Gaura coccinea,* 28 chromosomes, associations not completely determinable, plus three supernumerary chromosomes. 11. *Stenosiphon linifolium,* three pairs and two rings of four. All drawings × 1600.

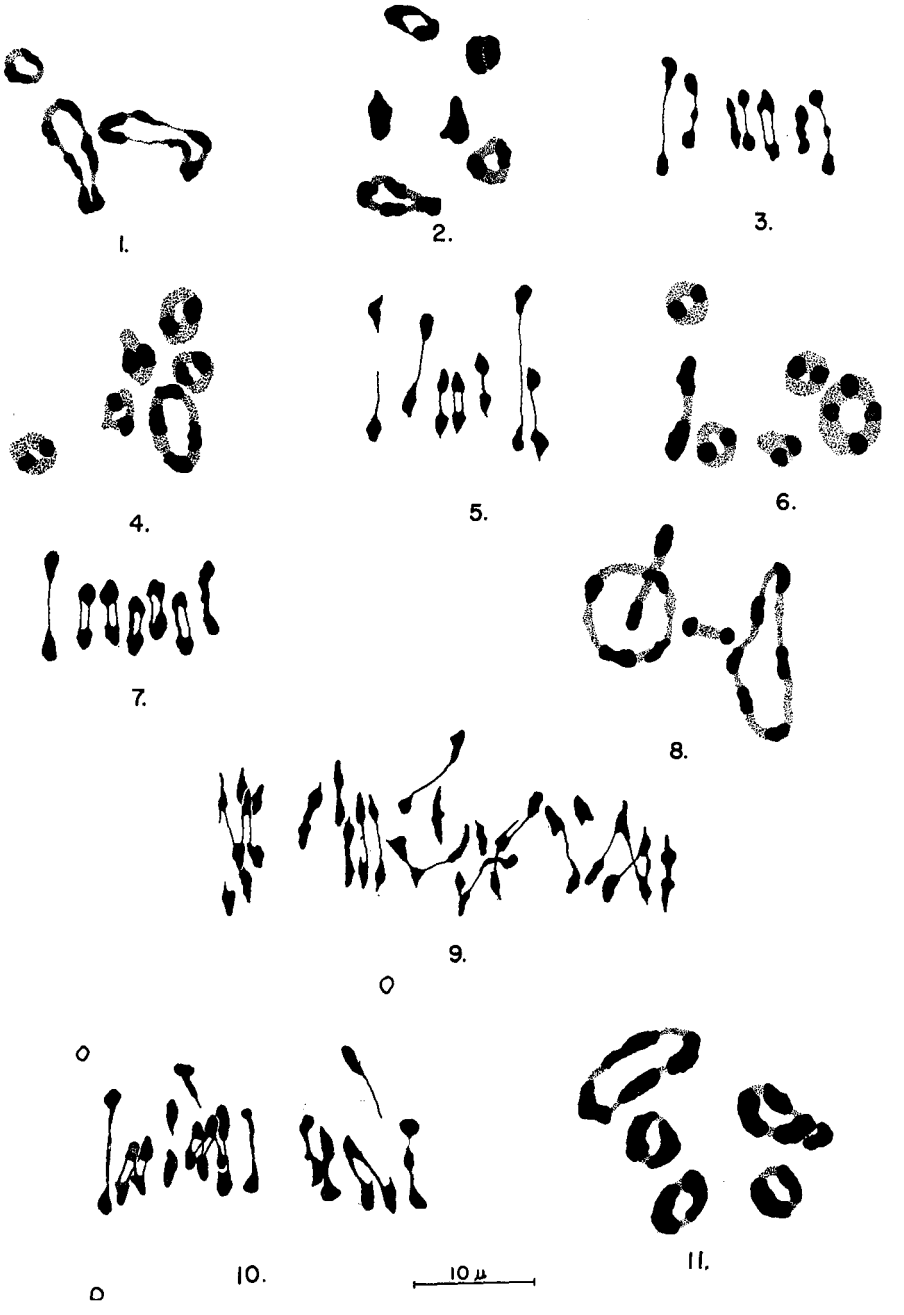


PLATE 1

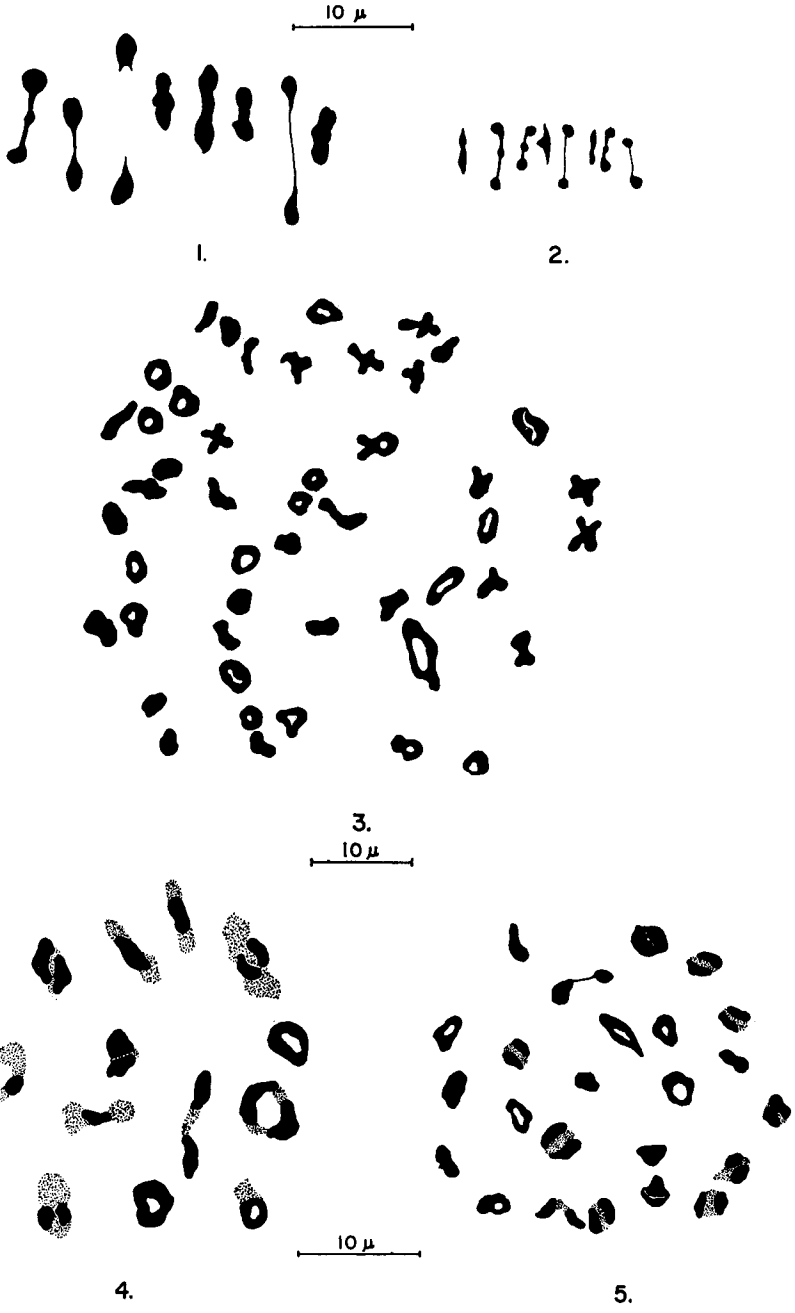


PLATE 2. Camera lucida drawings of chromosomes during meiosis in species of *Ludwigia* and *Jussiaea*. Figures 1 and 2, first metaphase; figures 3-5, diakinesis. 1. *Ludwigia maritima*, eight pairs. 2. *Jussiaea repens* var. *peploides*, eight pairs. 3. *Jussiaea peruviana*, 48 pairs. 4. *Jussiaea leptocarpa*, sixteen pairs. 5. *Ludwigia natans*, 24 pairs. Figures 1, 2, 4, and 5, × 1600; figure 3, × 1350.

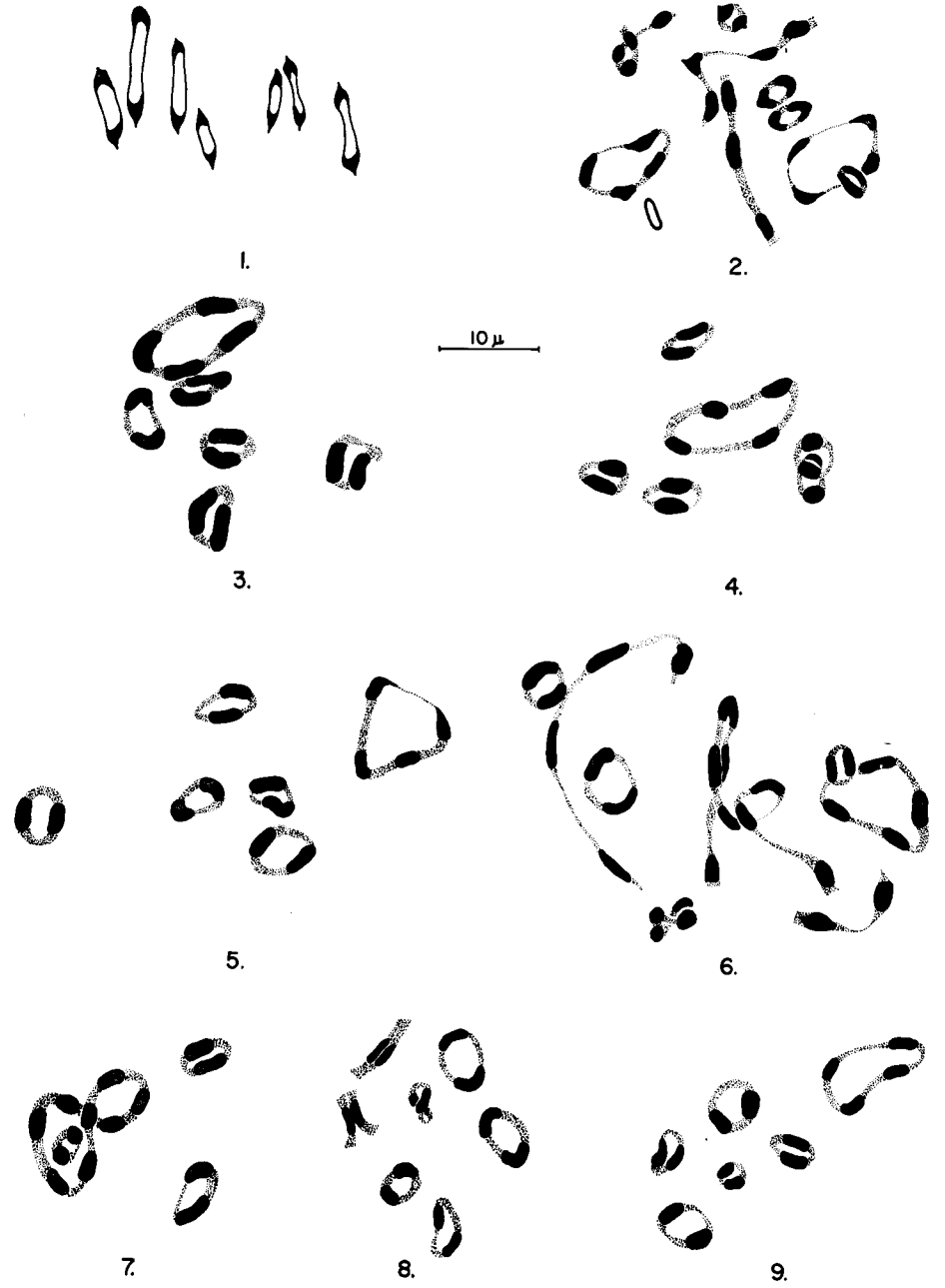


PLATE 3. Camera lucida drawings of chromosomes during meiosis in species of *Oenothera* subgenus *Anogra*. Figure 1, first metaphase; figures 2-9, diakinesis. 1. *Oeonthera californica* (Great Basin), seven pairs. 2. *Oenothera californica* (Coastal Ranges), four pairs, two chains of four, two rings of four, chain of three and one univalent. 3. *Oenothera deltoides* var. *deltoides*, five pairs and a ring of four. 4. *Oenothera engelmanni*, five pairs and a ring of four. 5. *Oenothera nuttallii*, five pairs and a ring of four. 6. *Oenothera nuttallii*, four pairs, two rings of four, a chain of four, and a chain of eight. 7. *Oenothera pallida*, three pairs and a ring of eight. 8. *Oenothera runcinata*, seven pairs. 9. *Oenothera trichocalyx*, five pairs and a ring of four. All drawings × 1350.

which are structurally homozygous but with single translocations occasionally found in the colonies. The only exception to this is *Oe. pallida* in which associations of intermediate size occur. Two of the species have tetraploid representatives which because of their chromosome associations at meiosis (see Hecht, 1942; Lewis et al., 1958, and Snow, 1959) and also because of their morphological similarity to a diploid strongly suggest that they are autotetraploids.

*Oenothera: Calylophis.* The meiotic investigations given here indicate that *Oe. serrulata* is a diploid with rings of intermediate size. This is consistent with the reports of Lewis et al. (1958) and Linder and Brun (1957).

*Oenothera: Hartmannia.* Reports for this subgenus so far include two species with complete rings of fourteen and one species with polyploidy (Hagen, 1950). One of the species reported here, *Oe. deserticola,* was structurally homozygous. Three gametic numbers, 7, 14 and 21, have now been reported for *Oe. speciosa,* including the hexaploid given in this paper. From the investigations to date, the typical variety is composed of diploids having from seven pairs to two rings of four and three pairs. The variety *childsii* has been studied by Hagen (1950) who reports a 2n number ranging from 28 to 35 chromosomes, apparently in different individuals. The two plants of this variety reported here are tetraploid and hexaploid. Because there is a hexaploid in the species, geographically very close to the tetraploid, Hagen's plant with 35 chromosomes was probably a pentaploid hybrid between the tetraploid and hexaploid and the plants with numbers between 20 and 35 may have been progeny of this hybrid.

*Oenothera: Kneiffia.* Two diploids are reported here, one, *Oe. spachiana,* with small chromosomes compared to the other Oenotheras studied (see plate 4). Both *Oe. fruticosa* and *Oe. tetragona* are polyploid; the first including a tetraploid and an octoploid reported by Hecht (1942), and the second including a tetraploid and a hexaploid. Hagen (1950) studied a tetraploid collection in which he found configurations of from 14 pairs to seven rings of four, and he suggests that "... this strain was derived from a structurally homozygous diploid." The tetraploids given in this paper could not be analyzed, but the hexaploid showed two associations of six plus five associations of four.

*Oenothera: Lavauxia.* This subgenus has at least one species with a ring of fourteen and four with very little translocation heterozygosity (Hagen, 1950). The species reported here is intermediate in this respect with a ring of four and a ring of six.

*Oenothera: Raimannia.* A detailed study of fourteen of the nineteen species of this subgenus was made by Hecht (1950). The observations included here consider two additional species and a few of the species which he studied. In one species not investigated by Hecht (1950), *Oe. coronopifolia,* there are both diploid and tetraploid representatives. The tetraploid plant had a chain of eight chromosomes, four rings of four and two pairs.

Another species not reported by Hecht (1950) is *Oe. humifusa.* In the plant studied here it was not possible to get an exact analysis but there was one large ring, probably of twelve chromosomes, but possibly of fourteen. This would be typical of many of the other species reported by Hecht.

The counts given here for *Oe. laciniata* also corroborate Hecht's analysis of this group,

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PLATE 4. Camera lucida drawings of chromosomes during meiosis in species of *Oenothera.* Figures 1-8, 12, and 13, first metaphase; figures 9-11, diakinesis. 1. *Oenothera serrulata* var. *pinifolia,* five pairs and a ring of four. 2. *Oenothera spachiana,* seven pairs. 3. *Oenothera speciosa,* seven pairs. 4. *Oenothera brachycarpa* var. *wrightii,* seven pairs. 5. *Oenothera taraxacides,* two pairs, a ring of four, and a ring of six. 6. *Oenothera caespitosa* var. *marginata,* five pairs and a chain of four. 7. *Oenothera albicaulis,* seven pairs. 8. *Oenothera laciniata* var. *grandiflora,* seven pairs. 9. *Oenothera laciniata* var. *pubescens,* a ring of fourteen. 10. *Oenothera tetragona,* a ring or six, a chain of six, four rings of four, one chain of four, and five pairs. 11. *Oenothera coronopifolia,* a chain of eight, four rings of four, and two pairs. 12. *Oenothera tubicula,* seven pairs. 13. *Oenothera greggii* var. *lampasana,* five pairs and a ring of four. All drawings × 1600.

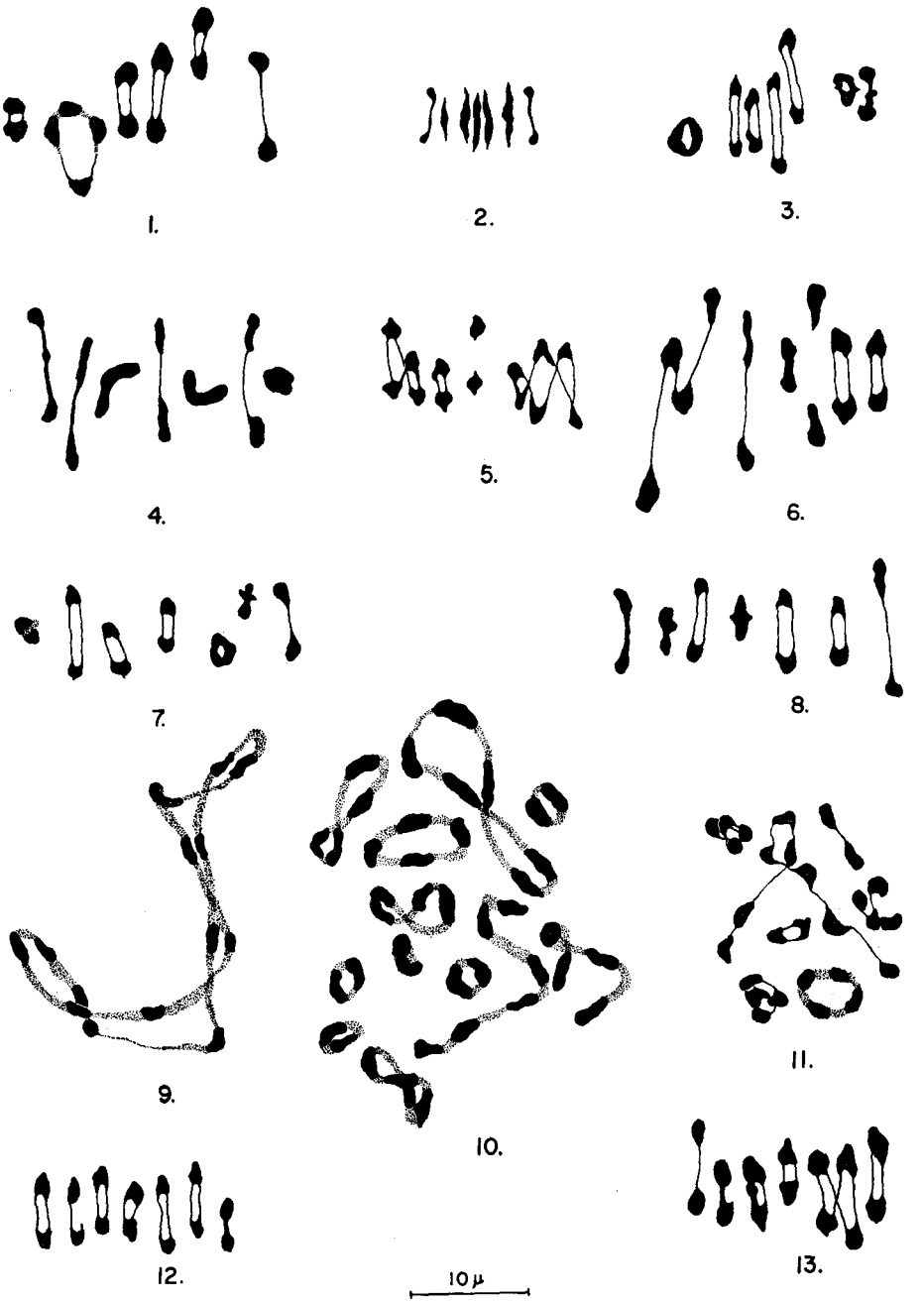


PLATE 4

the large flowered variety *grandiflora* having seven pairs (it also has rings of intermediate size) and the small-flowered *Oe. pubescens* having a ring of fourteen. The two counts of the typical variety could not be analyzed exactly, but one had a large ring, probably of fourteen chromosomes.

*Oenothera: Salpingia.* A gametic number of seven for all of the collections in the three species reported here indicates that this may be a strictly diploid subgenus. Rings of both small and intermediate sizes occur, but large rings have not been found.

## SUMMARY AND CONCLUSIONS

A study of the meiotic chromosomes of six genera, *Gaura, Jussiaea, Ludwigia, Lopezia, Oenothera* and *Stenosiphon,* of the Onagraceae is reported here. The findings of this study and similar studies in these or closely related genera allow some interesting comparisons and point out areas in which additional work is needed.

The basic chromosome number was found to be the same for all of the species of each genus, but differed between some of the genera. Three basic numbers were found in the genera reported here. *Gaura, Oenothera* and *Stenosiphon* are all based upon the number seven and appear to be quite closely related to each other. *Jussiaea* and *Ludwigia* have a basic number of eight and have been suggested by other authors (Brenan, 1953; Hara, 1953) to be congeneric, a suggestion to which the evidence presented here lends support. It now appears that *Lopezia* has a basic number of 10.

Observations have been made of supernumerary chromosomes in four tetraploid plants of *Gaura coccinea.* These were found to resemble most closely those reported by Cleland (1951).

Polyploidy has been found in four of the six genera reported here and appears to be an important factor in the evolution of most genera in the family. *Lopezia* and *Stenosiphon* are the only genera reported here which did not have polyploid species. The highest level of polyploidy was a dodecaploid, *Jussiaea peruviana.* Polyploidy in *Oenothera* appears to be most advanced in the subgenus *Kneiffia* in which there are two species with no known diploid representatives and one of these is reported (Hecht, 1942) to have an octoploid level. Hexaploids were found in *Gaura, Ludwigia* and *Oenothera.* Tetraploids are known in all four of the genera reported here to be polyploids.

It appears that polyploid species in the family may have originated in two ways. In the polyploid species of *Oenothera,* subgenera *Hartmannia, Kneiffia, Anogra* and *Raimannia,* and also in the genus *Gaura,* the meiotic configurations strongly suggest them to be of autoploid origin (Lewis et al., 1958; Snow, 1959). This was strengthened further by the work of Hecht (1942) when he treated a diploid *Oe. rhombipetala* having a ring of four and five pairs with colchicine and obtained tetraploids with an association of eight chromosomes, some quadrivalents and a few bivalents. Such multivalent associations were common in all of the polyploid species which were examined here and by other workers who have reported observations in the above mentioned groups. In some of the higher polyploid levels, however, such as in *Oe. speciosa* var. *childsii* (Hagen, 1950) and in *Oe. fruticosa* and in *Gaura coccinea* the pattern may be complicated further by some hybridization resulting in an auto-allopolyploid. In all of these, however, there is a high degree of multivalent association.

The polyploid species of *Oenothera,* subgenera *Spaerostigma* and *Eulobus,* have been found (Lewis et al., 1958) to have meiotic configurations composed of bivalents such as would be expected if they had originated through hybridization and were therefore allopolyploids. Polyploid species which exhibit the allopolyploid pairing are more common in the family and scattered through several genera including: *Gayophytum, Epilobium, Boisduvalia, Clarkia,* and *Jussiaea* (Lewis et al., 1958).

It has been suggested by Dr. Munz (oral comm.) that the subgenera of *Oeonthera* which exhibit the autoploid type of origin may be distinguished from those which are of the allo-

ploid type on morphological grounds. The autoploid subgenera have four-lobed stigmas and the others have stigmas of the sphaerical type. Polyploids have not yet been reported for the subgenera *Calylophis* and *Salpingia* which have stigmas of the discoid type. Additional morphological studies are now needed in the various polyploids in conjunction with geographical, ecological and chromosome studies in order to delimit the true biological species in these complexes.

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