Aliso: A Journal of Systematic and Evolutionary Botany

Volume 4 | Issue 1 Article 3

1958

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ALISO

VOL. 4, NO. 1, pp. 73-86 APRIL 25, 1958

OBSERVATIONS OF MEIOTIC CHROMOSOMES IN THE ONAGRACEAE[1]

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INTRODUCTION

Chromosome studies in the Onagraceae are well known from the extensive work of many investigators on the ring-forming species of *Oenothera* (see Cleland, 1950). In another genus, *Clarkia,* chromosome number has been determined for all the known species and several species have been studied in detail in regard to structural heterozygotes and supernumerary chromosomes (for references, see Lewis and Lewis, 1955). In both of these genera, chromosome studies have contributed greatly to an understanding of phylogenetic relationships, and in the latter they have been of great value in the delimitation of species. Consequently, we have examined chromosomes of a number of other taxa of the Onagraceae, because we have been curious to know the pattern of chromosome differentiation in the family, and because we think that such data are indispensable to an understanding of phylogenetic relationships within the family. The sampling has been as diverse as opportunity has permitted and does not constitute a systematic attempt to thoroughly investigate the family. The nomenclature used follows the most recent taxonomic treatments by Munz, particularly that which will appear in "A California Flora" (Munz and Keck, 1958), which covers most of our material. We are very grateful to Dr. Munz for checking the identification of our collections, vouchers of which are in the herbarium of the University of California at Los Angeles. Our observations, summarized in Table 1, suggest the need for taxonomic reevaluation in several taxa. Such reevaluation should be made, however, only in conjunction with careful studies of morphological, ecological, and other traits associated with chromosomal differences.

Meiosis in squash preparations of microsporocytes has been examined in all instances, in order to determine the prevalence of translocation heterozygotes that are frequent in wild populations of several genera. Buds were fixed in 1:3 acetic alcohol, hydrolysed for varying lengths of time, depending on the species, in equal parts of 95 percent ethyl alcohol and concentrated HCl at room temperature, and stained with acetocarmine. All samples were taken from wild populations unless otherwise indicated. In some instances, only chromosome number could be determined, because only late meiotic stages were available; however, when possible, chromosome associations at diakinesis or first metaphase were determined. Translocation heterozygotes are indicated by Arabic subscripts showing the number of chromosomes involved and whether the maximum configuration is a ring (r) or a chain (ch). In polyploids, where association of more than two chromosomes may be due to duplication or translocation, maximum chromosome association is indicated by Roman subscripts. Supernumerary chromosomes (s), when present, have been indicated. Bridge-fragment configurations indicative of paracentric inversions were not observed in any of the

[1]This work has been supported by Grant 3596 from the National Science Foundation.
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samples. Since our observations were made independently, the person examining each collection is indicated. However, because of mutual interest and propinquity, most of the preparations, except some of the older ones by the senior author, have been examined by at least two of us. The senior author has examined preparations of all the material showing unusual configurations, supernumerary chromosomes, or a new number for the genus.

TABLE 1. CHROMOSOME NUMBERS AND MEIOTIC ASSOCIATION IN SPECIES OF ONAGRACEAE

	Gametic number	*Meiotic association*[1]	*Locality*[2] *and collector*	*Investigator*
Boisduvalia				
densiflora (Lindl.) Wats. var. *densiflora*	10	10_{II}	Mather, Tuolumne Co., *H. Lewis 1643.*	L
	10	10_{II}	Auberry, Fresno Co., *Raven & H. Lewis 9374.*	V
stricta (Gray) Greene.	9	9_{II}	Drum Valley, Tulare Co., *Raven & H. Lewis 9357.*	V
tocornalii Gay.	19	19_{II}	Estero Quimo, Nuble, Chile, *L. Constance 3553* (garden progeny).	V
Circaea				
alpina L. var. *pacifica* (Aschers. & Magnus) Jones.	11	11_{II}	Mather, Tuolumne Co., *H. & M. Lewis 1612.*	L
Clarkia				
purpurea (Curt.) Nels. & Macbr. subsp. *purpurea.*	26		4.4 miles n. of Lincoln, Placer Co., *H. Lewis 980.*	L
Epilobium				
adenocaulon Hausskn. var. *parishii* (Trel.) Munz.	18	18_{II}	Kaweah River, Tulare Co., *H. Lewis 1094.*	W
exaltatum Drew.	18	18_{II}	West shore Mono Lake, Mono Co., *M. & H. Lewis 628.*	L
	18		Green Valley Campground, San Bernardino Mts., San Bernardino Co., *H. Lewis 1657.*	W
glaberrimum Barbey var. *glaberrimum.*	18	18_{II}	Cedar Creek Campground, Greenhorn Mts., Kern Co., *H. Lewis 1661.*	V
glaberrimum var. *fastigiatum* (Nutt.) Trel.	18	18_{II}	Slate Creek Valley, Mono Co., *M. Lewis 354.*	L
paniculatum Nutt. f. *adenocladon* Hausskn.	12	12_{II}	San Miguel Hills, San Francisco Co., *Raven 11306.*	W
paniculatum f. *subulatum* Hausskn.	12		Near Pleyto, Monterey Co., *H. Lewis 1681.*	W
paniculatum var. *tracyi* (Rydb.) Munz.	12		Mather, Tuolumne Co., *H. & M. Lewis 1627.*	L

[1]Association of chromosomes at diakinesis or first metaphase, if this was determined; when more than one plant was examined, the number is indicated in parentheses. Translocation configurations are indicated by Arabic subscripts: r=ring, ch=chain. Supernumerary chromosomes are indicated by the symbol s.

[2]All localities in California, unless otherwise indicated.

[3]This plant was certainly hexaploid and had several multivalents in each cell, but the exact number of chromosomes could not be determined.

	Gametic number	Meiotic association[1]	Locality[2] and collector	Investigator
watsonii Barbey var. *franciscanum* (Barbey) Jeps.	18	18_{II}	Tocaloma, Marin Co., *H. & M. Lewis 1613.*	L
Gaura				
brachycarpa Small.	7	7_{II}	Burnet, Burnet Co., Texas, *Chambers & Rollins 1129.*	W
coccinea Nutt. ex Pursh var. *epilobioides* (H.B.K.) Munz.	7	$4_{II}+1_{6r}$	15 mi. e. Fort Stockton, Texas, *H. & M. Lewis 1631.*	L
	21 ?[3]		Near Oracle, Santa Catalina Mts., Pima Co., Arizona, *H. Lewis 1078.*	W
odorata Sessé ex. Lag.	7	$5_{II}+1_{4r}$	Near Burnet, Burnet Co., Texas, *Chambers & Rollins 1130.*	W
	14	7_{IV}	Del Rio, Valverde Co., Texas, *Chambers & Rollins 1162.*	W
sinuata Nutt. ex Seringe.	14	$6_{II}+4_{IV}$	S. of Lampasas, Burnet Co., Texas, *Chambers & Rollins 1125.*	W
Gayophytum				
humile Juss. var. *humile.*	7	7_{II}	Near Sagehen Creek, Sierra-Nevada Co. line, *Ornduff 4343.*	R
nuttallii T. & G. *sensu latissimo.*	7	1_{14r} (6)[1]	Mather, Tuolumne Co., *H. & M. Lewis 1611.*	L
	7	$5_{II}+1_{4r}$	Kaiser Pass, Fresno Co., *Wedberg & Cohen in 1957.*	W
	7	$3_{II}+2_{4r}$	Same.	W
	7	$1_{II}+3_{4r}$	Same.	W
	7	7_{II} (2)	Pine Flat, Tulare Co., *H. Lewis 1645.*	LV
	7	$2_{II}+1_{6r}+1_{4r}$	Near Redwood Meadow, Tulare Co., *H. Lewis & Wedberg 1108.*	R
	7	$3_{4r}+1_{II}$	Same.	R
	7	7_{II} (2)	Greenhorn Mts., Kern Co., *H. Lewis 1626.*	LV
	7	$5_{II}+1_{4r}$	Same.	V
	7	1_{14r} (2)	Upper Chilao Recreation Area, San Gabriel Mts., Los Angeles Co., *H. Lewis 1104.*	R
	7	1_{14r} (2)	Same, *H. Lewis 1105.*	R
	7	1_{14r} (2)	Charleton Flats, San Gabriel Mts., Los Angeles Co., *H. Lewis 1103.*	R
	14	$12_{II}+1_{IV}$	Near Atlanta, Elmore Co., Idaho *Mosquin 65.*	R
	14	14_{II}	Anderson Ranch Dam, Elmore Co., Idaho, *Mosquin 61.*	R
	14	14_{II}	Near Sagehen Creek, Nevada-Sierra Co. line, *Ornduff 4342.*	R
	14	14_{II} (2)	Mather, Tuolumne Co., *H. & M. Lewis 1614.*	L
	14	14_{II}	Slate Creek Valley, Mono Co., *M. Lewis 280.*	L
	14	14_{II}	Same, *M & H. Lewis 355.*	L
	14	14_{II}	Leevining Creek, Mono Co., *H. & M. Lewis 1659.*	L

	Gametic number	Meiotic association[1]	Locality[2] and collector	Investigator
	14	14_{II}	Silver Lake, Mono Co., *H. & M. Lewis 1660.*	V
	14	14_{II}	Near Redwood Meadow, Tulare Co., *H. Lewis & Wedberg 1107.*	W
	14	14_{II} (3)	South Fork Meadows, San Bernardino Mts., San Bernardino Co., *Raven, Mosquin, & Wedberg 11176.*	W
	14	14_{II} (3)	Below South Fork Meadows, San Bernardino Mts., San Bernardino Co., *Raven, Mosquin, & Wedberg 11191.*	W
	14	(2)	Green Valley Public Camp, San Bernardino Mts., San Bernardino Co., *H. Lewis 1658.*	L
	14	14_{II}	Same.	L
	14	14_{II}	Coldbrook Public Camp, San Bernardino Mts., San Bernardino Co., *H. & M. Lewis 1648.*	L
	14		Same, *H. & M. Lewis 1651.*	L
	14	$14_{II}+1s$	Same.	L
	14	$10_{II}+2_{IV}$	Same, *H. & M. Lewis 1649.*	L
	14	14_{II}	Vista Grande Ranger Station, San Jacinto Mts., Riverside Co., *Raven & Snow 11088A.*	W
	14	14_{II}	Same, *Raven & Snow 11100.*	W
racemosum T. & G.	14	14_{II}	Slate Creek Valley, Mono Co., *H. Lewis 1632.*	L
ramosissimum T. & G.	7	7_{II}	Near Westgard Pass, White Mts., Inyo Co., *H. Lewis 1089.*	W
	7	7_{II}	Coldbrook Camp, San Bernardino Mts., San Bernardino Co., *H. & M. Lewis 1650.*	L
	7	7_{II} (3)	Camp Angeles, San Bernardino Mts., San Bernardino Co., *Raven, Mosquin & Wedberg 11195.*	W
Heterogaura *heterandra* (Torr.) Cov.	9	9_{II}	Davy Brown Public Camp, San Rafael Mts., Santa Barbara Co., *H. & M. Lewis 1628.*	L
Lopezia *lineata* Zucc.	10	10_{II}	Cultivated, U. C. L. A. campus, Los Angeles Co., *Raven 11404.*	R
Oenothera: Anogra *californica* Wats. var. *californica.*	14		Littlerock, Los Angeles Co., *H. Lewis & Wedberg 1690.*	W
californica var. *glabrata* Munz.	14	$2_{VIII}+2_{IV}+2_{II}$	Near Pala, San Diego Co., *H. Lewis 1082.*	W
deltoides Torr. & Frem. var. *deltoides.*	7	$5_{II}+1_{4r}$	About 10 mi. s. of Garnet, Riverside Co., *H. Lewis 1622.*	L
deltoides var. *cognata* (Jeps.) Munz.	7		14 mi. s. of Greenfield, Kern Co., *H. Lewis 1662.*	L
Oenothera: Calylophis *serrulata* Nutt. var. *drummondii* T. & G.	7	$4_{II}+1_{6r}$	Austin to Bastrop, on Highway 71, Texas, *H. & M. Lewis 1636.*	L

	Gametic number	Meiotic association[1]	Locality[2] and collector	Investigator
Oenothera: Chylismia				
brevipes Gray.	7	7_{II}	Box Canyon, Riverside Co., *H. Lewis 1625.*	L
cardiophylla Torr. var. *cardiophylla.*	7	7_{II}	Box Canyon, Riverside Co., *H. Lewis 1619.*	L
	7	7_{II}	Fish Creek Canyon, Split Mt., San Diego Co., *H. & M. Lewis 1641.*	L
	7	7_{II}	80 km. n. of San Felipe, Norte, Baja California, Mexico, *H. & L. Lewis 1617.*	L
clavaeformis Torr. & Frem. var. *clavaeformis.*	7	7_{II}	2.5 mi. w. of Boron, Kern Co., *Mathias 3192.*	R
	7	7_{II}	Highway 395 n. of junction with Highway 138, San Bernardino Co., *Wedberg in 1957.*	W
clavaeformis var. *aurantiaca* (Wats.) Munz.	7	7_{II}	Box Canyon, Riverside Co., *H. Lewis 1621.*	L
clavaeformis var. *peirsonii* Munz.	7	7_{II}	Fish Creek Canyon, Split Mt., San Diego Co., *H. & M. Lewis 1638.*	L
	7		Same.	L
	7	7_{II} (4)	Coyote Canyon, Borrego Valley, San Diego Co., *H. & M. Lewis 1618.*	L
	7	$5_{II}+1_{4r}$ (7)	Same.	L
clavaeformis var. *purpurascens* (Wats.) Munz.	7	7_{II} (11)	12 mi. s. of Bishop, Inyo Co., *Lewis & Venkatesh 1083.*	V
	7	$7_{II}+2s$	Same.	V
	7	$7_{II}+1s$	Same, *H. & M. Lewis 1654.*	V
	7	$7_{II}+4s$	Same.	V
	7	$7_{II}+5s$	Same.	V
heterochroma Wats. var. *heterochroma.*	7	7_{II}	Walker Lake, Mineral Co., Nevada, *Raven 11247.*	R
	7	7_{II}	Grapevine Canyon, Inyo Co., *Raven 11241.*	R
	7	7_{II} (2)	Caliente, Lincoln Co., Nevada, *Raven 11268.*	R
Oenothera: Eulobus				
leptocarpa Greene.	7	7_{II}	Calf Canyon, La Panza Range, San Luis Obispo Co., *H. Lewis & Chambers 1680.*	V
	7	7_{II} (3)	Latigo Canyon, Santa Monica Mts., Los Angeles Co., *Venkatesh 6.*	V
	7	7_{II} (2)	Same, *Venkatesh 7.*	V
	7		South Sepulveda Way, Santa Monica Mts., Los Angeles Co., *H. Lewis 1629.*	L
	7	7_{II} (11)	Mulholland Drive, Santa Monica Mts., Los Angeles Co., *Venkatesh 2.*	V
	7	7_{II}	Same, *Venkatesh 4.*	V
	7	7_{II}	Decker Canyon, Los Angeles Co., *Mathias 3159.*	R

	Gametic number	Meiotic association[1]	Locality[2] and collector	Investigator
	7	7_{II}	W. of Cabazon, Riverside Co., *H. Lewis 1679.*	V
	7		Ballena, San Diego Co., *Raven & Snow 9581.*	L
	14	14_{II}	Call Mountains, San Benito Co., *Raven 10875.*	V
	14	14_{II}	Little Sycamore Canyon, Santa Monica Mts., Ventura Co., *H. Lewis 1646.*	L
	14	14_{II} (8)	Topanga Canyon, Santa Monica Mts., Los Angeles Co., *Venkatesh 5.*	V
	14	14_{II} (6)	Mulholland Drive, Santa Monica Mts., Los Angeles Co., *Venkatesh 3.*	V
	14	14_{II}	Soledad Canyon, Los Angeles Co., *H. Lewis & Thompson 1615.*	L
	14		Pushwalla Canyon, Riverside Co., *H. & M. Lewis 1610.*	L
	14	14_{II}	S. of Garnet, Riverside Co., *H. Lewis 1620.*	L
	14		Borrego Valley, San Diego Co., *H. & M. Lewis 1644.*	L
	14	14_{II}	Santa Catalina Mts., Pima Co., Arizona *H. Lewis 1075.*	V
	14	14_{II}	Same, *H. Lewis 1077.*	V
Oenothera: Salpingia *hartwegii* Benth. var. *toumeyi* (Small) Munz.	7		Near Oracle, Santa Catalina Mts., Pima Co., Arizona, *H. Lewis 1079.*	W
Oenothera: Sphaerostigma *alyssoides* H. & A. var. *villosa* Wats.	7	7_{II}	E. of Panaca, Nye Co., Nevada, *Raven 11255.*	W
	7	7_{II} (2)	Highway 6, 62 mi. south-west of Delta, Millard Co., Utah, *Mathias 3025.*	L
andina Nutt. var. *andina.*	14	14_{II}	Eagle Lake, Lassen Co., *Ornduff 4205.*	R
bistorta Nutt. var. *bistorta.*	7	7_{II}	Playa del Rey, Los Angeles Co., *Wedberg I.*	W
bistorta var. *hallii* (Davids.) Jeps.	7	7_{II}	Morongo Canyon, Riverside Co., *H. Lewis 1682.*	W
bistorta var. *veitchiana* Hook.	7		Point Dume, Los Angeles Co., *H. Lewis 1634.*	L
	7	7_{II}	Same, *Wedberg in 1957.*	W
	7	7_{II}	Same, *Wedberg H.*	W
	7	7_{II}	Etiwanda Ave., San Bernardino Co., *Wedberg L.*	W
	7		Temescal Canyon, Riverside Co., *H. Lewis 1630.*	L
	7	7_{II}	Same.	L
	7	7_{II}	Alberhill, Riverside Co., *Wedberg B2.*	W
boothii Dougl. ex Hook.	7		Walker Lake, Mineral Co., Nevada, *Raven 11246.*	W
	7	$4_{II}+1_{6r}$	15 mi. n. of Nixon, Washoe Co., Nevada, *Ornduff 4203.*	R

	Gametic number	Meiotic association[1]	Locality[2] and collector	Investigator
	7	7_{II}	10 mi. w. of Lockes, Nye Co., Nevada *Thompson & Mathias 1692.*	L
chamaenerioides Gray.	7	7_{II} (3)	Organ Pipe National Monument, Pima Co., Arizona, *H. & M. Lewis 1639.*	L
contorta Dougl. ex Hook. var. *epilobioides* (Greene) Munz.	14	14_{II}	Mather, Tuolumne Co., *H. Lewis 1665.*	V
	14	14_{II}	Simmler to Creston, San Luis Obispo Co., *H. & M. Lewis 1609.*	L
	14	14_{II}	Vandeventer Flat, Riverside Co., *Wedberg N2.*	W
	14	14_{II}	Near Julian, San Diego Co., *H. & M. Lewis 1672.*	W
	21	21_{II}	Mouth of Kern River Canyon, Kern Co., *H. Lewis & Wedberg 1671.*	W
contorta var. *flexuosa* (A. Nels,) Munz.	7	7_{II}	Westgard Pass, Inyo Co., *H. Lewis 1091.*	W
contorta var. *strigulosa* (F. & M.) Munz.	14	14_{II}	Arroyo Grande to Edna, San Luis Obispo Co., *Lewis, Thompson, & Chambers 1664.*	V
decorticans (H. & A.) Greene var. *decorticans.*	7	7_{II}	Paso Robles, San Luis Obispo Co., *Lewis & Thompson 1101.*	W
decorticans var. *condensata* Munz.	7	7_{II}	Box Canyon, Riverside Co., *H. Lewis 1663.*	L
	7	7_{II}	Borrego Valley, San Diego Co., *Wedberg C2.*	W
	7	7_{II}	Same, *H. Lewis 1624.*	L
decorticans var. *desertorum* Munz.	7	7_{II}	Sherwin Grade, Mono Co., *H. Lewis 1673.*	W
	7	7_{II}	Westgard Pass, Inyo Co., *H. Lewis 1085.*	W
	7		Near Havillah, Kern Co., *H. Lewis 1106.*	W
	7	7_{II}	Same.	W
	7	$5_{II}+1_{4r}$	Near Randsburg, Kern Co., *Wedberg in 1957.*	W
dentata Cav. var. *campestris* (Greene) Jeps.	7	7_{II} (2)	Kern River Canyon, Kern Co., *H. Lewis & Wedberg 1109.*	W
	7	$5_{II}+1_{4r}$	Same.	W
	7	$5_{II}+1_{4r}$	Mouth of Kern River Canyon, Kern Co., *H. Lewis, Mathias, & Snow 1675.*	W
dentata var. *johnstonii* Munz.	7	7_{II}	Highway 395 n. of junction with Highway 138, San Bernardino Co., *Wedberg in 1957.*	W
	7	$5_{II}+1_{3ch}+1_{I}$	Pearblossom, Los Angeles Co., *H. Lewis & Wedberg 1691.*	W
dentata var. *parishii* (Abrams) Munz.	7	7_{II}	Wheeler Ridge, Kern Co., *H. Lewis 1684.*	L
	7	$5_{II}+1_{4r}$	Mouth of Kern River Canyon, Kern Co., *H. Lewis 1683.*	W
micrantha Hornem. ex Spreng var. *micrantha.*	7	7_{II}	Near Paso Robles, San Luis Obispo Co., *H. Lewis & Thompson 1100.*	W
	7	7_{II} (2)	Soledad Canyon, Los Angeles Co., *H. Lewis 1677.*	W
	7		11 mi. w. of Riverside, Riverside Co., *Snow & Mosquin in 1957.*	W

	Gametic number	Meiotic association[1]	Locality[2] and collector	Investigator
	14	14_{II}	Lower San Juan Campground, Santa Ana Mts., Orange Co., *H. Lewis 1642.*	L
micrantha var. *exfoliata* (A. Nels.) Munz.	7	7_{II}	Whitewater Canyon, Riverside Co., *Wedberg E.*	W
	7	7_{II}	Borrego Valley, San Diego Co., *H. & M. Lewis 1637A.*	L
	7	7_{II}	Same, *H. & M. Lewis 1637B.*	L
	7	7_{II}	Same, *Wedberg C3.*	W
micrantha var. *ignota* Jeps.	7	7_{II}	Mouth of Kern River Canyon, Kern Co., *H. Lewis 1670.*	W
	7	7_{II} (3)	Soledad Canyon, Los Angeles Co., *H. Lewis 1676.*	W
	7		Pearblossom, Los Angeles Co., *H. Lewis & Wedberg 1692.*	W
	7		Vandeventer Flat, Riverside Co., *Wedberg N1.*	W
	7	7_{II}	Alberhill, Riverside Co., *Wedberg B1.*	W
	7		Same.	W
	14		Soledad Canyon, Los Angeles Co., *H. Lewis & Thompson 1616.*	L
	14	14_{II}	7.7 mi. e. Hemet, Riverside Co., *Wedberg O.*	W
	14	14_{II}	Banning to Idyllwild, Riverside Co., *H. Lewis 1667.*	W
	14	14_{II}	Near Julian, San Diego Co., *H. & M. Lewis 1669.*	W
	14	$12_{II}+1_{IV}$	Same.	W
micrantha var. *jonesii* (Lévl.) Munz.	7	7_{II}	Near Paso Robles, San Luis Obispo Co., *H. Lewis & Thompson 1099.*	W
	7	7_{II}	Upper San Juan Campground, Santa Ana Mts., Riverside Co., *H. Lewis 1655.*	V
	7	7_{II}	Banning to Idyllwild, Riverside Co., *Wedberg M.*	W
	14	14_{II}	Little Sycamore Canyon, Santa Monica Mts., Ventura Co., *H. Lewis 1666.*	V
	21	21_{II}	Davy Brown Campground, San Rafael Mts., Santa Barbara Co., *H. Lewis 1647.*	L
	21		Cachuma Guard Station, San Rafael Mts., Santa Barbara Co., *H. Lewis 1678.*	W
refracta Wats.	7	$5_{II}+1_{4r}$	Box Canyon, Riverside Co., *H. Lewis 1623.*	L
	7	$3_{II}+2_{4r}$	Same, *H. Lewis 1633.*	
	7	$2_{II}+1_{10r}$	About 20 mi. e. of Yuma, Yuma Co., Arizona, *H. & M. Lewis 1640.*	L
Oenothera: Taraxia *palmeri* Wats.	7	7_{II}	Elkhorn Valley Road, Temblor Range, San Luis Obispo Co., *H. Lewis & Thompson 1635.*	L
tanacetifolia T. & G.	21		Near Beckworth, Plumas Co., *Ornduff 4347.*	W

DISCUSSION

Boisduvalia. Each of the three species examined has a different chromosome number. *Boisduvalia tocornalii* is a tetraploid with a number equal to the sum of the other two species, which are both from California. There is apparently no direct relationship, however, between this South American species and those from North America. Nevertheless, the pattern of chromosomal differentiation in this genus may parallel that in *Clarkia,* in which different basic numbers are frequently combined in polyploids.

Circaea. Our observations agree with those previously reported for *C. alpina* and two other species (Udding, 1929).

Clarkia. No chromosome observations of *C. purpurea purpurea* have previously been published. The gametic number of 26 is the same as has been reported for other subspecies of *C. purpurea* (Lewis and Lewis, 1955).

Epilobium. All of the species we have examined, save one, have a gametic number of 18, which is the basic number reported for some two dozen other species from the northern and southern hemispheres (see Darlington and Wylie, 1956). The one exception is an annual species, *E. paniculatum,* that has a gametic number of 12. This suggests to us that the original basic number of the genus was probably 6 and that most of the species of this widely distributed genus are hexaploid.

Gaura. Our samples have shown a great deal of diversity in chromosome arrangement and polyploidy, but no deviation from a basic number of 7. Translocation heterozygotes are apparently common in *Guara,* but in our material the rings have all been small. A ring of 12, however, has been reported by Bhaduri (1942) in *G. biennis.* Polyploidy may or may not prove to be taxonomically significant upon more extensive and careful study. One tetraploid plant of *G. odorata,* which is morphologically very similar to our diploid collection, showed a variable number of quadrivalents at diakinesis with a maximum of 7, which suggests that it was an autoploid rather than a plant with seven independent reciprocal translocations.

Gayophytum. No deviation from a gametic number of 7 or 14 has been found in any of our diverse assemblage of material. Consequently, our observations do not substantiate the report of Johansen (1933) of a gametic number of 11 for this genus. The collections that we have referred to *G. humile* and *G. ramosissimum* are diploid and regularly formed 7 pairs, whereas our collection of *G. racemosum* is tetraploid with 14 pairs. The remainder of the collections belong to a morphologically diverse complex that, for convenience, is referred to *G. nuttallii.* It consists of diploids and tetraploids both of which may be heterozygous for translocations. Among the diploids, populations from two widely separated areas (central Sierra Nevada and San Gabriel Mountains), form rings of 14, involving all of the chromosomes. These plants are apparently self-pollinated and every individual examined had a ring of 14. There can be little doubt, therefore, that these populations consist of complex heterozygotes comparable to those that are well known in *Oenothera.* The other diploids in this complex (these have sometimes been referred to *G. diffusum*) have larger flowers and are undoubtedly outcrossed; at meiosis they form 7 pairs or one or more rings of four. The relationship between these two classes of diploids is probably comparable to that between euoenotheras such as *Oenothera hookeri* and *Oe. biennis.* However, most of the populations of the *Gayophytum nuttallii* complex that we have examined (including those usually referred to *G. nuttallii,* as well as those sometimes referred to *G. lasiospermum* and some material referred to *G. diffusum*) are tetraploid and usually form 14 pairs at meiosis, but sometimes may have one or two rings of 4. Most of these populations are rather small-flowered and, since the pollen of a flower is deposited directly on the stigma, are probably autogamous to a high degree. Some of these populations are scarcely distinguishable from the diploid populations in the San Gabriel Mountains that form a ring of 14. On the other hand, some of the tetraploid collections *(Mosquin 61, 65)* are comparable in many respects to the large-flowered, pair-forming diploids and may, like them, be outcrossed. One tetraploid plant *(H. & M. Lewis 1651)* had 29 chromosomes. The supernumerary chromosome was indistinguishable from members of the normal complement and frequently was associated with a normal pair to form a trivalent. The extra chromosome was homologous, therefore, at least in part, with the chromosomes of one of the normal pairs. A supernumerary chromosome of comparable appearance and behavior has been found in *Clarkia rhomboidea* (Lewis, 1951). In both instances, the plants with an extra chromosome may have been trisomics.

Heterogaura. This monotypic genus is sometimes included in *Gaura* because of the similarity of their few-seeded indehiscent fruits. A summation of all morphological traits suggests, however, that this similarity is the result of parallel specialization in separate lineages. In totality of characters, *Heterogaura* is most similar to *Clarkia* and is probably closely related to it, whereas *Gaura* is assuredly more closely allied to *Oenothera.* The gametic number of 9 in *Heterogaura,* in contrast to the consistent basic number of 7 in *Gaura,* supports this suggested relationship.

Lopezia. Täckholm (1914) reported a gametic number of 11 for *L. coronata,* which, with the number 10 reported here, suggests that *Lopezia* may be comparable to *Boisduvalia* and *Clarkia* in having more than one basic number.

Oenothera. The material we have examined belongs to diverse subgenera that have had little or no previous study. In all instances the gametic number has been 7, 14, or 21, although supernumerary chromosomes have been observed in one population of *Oe. clavaeformis* var. *purpurascens* (Chylismia). These supernumeraries, which varied from 0 to 5 in different plants, are like those in *Clarkia* (Håkansson 1945, 1949; Lewis 1951) in that they are indistinguishable in size and appearance from members of the normal chromosome complement, although they usually do not pair with them. The extra chromosomes in *Oe. clavaeformis* differ considerably in size from the small supernumerary fragment in *Oe. hookeri* studied by Cleland (1951), the only other report of supernumerary chromosomes from wild populations of *Oenothera.* One plant of *Oe. clavaeformis* with 5 extra chromosomes (fig. 2c) is of particular interest because it frequently showed 6 pairs, a trivalent, and 4 univalents at diakinesis or first metaphase, suggesting that one of the supernumerary chromosomes was perhaps a duplicate of one of the ordinary chromosomes and may be comparable to the supernumerary chromosome described above in *Gayophytum nuttallii.* On the other hand, the homology of the supernumerary chromosome that pairs with the normal complement may be due to translocation between a non-homologous supernumerary and a normal chromosome, particularly since reciprocal translocation is a common phenomenon in this genus.

Translocation heterozygosity has been reported in several subgenera of *Oenothera* (see Hagen, 1950) including Euoenothera, Raimannia, Hartmannia, Lavauxia, and Anogra, with all but the last including complex heterozygotes that form a ring of 14. We have found translocation heterozygotes in three additional subgenera, Sphaerostigma, Chylismia, and Calylophis. None of these, however, had a ring of 14 and for the most part the rings were small, involving 4 or 6 chromosomes. The exceptions are a ring of 10 in *Oe. refracta* and rings of 8 in the tetraploid species *Oe. californica.*

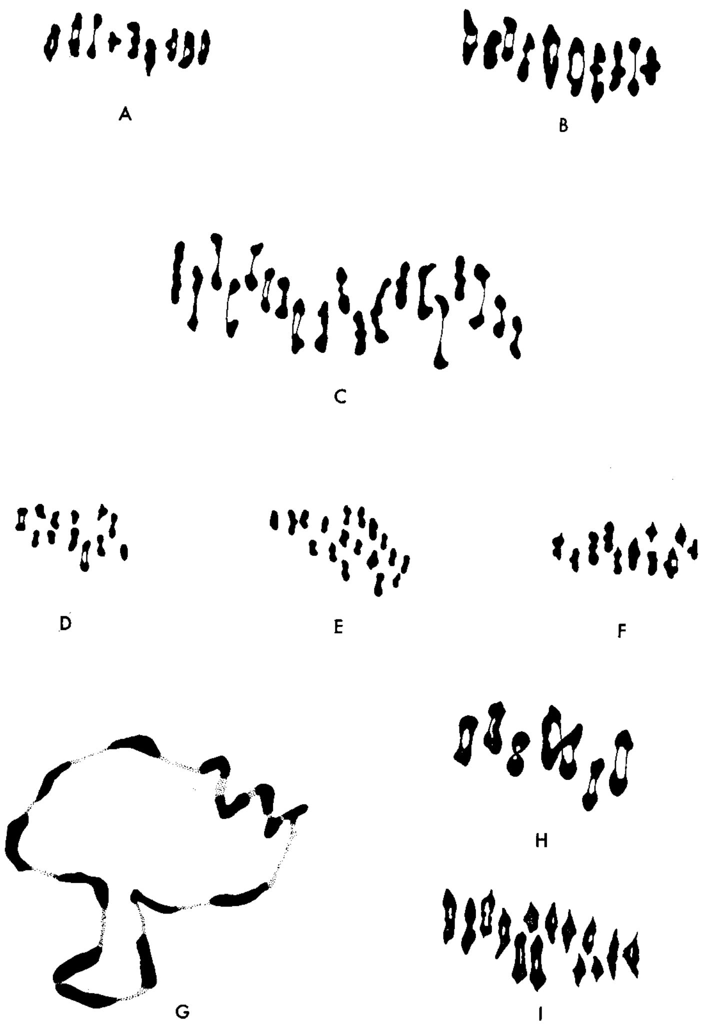

FIGURE 1. Camera lucida drawings of meiotic chromosome complements of the species indicated. A-F, H, I, first metaphase; G, diakinesis. A. *Boisduvalia stricta,* nine pairs. B. *Boisduvalia densiflora,* ten pairs. C. *Boisduvalia tocornalii,* nineteen pairs. D. *Epilobium paniculatum* f. *adenocladon,* twelve pairs. E. *Epilobium glaberrimum fastigiatum,* eighteen pairs. F. *Circaea alpina pacifica,* eleven pairs. G. *Gayophytum nuttallii,* ring of fourteen. H. *Gayophytum nuttallii,* five pairs and a ring of four. I. *Gayophytum nuttallii,* fourteen pairs. All drawings × 1200.

An unusual translocation configuration of a chain of 3 and a univalent instead of a ring of 4 was consistently present in one plant of *Oe. dentata* var. *johnstonii.* Comparable configurations have been found, however, in occasional individuals of several species of *Clarkia* and have been specially studied in *C. amoena* (Håkansson 1944; Hiorth 1947, 1948, as *Godetia whitneyi*) and *C. unguiculata* (Lewis, 1954).

Polyploidy has been found in six of the nineteen species of *Oenothera* we have examined and these six species belong to four subgenera. *Oenothera californica* and *Oe. andina* may be tetraploid species and *Oe. tanacetifolia* may be a hexaploid species. We have reservations as to the uniformity of ploidy level in these species, however, because the samples are few and three other species, *Oe. leptocarpa, Oe. contorta,* and *Oe. micrantha,* as delimited here, have both diploid and tetraploid populations, and the latter two also have hexaploid populations. The diploid and tetraploid populations of *Oe. leptocarpa* have different but overlapping distributions: the diploids are apparently confined to the coastal side of the mountains and the tetraploids are primarily in the desert. The spatial and ecological relationships of the three levels of ploidy in *Oe. contorta* and *Oe. micrantha* are more obscure. When carefully studied, these taxa can probably be resolved taxonomically into two or more readily delimitable species, although perhaps with a residual array of populations that can only be recognized as a polyploid complex.

SUMMARY AND CONCLUSIONS

Supernumerary chromosomes comparable in size and appearance to members of the normal set have been found in *Clarkia, Gayophytum,* and in *Oenothera,* to which the other two genera are closely related. Whether these supernumerary chromosomes are causally related to translocation heterozygotes, as suggested by Lewis (1951), and whether they play an adaptive role in the populations in which they occur, remain moot points. Without exception, however, the species in which supernumeraries have been found are also characterized by translocations.

The prevalence of translocation heterozygosity in *Oenothera* and the three closely related genera, *Clarkia, Gayophytum,* and *Gaura,* suggests that this heterozygosity is an integral part of their adaptive genetic system, of which the complex heterozygotes that characterize many populations of *Oenothera* and some populations of *Gayophytum* and probably *Gaura* (Bhaduri 1941, 1942) represent special cases.

Polyploidy is found to some degree in most of the genera and some *(Epilobium* and perhaps *Zauschneria)* may consist today of only polyploid species or perhaps may have been of polyploid origin. *Epilobium,* as indicated above, probably has a basic number of 6; the origin of the basic number 15 in *Zauschneria* (Clausen, Keck, and Hiesey, 1940) is at present obscure.

The basic number is apparently constant within most genera, such as in the large genus *Oenothera,* but frequently differs between genera. In other words, the family has no characteristic basic number. Three genera, *Clarkia, Boisduvalia,* and *Lopezia,* are characterized by more than one basic number. A study of changes in basic number in these genera (e.g., Lewis and Roberts, 1956) may indicate how the stage has been set for generic differentiation.

Chromosome size varies a great deal in the family but is apparently similar, for the most part, within each genus, although a notable exception is found in the size differences that characterize different species of *Clarkia* (Håkansson 1943, as *Godetia*). Among the genera we have examined, the smallest chromosomes have consistently been those of *Epilobium* (fig. 1D, E), whereas the largest have been those of *Lopezia* (fig. 2H). In *Oenothera clavaeformis,* there has been a suggestion of a chromosome

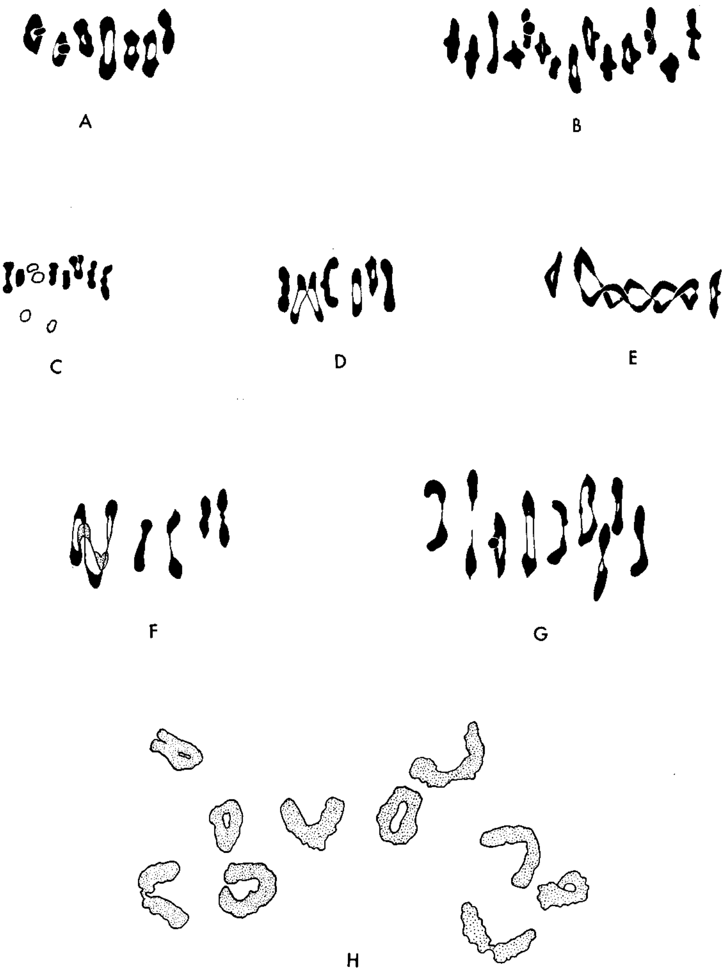

FIGURE 2. Camera lucida drawings of meiotic chromosome complements of the species indicated. A-G, first metaphase; H, diakinesis. A. *Oenothera micrantha exfoliata,* seven pairs. B. *Oenothera leptocarpa,* fourteen pairs. C. *Oenothera clavaeformis purpurascens,* six pairs, one trivalent, and four univalents. The four univalents and one member of the trivalent are supernumerary chromosomes. D. *Oenothera clavaeformis peirsonii,* five pairs and a ring of four. E. *Oenothera refracta,* two pairs and a ring of ten. F. *Gaura coccinea epilobioides,* four pairs and a ring of six. G. *Heterogaura heterandra,* nine pairs. H. *Lopezia lineata,* ten pairs. All drawings × 1200.

size difference between races within the species (fig. 2C, D) but, inasmuch as the samples were collected in the wild, we are uncertain how much of the difference may be attributable to the environment.

The value of chromosome studies to an understanding of phylogenetic relationship in the Onagraceae was surmised by Johansen (1929). Although the relationships he suggested suffered from inadequate and sometimes erroneous observations, as well as an overevaluation of chromosome number, his thesis still holds. The results of our limited survey indicate some of the potentialities of future studies of this kind for an understanding of phylogenetic relationships and the delimitation of species.

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