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DIFFERENTIAL CHIASMA FREQUENCIES IN SELF-POLLINATING AND CROSS-POLLINATING SPECIES OF THE GENUS *GILIA*

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INTRODUCTION

Evidence has been accumulating which indicates that there is a direct correlation between chiasma frequency and the breeding systems in flowering plants. Stebbins, Valencia and Valencia (1946) first proposed this hypothesis and postulated a selective value for higher chiasma frequency in self-pollinators because it would give them greater gene recombination. A lower chiasma frequency is found in cross pollinators, presumably, because they obtain gene recombination through their mode of reproduction. In the genera *Sitanion*, *Elymus*, and *Agropyron* this chiasma frequency-breeding type correlation seems good, and these authors have suggested that such a correlation may exist in the tribe *Hordeae* as a whole. Garber (1950) obtained data on chiasma frequency and breeding behavior in a number of taxonomic entities in the genus *Sorghum*. Grant (1958) has shown that this work indirectly supports the general hypothesis in that a positive correlation exists between the breeding behavior of the species in their native habitats and the chiasma frequency observed. Further work by Garber (1956) in the genus *Collinsia* has shown an almost perfect correlation between chiasma frequency and floral structural characteristics which separate taxa. The taxa with high chiasma frequency are predominantly self-pollinators and those with low chiasma frequency are predominantly cross-pollinators. Grant (1950) has shown a similar correlation in *Gilia achilleaeifolia*, an outcrosser, and *G. millefoliata*, a selfer. Stebbins (1959) compared the chiasma frequencies reported for a number of species in the genus *Crepis* by several workers (Richardson, 1935; Koller, 1935; Tobgy, 1943; Sherman, 1946). He suggests there may be some significance to the fact that three self-compatible species of the *C. foetida* complex have higher chiasma frequencies than their cross-fertilizing relatives.

The genus *Gilia* contains both self-pollinating and cross-pollinating species or subspecies in a number of subgenera, representing a diversity of forms with a wide and varied geographical distribution. Considerable information on the breeding mechanisms, taxonomy, genetics and cytogenetics is available due to the investigations of Grant (1950; 1952a, b, c, 1954a, b, 1956) and V. and A. Grant (1954, 1956a, b). The genus presents an excellent medium in which to test the hypothesis that chiasma frequency and breeding systems are correlated. Heretofore data have been obtained from other studies and re-evaluated. The study reported here has been undertaken in order to obtain direct evidence bearing on this hypothesis.

MATERIAL AND METHODS

Six pairs of closely related species or subspecies in the genus *Gilia*, one of which is a self-pollinator or facultative crosser and the other a cross-pollinator were selected for comparison of their chiasma frequencies. Table I lists these paired species and gives collection numbers and geographical strains. Except for one species, *G. tricolor*, which was grown in a garden

bed, all plants were grown in six inch pots in a glass house with temperature and humidity control.

Buds were taken periodically from 8 a.m. to 5 p.m. from all species as they became available over approximately a two month period extending from late April to the middle of June, 1958. These were fixed in a 3-1 absolute alcohol-glacial propionic acid mixture.

TABLE 1. *Taxa of genus Gilia used in this investigation.*

SPECIES OR SUBSPECIES	BREEDING SYSTEM	CULTURAL NUMBER ¹ & GEOGRAPHICAL STRAIN
Section <i>Gilia</i> :		
<i>G. capitata chamissonis</i>	facultative crosser	3315: Pt. Reyes Penin., Marin Co.
<i>G. capitata capitata</i>	obligate crosser	3314: Mayacama Mt., Napa Co.
<i>G. achilleaefolia multicaulis</i>	selfer	3331: Kings Mt., San Mateo Co.
		3332: Woodside, San Mateo Co.
		3333: Blythdale, Canyon, Marin Co.
		3329: School Canyon, San Luis Obispo Co. †: School Canyon, San Luis Obispo Co.
<i>G. achilleaefolia achilleaefolia</i>	crosser	
<i>G. millefoliata</i>	selfer	3338: Pt. Reyes Penin., Marin Co.
<i>G. tricolor</i>	crosser	8640: Byron, Contra Costa Co.
		Garden Bed ^o : Unknown
Section <i>Arachnion</i> :		
<i>G. ochroleuca ochroleuca</i>	selfer	3210: Inyokern, Kern Co.
<i>G. ochroleuca bizonata</i>	crosser	3269: Mt. Pinos, Ventura Co.
<i>G. minor</i>	selfer	3339: Homewood Canyon, Inyo Co.
<i>G. tenuiflora</i>	crosser	3334: Arroyo Seco, Monterey Co.
Section <i>Saltugilia</i> :		
<i>G. australis</i>	selfer	331*: Cajon Pass, San Bernardino Co.
<i>G. splendens</i>	crosser	300*: Tassajara, Monterey Co.
		302*: Bayless Park, San Bernardino Mts.

¹All culture numbers from Grant, except: *Culture numbers of H. Latimer; ^oNaturalized in bed at Rancho Santa Ana Botanic Garden; †Collection of H. S. Brown.

Permanent propiono-carminic squash preparations were made using the improved technique of Beeks (1955). Except for 3 species, where material was scarce, at least fifty pollen-mother cells, representing stages from diplotene through metaphase I, were examined for each species and the chiasmata per pollen-mother cell determined.

Due to terminalization, it is necessary to compare the chiasma frequencies of the paired species at similar stages of the meiotic process. The fact that the chromosomes continually contract during prophase and early metaphase I of meiosis (Belling, 1928; Darlington, 1933; Swanson, 1957) suggested that the total length of the chromosomal complement of a cell be used as a measure of the meiotic stage. Each chromosomal complement was drawn by camera lucida and traced by a line running lengthwise through the center of the drawings of chromosomes. Chromosome lengths were measured with a tachometer on these mid-line camera-lucida drawings. The total chromosomal lengths thus determined are for comparison only, being in inches of camera-lucida drawing. Classification of the drawings according to visually determined meiotic stages showed little discrepancy with the continued decrease in measured chromatin length from diplotene through metaphase I. Only where the chromosomes increase in length at late metaphase I is any serious discrepancy evident. This phase-length discrepancy is obvious and is handled by visual classification. Due to this discrepancy

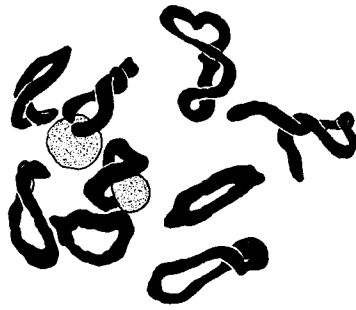


Fig. 1. Camera-lucida drawings of *Gilia millefoliata* meiotic figures.—a. Late diplotene (XTA 19, chromatin length 24 "units"). b. Early diakinesis (XTA 16, chromatin length 18 "units"). c. Metaphase (XTA 14, chromatin length 12 "units").

and the fact that the chromosomes have a limit of contraction, the comparison tables show a division of metaphase I classes.

The data on total length of chromatin in a complement were divided into classes of five length-stage units each and the mean chiasma frequency for each class determined. These data are presented in tables 2 through 7 which give a comparison of chiasmata per length-stage for each of the six species pairs investigated. To test the differences indicated in these tables further, the significance of the difference between means of each inbreeder and out-

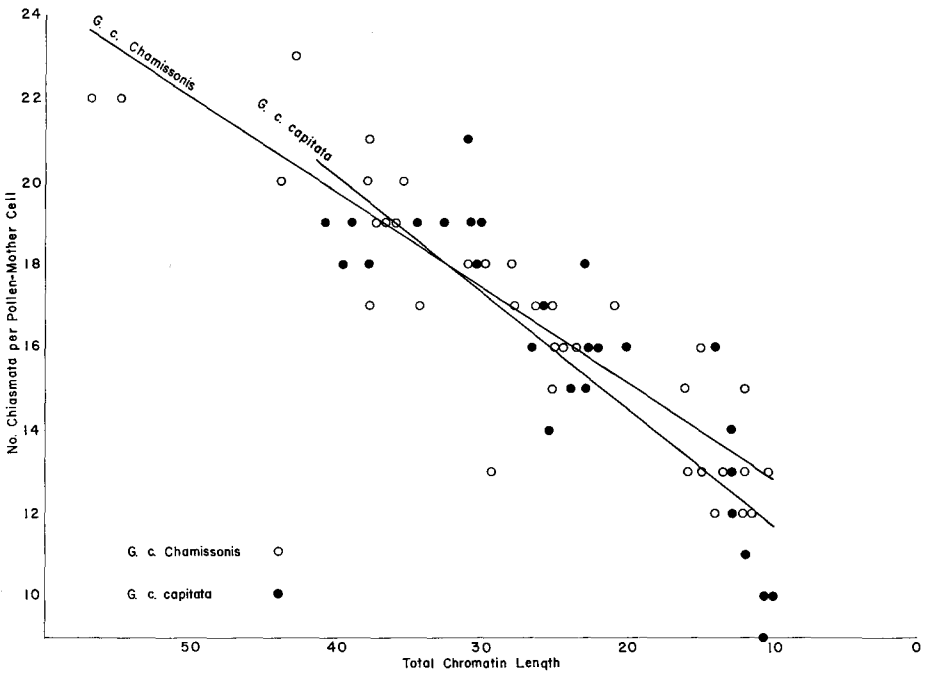


Fig. 2. Regression of chiasma frequency against stage of meiosis (as represented by total length of chromatin in arbitrary units) in *Gilia capitata chamissonis* and *G. capitata capitata*.

TABLE 2. Chiasma frequency at comparative stages of meiotic division I.

TOTAL LENGTH* OF CHROMATIN	<i>Gilia capitata chamissonis</i>			<i>Gilia capitata capitata</i>				
	AVERAGE	RANGE	STD. DEV.	NO. PMC	AVERAGE	RANGE	STD. DEV.	NO. PMC
60-55	22.00			1				
55-50	22.00			1				
50-45								
45-40	21.50	20-23		2	19.00			1
40-35	19.28	17-21	0.8	7	18.33	18-19	1.2	3
35-30	17.75	17-18	1.4	4	19.17	18-21		6
30-25	<u>16.44</u>	13-18	1.7	9	<u>15.67</u>	14-17	0.8	3
25-20	<u>16.25</u>	16-17	1.3	4	<u>16.00</u>	15-18	1.1	6
20-15	<u>14.67</u>	13-16	0.8	3				
15-10	12.89	12-15	0.7	9	11.88	10-16	2.2	8
10-15	10.73	10-12	1.0	15	9.95	9-11	0.6	19
15-20	11.00			<u>1</u>	10.27	9-11	0.6	<u>11</u>
				56				57

*In inches as measured by tachometer on camera lucida drawings at bench level. Further explanation in text.

≡ Indicates the range of diakinesis for each species as determined by visual inspection.

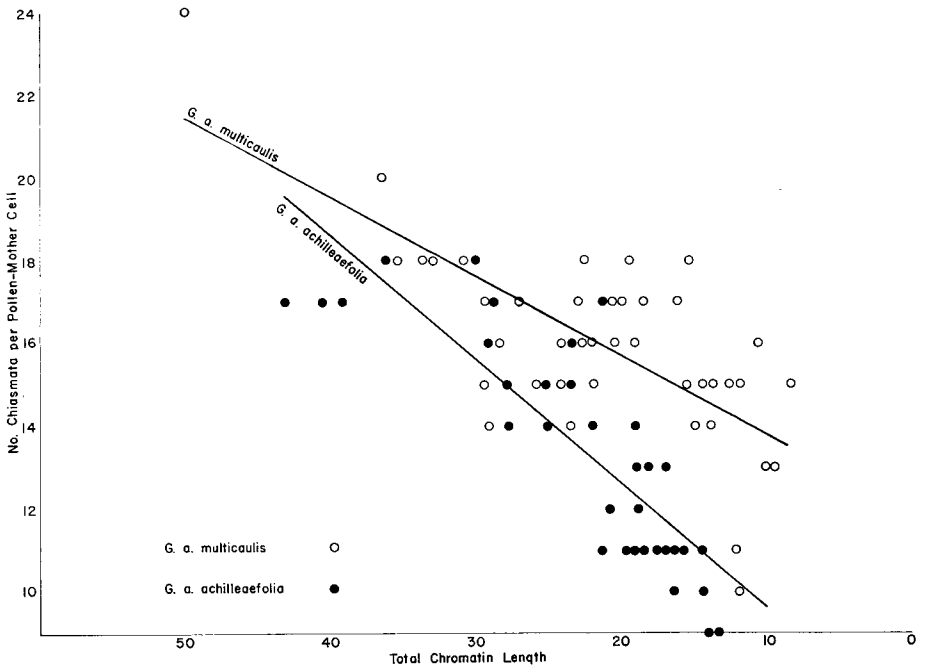


Fig. 3. Regression of chiasma frequency against stage of meiosis (as represented by total length of cromatin in arbitrary units) in *Gilia achilleaeifolia multicaulis* and *G. a. achilleaeifolia*.

TABLE 3. *Chiasma frequency at comparative stages of meiotic division I.*

TOTAL LENGTH* OF CHROMATIN	<i>G. achilleaeifolia multicaulis</i>			NO. PMC	<i>G. achilleaeifolia achilleaeifolia</i>			NO. PMC
	AVERAGE	RANGE	STD. DEV.		AVERAGE	RANGE	STD. DEV.	
50-45	24.00			1				
45-40					17.00			2
40-35	19.00	18-20		2	17.33	17-18	0.5	2
35-30	18.00			3	18.00			1
30-25	15.86	14-17	1.8	7	15.43	14-17	1.5	7
25-20	16.09	14-18	0.9	11	14.33	12-17	2.2	7
20-15	16.62	15-18	1.4	8	11.82	10-14	1.4	17
15-10	13.92	10-16	1.8	12	9.80	9-11	0.8	5
10-5	14.00	13-15		2				
5-10	11.50	10-13		2	10.00			1
10-15	13.00	12-14	3.9	3	10.14	9-11	1.0	7
20-25					10.00	9-11	0.5	6
				51				55

*In inches as measured by tachometer on camera lucida drawings at bench level. Further explanation in text.

≡ Indicates the range of diakinesis for each species as determined by visual inspection.

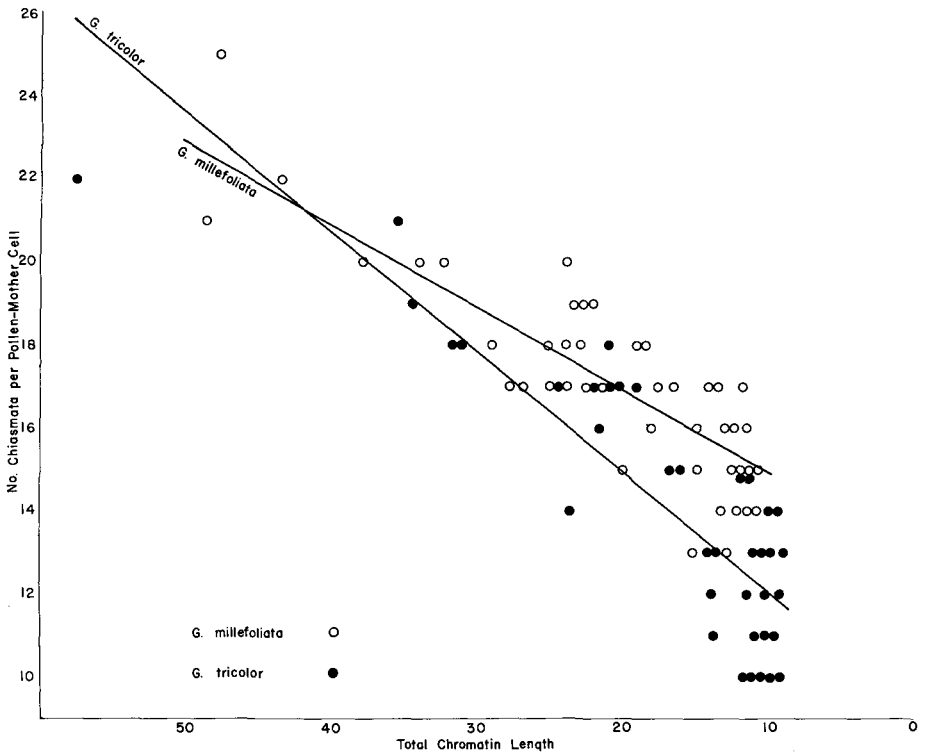


Fig. 4. Regression of chiasma frequency against stage of meiosis (as represented by total length of chromatin in arbitrary units) in *Gilia millefoliata* and *G. tricolor*.

TABLE 4. Chiasma frequency at comparative stages of meiotic division I.

TOTAL LENGTH* OF CHROMATIN	<i>Gilia millefoliata</i>				<i>Gilia tricolor</i>			
	AVERAGE	RANGE	STD. DEV.	NO. PMC	AVERAGE	RANGE	STD. DEV.	NO. PMC
60-65					22.00			1
55-50								
50-45	22.00	19-25		2				
45-40	22.00			1				
40-35	20.00			1	21.00			1
35-30	20.00			2	18.33	18-19	1.2	3
30-25	17.40	17-18	0.4	5				
25-20	17.90	15-20	1.3	10	16.78	14-18	0.8	9
20-15	16.50	13-18	1.7	6	15.67	15-17		3
15-10	15.45	14-17	1.6	22	11.74	10-15	1.9	19
10-5					12.00	9-14	1.5	9
5-10	13.20	13-14		5	11.28	10-13	0.6	7
				54				52

*In inches as measured by tachometer on camera lucida drawings at bench level. Further explanation in text.

— Indicates the range of diakinesis for each species as determined by visual inspection.

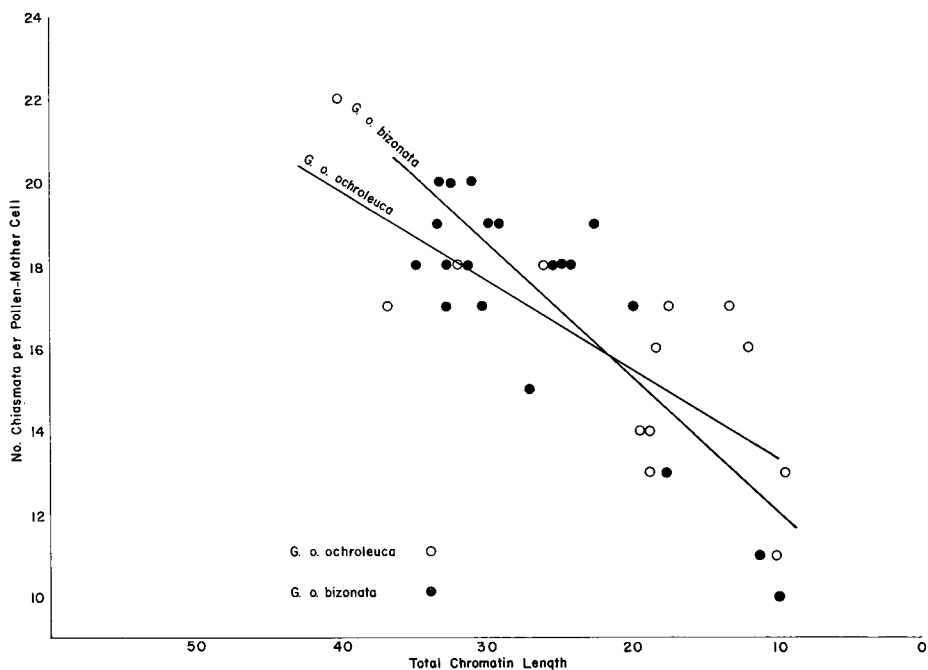


Fig. 5. Regression of chiasma frequency against stage of meiosis (as represented by total length of chromatin in arbitrary units) in *Gilia ochroleuca ochroleuca* and *G. o. bizonata*.

TABLE 5. Chiasma frequency at comparative stages of meiotic division I.

TOTAL LENGTH* OF CHROMATIN	<i>Gilia ochroleuca ochroleuca</i>				<i>Gilia ochroleuca bizonata</i>			
	AVERAGE	RANGE	STD. DEV.	NO. PMC	AVERAGE	RANGE	STD. DEV.	NO. PMC
45-40	22.00			1				
40-35	17.00			1				
35-30	18.00			1	18.50	17-20	1.1	10
30-25					17.83	15-19	1.7	6
25-20					18.50	18-19		2
20-15	14.80	13-17	1.5	5	15.00	13-17		2
15-10	16.50	16-17		2	11.00			1
10-5	12.00	11-13		2	10.00			1
				12				22

*In inches as measured by tachometer on camera lucida drawings at bench level. Further explanation in text.

≡ Indicates the range of diakinesis for each species as determined by visual inspection.

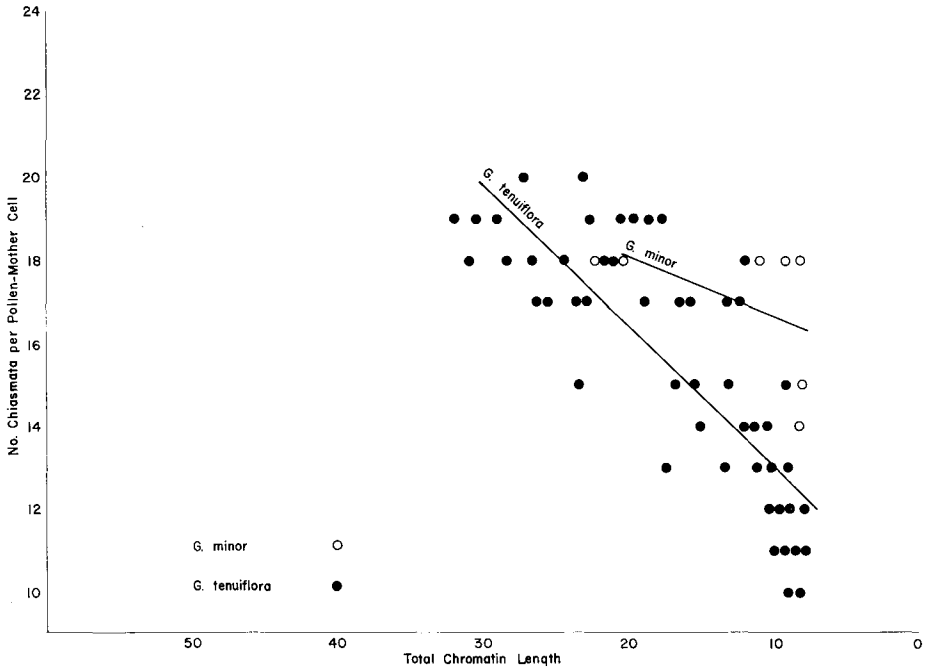


Fig. 6. Regression of chiasma frequency against stage of meiosis (as represented by total length of chromatin in arbitrary units) in *Gilia minor* and *G. tenuiflora*.

TABLE 6. Chiasma frequency at comparative stages of meiotic division I.

TOTAL LENGTH* OF CHROMATIN	<i>Gilia minor</i>				<i>Gilia tenuiflora</i>			
	NUMBER CHIASMATA/CELL			NO. PMC	NUMBER CHIASMATA/CELL			NO. PMC
AVERAGE	RANGE	STD. DEV.	AVERAGE		RANGE	STD. DEV.		
35-30					18.67	18-19	0.3	3
30-25					18.17	17-20	1.0	6
25-20	18.00			2	17.89	15-20	1.2	9
20-15					16.30	13-19	2.3	10
15-10	18.00			1	14.80	13-18	1.8	10
10-5	16.25	14-18	1.3	4	11.64	10-15	1.3	14
5-10					10.25	9-11	1.2	4
10-15	16.00			1	11.00	10-12		2
15-20					11.00			1
				8				59

*In inches as measured by tachometer on camera lucida drawings at bench level. Further explanation in text.

== Indicates the range of diakinesis for each species as determined by visual inspection.

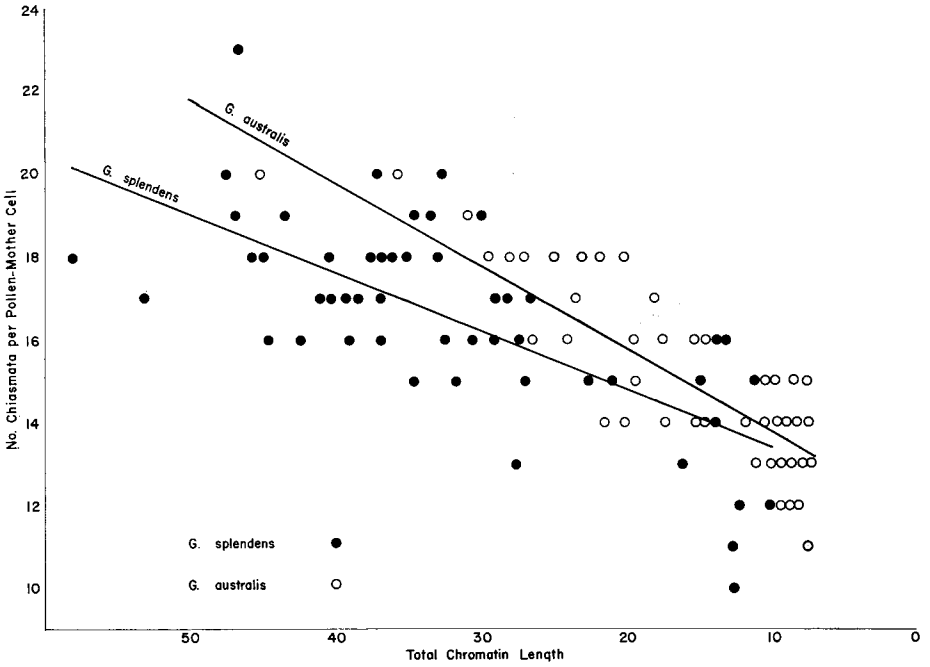


Fig. 7. Regression of chiasma frequency against stage of meiosis (as represented by total length of chromatin in arbitrary units) in *Gilia australis* and *G. splendens*.

TABLE 7. Chiasma frequency at comparative stages of meiotic division I.

TOTAL LENGTH* OF CHROMATIN	<i>Gilia australis</i>				<i>Gilia splendens</i>			
	NUMBER CHIASMATA/CELL			NO. PMC	NUMBER CHIASMATA/CELL			NO. PMC
AVERAGE	RANGE	STD. DEV.	AVERAGE		RANGE	STD. DEV.		
60-55					18.00			1
55-50					17.00			1
50-45	20.00			1	19.60	18-23	1.8	5
45-40					17.22	16-18	1.3	9
40-35	20.00			1	17.50	16-20	1.1	10
35-30	19.00			1	<u>17.30</u>	15-20	1.8	10
30-25	18.00			4	15.71	13-16	1.4	7
25-20	<u>16.43</u>	14-18	1.9	7	<u>15.80</u>	14-17	0.8	5
20-15	<u>15.43</u>	14-17	1.4	7	<u>14.50</u>	13-16	1.2	4
15-10	<u>14.40</u>	13-16	1.0	5	12.86	10-16	2.4	7
10-5	<u>13.30</u>	11-15	1.0	23				
5-10	11.00			1				
10-15	12.00	11-13	0.7	2	11.00	10-13	1.0	5
15-20					11.88	11-14	0.8	9
20-25					10.12	9-12	1.3	4
				<u>54</u>				<u>77</u>

*In inches as measured by tachometer on camera lucida drawings at bench level. Further explanation in text.

≡ Indicates the range of diakinesis for each species as determined by visual inspection.

TABLE 8. Comparison of mean chiasma frequency per meiotic stage and summations of paired species or subspecies of *Gilia*

SPECIES OR SUBSPECIES	BREEDING SYSTEM	NO. PMC	DIPLOTENE			NO. PMC	DIAKINESIS		
			AV. XTA	P ¹	SIG.		AV. XTA	P	SIG.
<i>G. capitata chamissonis</i>	facultative crosser	24	18.38	65%	o ²	4	16.25	74%	o
<i>G. capitata capitata</i>	obligate crosser	13	18.15			6	16.00		
<i>G. achilleaefolia multicaulis</i>	selfer	13	17.47	10%	o	19	16.32	3.4%	* ²
<i>G. achilleaefolia achilleaefolia</i>	crosser	12	16.25			7	14.43		
<i>G. millefoliata</i>	selfer	11	19.54	X	o	16	17.38	25%	o
<i>G. tricolor</i>	crosser	5	19.60			9	16.76		
<i>G. ochroleuca ochroleuca</i>	selfer	3	19.00	63%	o	5	14.80	X	o
<i>G. ochroleuca bizonata</i>	crosser	18	18.28			2	15.00		
<i>G. minor</i>	selfer	2	18.00	X	o	1	18.00	X	o
<i>G. tenuiflora</i>	crosser	18	18.11			20	15.55		
<i>G. australis</i>	selfer	14	17.57	67%	o	12	15.00	X	o
<i>G. splendens</i>	crosser	43	17.35			9	16.22		
Grouped Data	selfers	67	18.23	11%	?	57	16.23	5.6%	?
	crossers	109	17.71			53	15.58		

¹P=Probability that the observed is due to chance.

²Code:

**=Highly significant.

*=Significant.

?=Questionable significance.

o=No significance.

X=Indicates calculations impossible due to insufficient or reversed data, or results not on normal curve table.

TABLE 8. Comparison of mean chiasma frequency per meiotic stage and summations of paired species or subspecies of *Gilia* (continued)

SPECIES OR SUBSPECIES	BREEDING SYSTEM	METAPHASE I				ALL STAGE			
		NO. PMC	AV. XTA	P	SIG.	NO. PMC	AV. XTA	P	SIG.
<i>G. capitata chamissonis</i>	facultative crosser	28	11.86	66%	**	56	14.96	6.3%	?
<i>G. capitata capitata</i>	obligate crosser	38	10.45			57	12.79		
<i>G. achilleaefolia multicaulis</i>	selfer	19	13.53	X ²	**	51	15.57	X	**
<i>G. achilleaefolia achilleaefolia</i>	crosser	36	10.86			55	12.49		
<i>G. millefoliata</i>	selfer	27	15.04	19%	o	54	16.61	X	**
<i>G. tricolor</i>	crosser	38	14.66			52	13.60		
<i>G. ochroleuca ochroleuca</i>	selfer	4	14.25	0.5%	**	12	15.67	X	o
<i>G. ochroleuca bizonata</i>	crosser	2	10.50			22	17.27		
<i>G. minor</i>	selfer	5	16.20	X	**	8	16.88	X	**
<i>G. tenuiflora</i>	crosser	21	11.29			59	14.81		
<i>G. australis</i>	selfer	26	14.04	2.3%	*	52	15.21	X	o
<i>G. splendens</i>	crosser	25	11.88			77	15.32		
Grouped Data	selfers	109	13.74	X	**	233	15.64	X	**
	crossers	160	11.26			322	14.15		

crosser was calculated at diplotene, diakinesis and metaphase I for each species pair. The significance was also determined for the sum of the means of all self-pollinators and all cross-pollinators at each stage, and for the mean of the combined stages of each pair. The results of these calculations are presented in table 8.

Scatter diagrams suggested a linear relationship between chiasma frequency and chromatin length. This was borne out by high correlation coefficients between chiasma frequency and chromatin length for all species tested except one, *G. minor*, for which there was insufficient data. This type of relationship lends itself to correlation by regression coefficients. These were calculated and the regression line for each of the species drawn. Due to variation in the sample size of the classified data, the regression lines were calculated directly. The resulting comparative graphs, Fig. 2 through 7, were superimposed upon scatter diagrams of the data to show the linear relationships.

Because the number of chiasmata observed at any stage in meiosis is a function of both the original number of chiasmata formed and the rate of terminalization, it is necessary to test the significance of both of these quantities. It is impossible to determine if any of the diplotene stages observed contain the total chiasmata produced in that cell. Therefore, it must be assumed that the best estimate which can be made is from those figures closest to the actual process of crossing over. Arbitrarily, the earliest dual observed diplotene of each species pair, determined by chromatin length, was analyzed. The chiasma frequencies were obtained from the regression line graphs at this stage and are presented in table 9. Since the regression lines were determined from a comparison of chiasma frequency versus chromatin length, and the latter may be considered constant at any stage for the compared pair, the slope of the line is determined by the rate of terminalization. Both the differences in rate of terminalization (slope) and the differences in chiasmata at earliest dual-stage diplotene were subjected to a "T" test for significance. Table 10 shows the significance of the differences in rate of terminalization for the six paired species and subspecies. No significant difference in chiasma frequency at earliest observed dual-stage diplotene was found for any of the species pairs studied.

Camera lucida drawings of typical diplotene, diakinesis, and metaphase I figures showing reduction in chromatin length and chiasma frequency are presented in figure 1.

GENERAL CONSIDERATION OF RESULTS

A review of the grouped data in tables 2 through 7 gives the impression that the self-pollinators have a higher chiasma frequency than the cross-pollinators. It will be noted also that in all comparisons except one, *G. australis*-*G. splendens*, the highest chiasma frequency in the earliest class recorded is highest in the self-pollinators. This fact is more readily observed in the scatter diagrams in Fig. 2 through 7. When the mean chiasma frequencies at diplotene, diakinesis, and metaphase I are compared (Table 8) it is obvious again that the trend is toward a higher chiasma frequency in the self-pollinators. The grouped data at these three stages of all self-pollinators and all cross-pollinators studied appears highly indicative.

Table 10 shows that the difference in terminalization rates in the paired species varies greatly. Figures 2 through 7 show clearly that the difference in chiasma frequency as determined by tabular data at any meiotic state may permit widely different interpretation. The findings here confirm the work of Rai (1959) who has found that the rate of terminalization differs greatly in different varieties of the eggplant, *Solanum melangena*. Consequently, the mean chiasma frequency at successive stages of meiosis between these varieties also varies greatly. Apparently chiasma frequency and terminalization are independently controlled in *Gilia*; perhaps in a manner similar to that concluded by Rees (1955) for rye. The results presented here indicate the importance of using diplotene data if accurate comparative chiasma frequency determinations are to be made. It is possible that diakinesis and

metaphase I data may correlate with the actual relative chiasma frequencies, but spurious interpretation could result due to differential rates of terminalization. In extreme cases, metaphase I comparisons may be the reverse of actual chiasma frequencies at diplotene. This is indicated by the *G. tricolor*-*G. millefoliata* comparison where the difference in terminalization rate (Table 10) is significant and the regression lines cross at a point equivalent to late diplotene (Fig. 4).

TABLE 9. Comparative chiasma frequencies of paired species at first observed dual stage diplotene as determined from regression lines

TAXA	BREEDING SYSTEM	DUAL DIPLOTENE XTA FREQUENCY
<i>G. capitata chamissonis</i>	obligate selfer	19.75
<i>G. capitata capitata</i>	facultative crosser	20.11
<i>G. achilleaefolia multicaulis</i>	selfer	20.50
<i>G. achilleaefolia achilleaefolia</i>	crosser	20.13
<i>G. millefoliata</i>	selfer	20.98
<i>G. tricolor</i>	crosser	20.79
<i>G. ochroleuca ochroleuca</i>	selfer	18.73
<i>G. ochroleuca bizonata</i>	crosser	20.11
<i>G. minor</i>	selfer	18.10
<i>G. tenuiflora</i>	crosser	16.48
<i>G. australis</i>	selfer	20.77
<i>G. splendens</i>	crosser	19.05

In the light of the above, it is necessary to consider the diplotene data presented here critically with regard to the hypothesis being considered because it is the only data from which a true indication can be drawn. The mean chiasma frequency comparisons at diplotene (Table 8) indicate generally that the self-pollinators have a higher chiasma frequency. The mean comparison of grouped diplotene data in table 8 is impressive and would seem to support the hypothesis. However, these diplotene data may be criticized on the basis of total sample size and relative sample size within a comparison. It is believed that the reversals in diplotene comparisons shown in tables 8 and 9 may be due to unequal size of the samples. If the comparisons in which one of the samples is less than ten are disregarded, it

TABLE 10. Significance of the difference in terminalization rate of paired species or subspecies (Further explanation in text)

SELFER	CROSSER	SIGNIFICANCE
<i>G. capitata chamissonis</i>	<i>G. capitata capitata</i>	none
<i>G. achilleaefolia multicaulis</i>	<i>G. achilleaefolia achilleaefolia</i>	very high
<i>G. millefoliata</i>	<i>G. tricolor</i>	significant
<i>G. ochroleuca ochroleuca</i>	<i>G. ochroleuca bizonata</i>	none
<i>G. minor</i>	<i>G. tenuiflora</i>	close to significant
<i>G. australis</i>	<i>G. splendens</i>	very high

will be noted that the self-pollinators definitely exhibit a higher chiasma frequency. It is worthy of mention that the number of observations in these latter cases is greater than that used by Rai (1959), or the number of metaphase I counts reported in the paper by Stebbins, Valencia and Valencia (1946) in which the hypothesis being considered here was suggested.

When the significance of the difference in chiasma frequency was tested at the first observed dual diplotene stage, as determined from the regression lines, no positive evidence, except for *G. australis*-*G. splendens* was obtained. However, regardless of the lack of statistical significance, it should be noted that in all but two cases the self-pollinators showed a higher chiasma frequency than the cross-pollinators (Table 9). The two comparisons which show higher chiasma frequencies for the cross-pollinators in the test, *G. capitata cbamissonis*-*G. capitata capitata* and *G. ochroleuca ochroleuca*-*G. ochroleuca bizonata*, interestingly, also show no significance in their compared terminalization rates (Table 10). Regression line crossing in these cases could be due to sample size differences and variance.

The results obtained from the different analyses presented here on chiasma frequency in relation to breeding systems in six species pairs of the genus *Gilia* were mutually contradictory in terms of support for the hypothesis. Significantly, these contradictions point to a need for analysis of diplotene data if a resolution of the hypothesis is to emerge. Due to differing rates of terminalization, metaphase data may not indicate either a true difference in chiasma frequency or its true relative magnitude.

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