

3. An analysis of the chromosome complements in the microspores of plants heterozygous for the interchange indicated that of the four chromosomes constituting a ring, those with homologous spindle fiber attachment regions can pass to the same pole in anaphase I and do so in a considerable number of the sporocytes.

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* Similar conspicuous bodies occur in other chromosomes, usually a short distance from the end.

¹ Brink, R. A., *J. Hered.*, **18**, 266-70 (1927).

² Brink, R. A., and C. R. Burnham, *Am. Nat.*, **63**, 301-16 (1929).

³ Burnham, C. R., *Proc. Nat. Acad. Sci.*, **16**, 269-77 (1930).

THE INHERITANCE OF RUBRICALYX BUD COLOR IN CROSSES WITH OENOTHERA LAMARCKIANA¹

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Some years ago² the cross between *Oenothera Lamarckiana* and *Oe. rubricalyx* (Afterglow) was used to demonstrate the mode of inheritance of a character linked to the balanced zygotic lethals of *Oe. Lamarckiana*. The objection was raised³ that linkage between the gene for *rubricalyx* bud color and the lethals involved should give a different breeding behavior from that observed. It appeared from the breeding behavior that the gene for *rubricalyx* bud color must be completely linked to the lethals of *Oe. Lamarckiana* in certain plants of similar parentage to others in which the gene was independent of the lethals. At the time this seemed an anomalous situation. The crosses between *Oe. Lamarckiana* and *Oe. rubricalyx* have been repeated and a check has been kept on the chromosome configurations of the various hybrids in an attempt to determine the cause of the differences in the linkage relationships.

Oenothera Lamarckiana regularly produces two types of gametes, or complexes, known as *velans* and *gaudens*.⁴ There is a zygote lethal in *velans* and another in *gaudens* which prevent these complexes from appearing in the homozygous condition. I know of no reported occurrences of the loss of the characteristic lethals of these two complexes. In other words, the *velans* lethal and the *gaudens* lethal may be said to be completely linked in *Oe. Lamarckiana*.

Oenothera rubricalyx also produces two different complexes. One of these closely resembles *velans* of *Oe. Lamarckiana* and carries the *velans* lethal. This complex will provisionally be called modified-*velans*. The other complex has no lethal and is viable in the homozygous condition. The homozygous segregate is known as mut. *latifrons*. The complex appearing in homozygous condition in mut. *latifrons* will be called ^h*latifrons* (read haplo-*latifrons*).

The chromosome configuration⁵ of *Oe. Lamarckiana* consists of a ring of twelve and a pair. *Oenothera rubricalyx* has a ring of eight chromosomes and three pairs. Mutation *latifrons* has seven pairs of chromosomes.

In the first generation of crosses between *Oe. Lamarckiana* and *Oe. rubricalyx* there are three types of plants: *velans*^h*latifrons*, *gaudens*^h*latifrons*, and *gaudens*-modified-*velans*. The fourth possible type, *velans*-modified-*velans*, is inviable because of the *velans* lethal which is carried in both complexes.

Velans^h*latifrons* has narrow leaves, the *rubricalyx* growth habit, bluntly pointed buds, and a dark *rubricalyx* bud color. Hybrids of this constitution have a ring of eight chromosomes and three pairs.

The two other F_1 types, *gaudens*-modified-*velans* and *gaudens*^h*latifrons*, resemble each other closely. Both have broad leaves, tapering buds, a pale *rubricalyx* bud color, and both resemble *Oe. Lamarckiana* in growth habit. They differ in chromosome configuration; *gaudens*^h*latifrons* has a ring of eight chromosomes and three pairs, while *gaudens*-modified-*velans* has a ring of twelve and one pair.⁶

The three F_1 types are distinctly different in breeding behavior. *Gaudens*-modified-*velans* breeds true for pale *rubricalyx* bud color, tapering buds, the *Lamarckiana* growth habit, and chromosome configuration. This means that the gene for *rubricalyx* bud color, the *velans* lethal, and the *gaudens* lethal are all in the ring of twelve chromosomes; otherwise homozygous types should appear in the second generation.

Gaudens^h*latifrons* gives an F_2 consisting of two types of plants. One type has tapering buds, pale *rubricalyx* bud color, and has a ring of eight chromosomes and three pairs. This type is identical with the F_1 parent. The other type has somewhat blunter buds, a deep *rubricalyx* bud color, and has seven chromosome pairs. Both types are variable in leaf width and growth habit. In *gaudens*^h*latifrons*, therefore, the *gaudens* lethal and the gene for *rubricalyx* bud color must be in the ring of eight chromosomes, otherwise homozygous *gaudens* or homozygous green buds should appear in the F_2 . Similarly some of the genes for leaf width and growth habit must be in the freely pairing chromosomes since they segregate independently of the chromosome ring.

Velans^h*latifrons* gives a second generation in which growth habit and bud color segregate independently. The majority of the plants resemble

the F_1 parent in having the *rubricalyx* growth habit, extremely blunt buds, and in having a ring of eight chromosomes and three pairs. The other plants have the growth habit of mut. *latifrons*, more pointed buds, and

TABLE 1

PEDIGREE NUMBER	TYPE OF CROSS	<i>Lamarckiana</i> -HABIT	<i>Rubricalyx</i> -HABIT
555	<i>Lamarckiana</i> × <i>rubricalyx</i>	16	22
554	<i>Rubricalyx</i> × <i>Lamarckiana</i>	12	37
557	<i>Lamarckiana</i> × <i>latifrons</i>	5	33

TABLE 2

PEDIGREE NUMBER	PARENT PLANT	HABIT OF PARENT	<i>Lamarckiana</i> -HABIT		<i>Rubricalyx</i> -HABIT		<i>Latifrons</i> -HABIT	
			<i>Rubricalyx</i> BUDS	RED BUDS	<i>Rubricalyx</i> BUDS	RED BUDS	<i>Rubricalyx</i> BUDS	RED BUDS
776	555-5	<i>Rubricalyx</i>	..	20	7	5	2	
777	-8	"	..	28	3	7	5	
778	-9	"	..	23	5	9	3	
2040	-9	"	..	84	25	24	16	
779	-10	"	..	23	6	12	3	
780	-11	"	..	32	5	7	6	
781	-12	"	..	28	5	13	1	
782	-13	"	..	28	12	0	0	
2039	-13	"	..	62	18	11	5	
783	-16	"	..	9	4	5	0	
766	554-4	"	..	6	1	4	0	
767	-6	"	..	31	5	12	3	
768	-7	"	..	7	6	4	1	
769	-8	"	..	14	7	1	0	
770	-9	"	..	28	4	8	0	
771	-10	"	..	24	12	7	2	
772	-12	"	..	20	1	2	1	
773	-13	"	..	25	8	3	3	
786	557-6	"	..	7	4	9	2	
787	-7	"	..	11	6	5	0	
788	-8	"	..	23	9	4	3	
789	-9	"	..	22	10	9	1	
790	-10	"	..	30	7	3	4	
				(585)	(170)	(164)	(61)	
774	554-39	<i>Lamarckiana</i>	17	
2037	-39	"	19	
775	-46	"	25	
2038	-46	"	31	
			(92)					
784	557-4	"	? ⁸	15	..	
785	-5	"	?	39	..	
2035	-5	"	4	4	..	

seven pairs of chromosomes. In both types there are approximately three plants with *rubricalyx* bud color to one plant with the recessive red bud cone color carried in *velans*. In *velans*^h*latifrons*, therefore, the *velans*

lethal and the genes for growth habit and bud shape must be in the ring of eight chromosomes since they are inherited as a unit. But the genes for *rubricalyx* vs. red bud color must be in one of the pairing chromosomes since they segregate independently of the ring.

TABLE 3

PEDIGREE NUMBER	CONSTITUTION	GENERATION	GROWTH HABIT	BUD COLOR	CHROMOSOME CONFIGURATION
554-4	<i>Velans</i> ^h <i>latifrons</i>	F ₁	<i>Rubricalyx</i>	<i>Rubricalyx</i>	Ring 8, 3 pairs
-8	"	"	"	"	"
-9	"	"	"	"	"
-12	"	"	"	"	"
555-9	"	"	"	"	"
-10	"	"	"	"	"
2040-D	"	F ₂	"	"	"
-C	"	"	"	Red	"
2039-5	"	"	"	"	"
-5	^h <i>latifrons</i> ^h <i>latifrons</i>	"	<i>Latifrons</i>	<i>Rubricalyx</i>	7 pairs
-9	"	"	"	"	"
-16	"	"	"	"	"
2040-B1	"	"	"	"	"
-B2	"	"	"	"	"
-A1	"	"	"	Red	"
-A2	"	"	"	"	"
2035-3	<i>Gaudens</i> ^h <i>latifrons</i>	"	<i>Lamarckiana</i>	<i>Rubricalyx</i>	Ring 8, 3 pairs
-10	"	"	"	"	"
-11	"	"	"	"	"
-8	^h <i>latifrons</i> ^h <i>latifrons</i>	"	<i>Latifrons</i>	"	7 pairs
2037-7	<i>Gaudens</i> mod.- <i>velans</i>	"	<i>Lamarckiana</i>	"	Ring 12, 1 pair
2038-3	"	"	"	"	"
-15	"	"	"	"	"

The observed frequencies of phenotypes in the above crosses are given in tables 1 and 2. A list of the plants whose chromosome configurations were determined cytologically⁷ is given in table 3.

From the above observations it is apparent that the gene for *rubricalyx* bud color is "linked" with the *velans* and *gaudens* lethals in hybrids of the constitution *gaudens*-modified-*velans* because all three are in the ring of twelve chromosomes. And, similarly, the gene for *rubricalyx* bud color is independent of the *velans* lethal in hybrids of the constitution *velans*-^h*latifrons* because the two lie in different, independently assorting chromosome groups. The linkage between the gene for *rubricalyx* bud color and the *velans* lethal in the former case is thus not due to the presence of both in the same chromosome, but is due to the association in a ring of the two chromosomes which carry the gene and the lethal. In all three F₁ types the *Lamarckiana* lethals are in the chromosome rings, so neither *velans* nor *gaudens* can appear in homozygous condition in the F₂. The homozygous

segregates with all pairing chromosomes are homozygous ^h*latifrons* in each case.

¹ The experiments reported in this paper were started at the University of Michigan Botanical Gardens, Ann Arbor, Michigan.

² Shull, G. H., *Eugenics, Genetics and the Family*, 1, 86-99 (1923).

³ Emerson, Sterling, *J. Wash. Acad. Sci.*, 14, 277-284 (1924).

⁴ For a summary of the genetical behavior of *Oe. Lamarckiana* see: Renner, O., *Bibliot. Genet.*, 8 (1925).

⁵ Cleland, Ralph E., *Amer. Nat.*, 59, 475-479 (1925).

⁶ The chromosome configurations for *gaudens*-^h*latifrons* and *gaudens*-modified-*velans* were determined from *F*₂ plants only. A ring of twelve and a pair can come from the inbreeding of a form with the same chromosome configuration and from none other, so the configuration of the *gaudens*-modified-*velans* *F*₁ is certain. Forms with a second ring of four or six in addition to the ring of eight could give rise to a ring of eight and three pairs from inbreeding. But the chromosome configurations of hybrids of ^h*latifrons* and *gaudens* with *velans*, ^h*franciscana*, and *sulfurens* indicate that ^h*latifrons* has at least two chromosomes in common with *gaudens*. The only possible configuration for *F*₁ *gaudens*-^h*latifrons* is thus a ring of eight and three pairs. Even if a second ring were present in the *F*₁, the observed relationships between the gene for bud color, the *gaudens* lethal and the ring of eight chromosomes would remain unchanged.

⁷ The microscopic preparations were made by Miss Elizabeth Griffiths.

⁸ The two types in the *F*₂ from *gaudens*-^h*latifrons* were not recognized the first year and all plants were classed together.

COMPLETE ELIMINATION OF SELF-STERILITY IN THE ASCIDIAN *STYELA* BY FERTILIZING IN ALKALINE SOLUTIONS

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The discovery by Morgan¹ that removal of the membranes surrounding the unfertilized egg of the Ascidian *Ciona* made self-fertilization possible suggested a new and illuminating explanation of the phenomenon of self-sterility in these forms. Since it is known that sperm may penetrate the membrane itself without fertilization, Morgan's suggestion was that the test cells which lie between egg and membrane constitute the block which causes self-sterility. These cells are maternal tissue, with the maternal genetic constitution, and either mechanically or as a result of some secretion they might immobilize spermatozoa of like genetic constitution. Thus fertilization by sperm of the same individual would be prevented, even though there was no incompatibility between the gametes when they met. According to this view self-sterility in Ascidians is brought into line with the explanation of East and Parks² for self-sterility