THE LINKAGE RELATIONS OF CERTAIN GENES IN OENOTHERA

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One may now predict with some confidence that two characters, which are known to segregate independently in certain Oenothera crosses, will be found to be closely linked in other crosses. Instances of this sort are increasingly numerous. RENNER (1925, 1928) was the first to call proper attention to such differences in linkage relationships, though other cases of the same sort had been discussed earlier by DE VRIES, by RENNER, and by BLANCHARD and BARTLETT.

At present there are only two characters that do not show such variable linkage relationships. The better known case involves the flower size differences found in many species (C_o, etc. of RENNER 1925). The second is the *brevistylis* character (short styles and deformed stigmas—b_r of SHULL [1926]) of *Oe. Lamarckiana*. The two characters are alike in that they have never been found to be linked to any other characters, even when all other characters in a hybrid were linked through the presence of all 14 chromosomes in a single ring.

VARIABLE LINKAGE RELATIONSHIPS

A difference in the linkage relationships of *nanella* stature (*n*) was reported by DE VRIES (1913, p. 235) in the cross *Oe.* "*biennis*-Chicago" (that is, *Oe. chicagoensis*) × *Oe. Lamarckiana nanella* which produced twin hybrids in F_1. The *densa* twin (that is, *excellens·gaudens*, probably with the

configuration 10, 2, 2[1], with chromosomes 1·2 and 5·6 as pairs, and with *N* in 3·4 of *excellens* and therefore in the ring [EMERSON and STURTEVANT 1931]) bred true for tall stature and other F_1 characteristics; in other words *n* was completely linked to the *gaudens* lethal (*gaudens* lethal not in 1·2 or 5·6 and therefore in the ring) and to other characters by which these complexes differed. In the *laxa* twin (that is, *excellens·n velans*, probably with the configuration 6, 2, 2, 2, 2, with chromosomes 1·2, 3·4, 11·12, and 13·14 as pairs, and with *n* in the pairing chromosome 3·4) *nanella* appeared in 35 percent of the progeny; in other words *n* was independent of the *velans* lethal. In the *Oe. Lamarckiana* parental race (*velans·gaudens*), the gene *n* and the *velans* and *gaudens* lethals were almost completely linked (DE VRIES 1913, many examples).

RENNER (1917, pp. 221–225) reported that red mid-ribs (*R*) segregated independently of other genes in *rubens·velans* (probable configuration 12, 2, with *R* in the pairing chromosome 1·2 [EMERSON and STURTEVANT 1931]), while in *albicans·R gaudens* (probable configuration 8, 6) *R* was completely linked to the other genes involved (the genes in *rubens* and in *gaudens* were identical as far as could be determined).

The case reported by DOCTOR (COBB) BLANCHARD (COBB and BARTLETT 1919, COBB 1921, BLANCHARD 1929) was in *Oe. pratincola*, in which the β complex of strain E carried a recessive gene (*f*) for revolute leaves which was masked by the dominant in the α complex. *Oe. pratincola* E ($\alpha\cdot\beta$) had a ring of 14 chromosomes (KULKARNI 1929) and was heterozygous for several characters all showing complete linkage except that *f* became associated with α in about one percent of the gametes. When the new *f*-α was crossed to the β (*F*) of *Oe. pratincola* strain C, the F_1 had the configuration 12, 2 (KULKARNI 1929) and *f* was inherited independently of all other characters of α and β.

In his 1928 paper, RENNER gave a summary of the linkage relationships observed by him in different hybrids. For example, in *curvans·flavens* S_p[2] was linked to C_u, and *M* and *B* were independent, while in *flavens·flectens* S_p was linked to *B* with C_u and *M* independent. In *flavens·velans* (probable configuration 4, 4, 2, 2, 2) S_p and *B* were linked and *P*(*M*) and *R* were linked but independent of the former group. In *rubens·velans* (probable configuration 12, 2) *P*, *B* and S_p were linked and *R* was independent,

[1] Chromosome configurations are indicated by the convention used by STURTEVANT (1931). The numbers separated by commas indicate the numbers of chromosomes in the rings (or pairs): 10, 2, 2 indicates a ring of 10 and 2 pairs; 8, 6 indicates a ring of 8 and a ring of 6, etc.

[2] S_p is a gene for pointed buds and leaves, C_u for curved stems, *M* for marginate leaves (allelomorph of *P*, a gene for punctate stems), *B* for broad leaves, and *R* for red mid-ribs.

while in *curvans·rubens* and *curvans·velans* *R*, *P(M)*, *B*, S_p and C_u were all linked. In all the cases reported by RENNER the linkage was either extremely close or entirely lacking.

A similar situation was found by SHULL (1923a) in crosses between *Oe. Lamarckiana* and *Oe. rubricalyx* in which P^r (*rubricalyx* bud color) was linked to the *velans* and *gaudens* lethals in *gaudens*·modified-*velans* with the configuration 12, 2 (the pair probably was chromosome 1·2), but P^r was independent of the *velans* lethal in *ʰlatifrons·velans* with the configuration 8, 2, 2, 2 in which P^r was in the pairing chromosome 3·4 (cytology and interpretation by EMERSON [1930] and EMERSON and STURTEVANT [1931]). Linkage of sulfur flower color (*s*) and dwarf stature (*d*) to striped bud color (P^s) and to the *sulfurens* pollen lethal was found in *ʰfranciscana·sulfurens* with the configuration 10, 2, 2, while *s* and *d* were completely independent in *ʰfranciscana·ʰfranciscana* with 7 paired chromosomes (EMERSON 1931a). SHULL (1926) has found *n* (*nanella* stature) and *v* (old-gold flower color) to be independently inherited in all his crosses, but STURTEVANT (1931) found them to be very closely linked in *jugens·N* which had the configuration 10, 2, 2, with *v* in chromosome 1·2 and *n* in chromosome 3·4, both in the ring. There are many other cases of the same sort (see especially GERHARD 1929, and CLELAND and OEHLKERS 1930).

The apparent rule is that characters which are independently inherited in hybrids with pairing chromosomes will be linked in hybrids in which the chromosomes are in rings. By means of this rule it has been possible to identify certain genes with particular chromosomes (EMERSON and STURTEVANT 1931, pp. 410–412), as has been noted in some of the crosses reviewed above.

LINKAGE WITHIN CHROMOSOME 1·2

Chromosome 1·2 is defined as that chromosome which is present in *ʰHookeri* and in *gaudens* but not in *flavens* (EMERSON and STURTEVANT 1931, p. 403) and corresponds to RENNER'S linkage group II and to SHULL'S III. The gene *R* (red mid-ribs) is in chromosome 1·2 since it is independent of certain other characters in plants in which 1·2 is a pairing chromosome, but is linked to the same characters in plants in which 1·2 is in the ring (EMERSON and STURTEVANT 1931, p. 410).

Old-gold flower color has recently been found to be in chromosome 1·2. The evidence for placing *v* (old-gold) in chromosome 1·2 is as follows: The F_1 hybrid *R velans·N* had the configuration 6, 2, 2, 2, 2 and was heterozygous for the factor pairs *R r*, *V v*, *N n*, and P^r P^s (STURTEVANT 1931).

The backcross to $N\,(r\ v\ n\ P^r)$, using the multiple recessive as pollen parent, gave the following frequencies (culture 18 of 1931):

5 *R V N* P^r
1 *R V n* P^r
5 *r v N* P^r
4 *r v n* P^r

In the backcross of *R velans*·*N* to an *r v N* P^s, extracted from *franciscana*·*N* crosses, the following frequencies were observed (culture 20 of 1931):

9 *R V N* P^r
1 *r V N* P^r
7 *r v N* P^r
1 *r v N* P^3

The F_1 hybrid *R gaudens*·*N* had the configuration 10, 2, 2 and was heterozygous for the factor pairs *R r*, *V v*, and P^r *p* (STURTEVANT 1931). In the backcross to the extracted *r v* P^s (culture 19 of 1931) there were 2 *R V* P^r and 1 *r v* P^r.

In *Oe. R Lamarckiana* the gene *R* is carried in the pairing chromosome 1·2 which is common to *velans* and *gaudens*. Chromosome 1·2 is also carried in the complex *N* (EMERSON and STURTEVANT 1931). The pair 1·2 in *R velans*·*N* and in *R gaudens*·*N* is therefore identical and the linkage data for this chromosome should be comparable in both hybrids. In the backcrosses reported above there were 35 non-crossover gametes recovered (17 *R V* and 18 *r v*) and one crossover gamete (*r V*). This represents about 3 percent crossing over between *R* and *v*, but the data are too few to give an accurate indication of the linkage intensity. Since 1·2 was known to be a pairing chromosome in these hybrids, and since *R* is known to be in 1·2, it follows that *v* is also in 1·2. It should be noted in the *R velans*·*N* backcross that *n* segregated independently of the characters in chromosome 1·2.

It is probable that b_u (*bullata*) and s_p (double flowers), which SHULL (1925, 1927, 1928) has found to be linked to *v*, are also in chromosome 1·2 since most of his crosses were in *Oe. Lamarckiana* in which 1·2 is a pair.

LINKAGE WITHIN CHROMOSOME 3·4

Chromosome 3·4 is defined as that chromosome which is present in ^{h}*Hookeri* but not in *gaudens* and not in *flavens* (EMERSON and STURTEVANT

[3] This plant and the *P* recorded below from *flavens*·*N* selfed suggest mutation of P^r to *P*.

1931, p. 403) and corresponds to SHULL's linkage group I and to RENNER's I. The gene *P* (punctate stems) is in chromosome 3·4 since it is inherited independently of *R* in any hybrids in which 3·4 is a pairing chromosome but is linked to *R* in all hybrids in which both 1·2 and 3·4 are in a common ring (EMERSON and STURTEVANT 1931, p. 410). There are probably a series of allelomorphs of *P* (P^r, *rubricalyx* bud color with punctate stems; P^s, striped bud cones with punctate stems; *P*, green buds with punctate stems; and *p*, green buds with no punctation on the stems [see discussion in EMERSON 1931b, pp. 390–392]).

SHULL (1923b) found linkage with about 8 percent crossing over between P^r P^s and *S s* (yellow *versus* sulfur flowers) in certain crosses in which it was not known that 3·4 was a pairing chromosome. Since then EMERSON (1931b) has found the same relationship in the hybrid *s d* ^{h}*franciscana*·^{h}*latifrons* (configuration 4, 2, 2, 2, 2, 2) in which 3·4 was known to be a pairing chromosome (EMERSON and STURTEVANT 1931) and in which it was shown by cytological examination of plants in the backcross to *s d* ^{h}*franciscana* that both *P* and *s* were independent of the only ring present in the hybrid.

SHULL also found *n* to be linked to *s* and to P^r, but here again it was not known that 3·4 was a pairing chromosome. STURTEVANT (1931) has since found P^r and *n* to be linked in the hybrid ^{h}*franciscana*·*N* (configuration 6, 2, 2, 2, 2) in which chromosome 3·4 was known to be one of the pairs, and EMERSON (1931b) has found *n* and *s* to be linked in the hybrid *s d* ^{h}*franciscana*·*n velans* (configuration 6, 2, 2, 2, 2) in which 3·4 was again known to be one of the pairs.

From the above data it is evident that *P*, *n*, and *s* are all in chromosome 3·4 and that the observed linkage between these genes is due to their presence in a single chromosome. There is now additional data to support this conclusion. In the hybrid *s d* ^{h}*franciscana*·*N* (configuration 6, 2, 2, 2, 2[EMERSON 1931b]) chromosome 3·4 was known to be one of the pairs (EMERSON and STURTEVANT 1931). The following frequencies were observed in F_2 (culture 2305 of 1931):

14 P^r *S N V D*
5 P^r *S N V d*
3 P^r *S N v D*
2 P^r *S n V D*
1 P^r *S n V d*
2 P^r *S n v d*
1 P^s *S N v D*
3 P^s *s N V D*

The genes *v* and *d* (dwarf stature) were independent of the genes in chromosome 3·4. Disregarding these two genes, the frequencies for the genes in 3·4 were: 22 *P^r S N*, 5 *P^r S n*, 1 *P^s S N*, and 3 *P^s s N*, indicating very close linkage between these three genes. Unfortunately, there was no triple recessive to use for backcrossing, but backcrosses were obtained for *P^s n* (4 percent crossing over, total equals 25) and for *P^s s* (12.5 percent crossing over, total equals 40).

Revolute leaves (*f*) have been supposed by SHULL (1923b) to be in the same linkage group as *P*, *s*, and *n*. We have found close linkage with no crossing over between *f* and *s* in extensive cultures, but in no case has it been known that these genes were in pairing chromosomes.

The *velans* zygotic lethal which was similarly supposed to be in the same linkage group (SHULL 1923a, 1923b) has since been shown (EMERSON 1930) to be in a different chromosome. In the hybrid *^{h}latifrons·velans*, the configuration was 8, 2, 2, 2 and the factor pair *P^r P^s* was shown to be in one of the pairing chromosomes while the *velans* zygotic lethal was in the ring of 8 (since the only segregates with 7 pairs of chromosomes were *^{h}latifrons·^{h}latifrons*).

LINKAGE BETWEEN CHROMOSOMES 1·2 AND 3·4

Linkage between *R* in chromosome 1·2 and *P* in 3·4 was found by RENNER (1925) in *velans·flavens*. In this hybrid it is known that 1·2 and 3·4 of *velans* are in a ring of 4 with 1·4 and 2·3 of *flavens* (EMERSON and STURTEVANT 1931).

Linkage between *v* in chromosome 1·2 and *n* in 3·4 was found by STURTEVANT (1931) in the hybrid *jugens·N*. This hybrid had the configuration 10, 2, 2 and the pairs were 8·13, 11·12, chromosomes 1·2 and 3·4 of *N* being in the ring of 10 (EMERSON and STURTEVANT 1931). In addition to the counts previously recorded there was an F_2 with 8 *V P^r N* and 1 *v P^r n* (culture 25 of 1931).

The hybrid *flavens·N* had the configuration 4, 4, 2, 2, 2 (STURTEVANT 1931). One of the rings of 4 was made up of chromosomes 1·2 and 3·4 of *N* with 1·4 and 2·3 of *flavens*. The F_2 of this cross (culture 23 of 1931) showed linkage between *v*, *P^r* and *n*; the frequencies were 5 *p N V* (*lutescens*), 6 *P^r N V*, 1 *P^r n v*, and 1 *P N V*. The backcross to *N* (*P^r n v*) showed complete linkage between *n* and *v*—6 *P^r N V* to 6 *P^r n v* (culture 22 of 1931).

In the hybrid *accelerans·N*, *v* was found to be linked to *P^r*. The F_1 had the configuration 12, 2 (STURTEVANT 1931) with the pair known to be 5·6 (EMERSON and STURTEVANT 1931). In the backcross to *v P^s N* the following frequencies were obtained (culture 36 of 1931): 12 *v P^r* with erect

mid-rib hairs and appressed sepal tips (that is, the *N* complex was recovered) and 2 *V* P^s with strigose mid-rib hairs and spreading sepal tips (that is, the *accelerans* complex was recovered).

The F_1 *sulfurens·v hfranciscana* had the configuration 10, 2, 2, and was heterozygous for the factor pairs P^s *p*, *S s*, *V v*, The pairs were known to be 7·10 and 8·9 (EMERSON and STURTEVANT 1931). In the backcross to P^s *v s* there were (cultures 2380, 2381 of 1931): 17 *v*, P^s P^s, *S*; 4 *V*, P^s *p*, *s*; and 1 *V*, P^s *p*, *S*. The last plant was examined cytologically and found to have the configuration 10, 2, 2, indicating the constitution *S sulfurens·s v hfranciscana*. Otherwise there were no crossovers between *v* in chromosome 1·2 and P^s and *s* in chromosome 3·4.

LINKAGE RELATIONS OF *d* (DWARF STATURE)

It has previously been shown (EMERSON 1931a) that dwarf stature (*d*) was independent of *s* (chromosome 3·4) in a hybrid with 7 pairs of chromosomes, and that *d* was independent of both *s* and P^r in another hybrid with the configuration 4, 2, 2, 2, 2, 2 in which chromosome 3·4 was known to be a pair (*s d hfranciscana·hlatifrons* [EMERSON 1931b]). It has also been shown that *d* was in the ring of 10 in *sulfurens·s d hfranciscana* and consequently independent of the pairing chromosomes 7·10 and 8·9 (EMERSON 1931a; for chromosome identities see EMERSON and STURTEVANT 1931). In the F_2 from *s d hfranciscana·N* (described in the third section of this paper), *d* was independent of P^r, *s*, and *n* in chromosome 3·4 and also independent of *v* in chromosome 1·2.

The F_1 *s d hfranciscana·b_r velans* had the configuration 6, 2, 2, 2, 2 (EMERSON 1931b). In the backcross to *s d hfranciscana* there were (culture 2293 of 1931): 4 *S D* (2 plants with 7 pairs of chromosomes), 3 *S d* (1 with 7 pairs, 1 with configuration 6, 2, 2, 2, 2,), 1 *s D*, and 3 *s d* (1 with 7 pairs, 1 with 6, 2, 2, 2, 2). In the plants examined cytologically, *s* and *d* were each associated with the ring chromosomes in their inheritance in 2 cases and not so associated in 4 cases, indicating that neither *s* nor *d* was in the ring of 6. The ring in this hybrid was made up of chromosomes 5·8, 6·7 and 9·10 of *velans* and 5·6, 7·10 and 8·9 of *hfranciscana*.

The F_1 *jugens·s d hfranciscana* had the configuration 10, 2, 2 (STURTEVANT 1931) with chromosomes 7·10 and 11·12 as pairs (EMERSON and STURTEVANT 1931). In the F_2 (culture 26 of 1931) there were 12 *D S* and 3 *d s*. In the backcross *s d hfranciscana* × F_1 (culture 28 of 1931) there were 2 *D S* and 13 *d s*. Chromosome 3·4, which carried *s*, was in the ring of 10 in the F_1, and, since *s* and *d* were linked, *d* must also have been in the ring of 10 and consequently independent of chromosomes 7·10 and 11·12.

In the crosses reported above, *d* (dwarf stature) has been shown to be inherited independently of chromosomes 1·2, 3·4, 5·6, 7·10, 8·9 and 11·12 of *hfranciscana*, and consequently may be supposed to be carried in chromosome 13·14. A direct test of this point was available in the backcross of *s d hfranciscana·N* to *s d hfranciscana* in which *d* should never have been associated with the ring of 6 (chromosomes 7·10, 8·9 and 13·14 of *hfranciscana*), but, unfortunately, the proper plants were not examined cytologically.

FLOWER SIZE AT THE C_o LOCUS[4]

The best evidence of the independence of flower size was found by LANGENDORF (1930) in crosses between *Oe. biennis* and *Oe. Hookeri*. The F_1 *albicans·hHookeri* has been found usually to have all 14 chromosomes in a single ring (CLELAND and BLAKESLEE 1930). Due to the presence of a pollen lethal in *balbicans*, all functioning pollen was *hHookeri*, and through the great superiority of *hHookeri* over *balbicans* in gametophytic competition (RENNER 1921), all functioning eggs were also *hHookeri*. The F_2 thus consisted entirely of homozygous *Hookeri* plants and these were uniform for all characters involved except flower size. Of the parents, *Oe. biennis* had the smaller flowers (petal length 13 to 19 mm) and *Oe. Hookeri* had much larger (34 to 40 mm). The flower size of the F_1 was definitely intermediate (23 to 31 mm). In the F_2, flower size segregated sharply into two classes. Tests in the F_3 generation and backcrosses to *Oe. Hookeri* showed that small flower size was a simple Mendelian dominant in plants of the constitution *hHookeri·hHookeri*. LANGENDORF'S data for petal length in these crosses are summarized in table 1.

From this hybrid, *hHookeri* chromosomes alone were recovered in the F_2 and backcrosses; still half of the gametes carried the gene C_o (small flower size) from *balbicans*. Thus C_o is shown to have been inherited independently of all the chromosomes of *balbicans*. It has been suggested (EMERSON and STURTEVANT 1931, p. 414) that these conditions can be satisfied by the assumption that the gene had its locus at such a distance from the translocation point in some chromosome as to give 50 percent crossing over with that point.

[4] In comparing the measurements of flower size in different crosses and in the data of different authors, it should be borne in mind that the measurements reported cannot be exact. Flower size on a given plant may vary somewhat during the flowering season (see GATES 1917). A more important error can arise from measuring flowers at different times of day since the petals grow considerably between the time of opening in the evening and the time that the flowers wilt the following morning. Differences in petal shape in various species also make exact measurements difficult.

The case for *ʰalbicans·velans* (HOEPPENER and RENNER 1929) is not quite as clear as in the cross just described, since the data were not given in detail, but has one advantage in that cytological examinations were made on the plants studied. HOEPPENER and RENNER found that both large and small flowered F_2 plants had rings of 14 chromosomes.

CLELAND and OEHLKERS (1930) reported independent segregation for flower size in two hybrids, each having a ring of 14 chromosomes. The F_2 from *ʰHookeri·truncans* consisted of 27 plants of the F_1 constitution of which 17 had small flowers and 10 had large flowers, and 17 homozygous *Hookeri* plants of which 9 had small flowers and 8 large. The F_2 from *acuens·gaudens* bred true except for flower size: there were 38 plants with small flowers and 23 with large.

RUDLOFF (1921) reports that the small flowers of *Oe. purpurata* were dominant to the larger ones of *Oe. Hookeri* (F_1 could have not more than two pairs)[5] and that there was a simple monohybrid segregation, tested by raising F_2 and both types of backcrosses from both F_1's (*Hookeri* × *purpurata* and *purpurata* × *Hookeri*). There was also recombination for flower-size (not clearly monofactorial) in *ʰpurpurata·velans* (12, 2), *ʰpurpurata·gaudens* (10, 4 or 10, 2, 2), and *ʰpurpurata·albicans*. In these cases there can be no single chromosome of *purpurata* that is segregating freely of the rest in all cases, since *albicans* has no chromosome in common with *ʰHookeri*, *velans*, or *gaudens* (EMERSON and STURTEVANT 1931).

Students of Oenothera have accumulated numerous instances of the type of inheritance of flower size reported in the crosses reviewed above. Only a partial list of such cases will be presented.

Among the cases reported by DE VRIES is the cross *Oe. muricata* × *Oe. biennis* in which the F_1 (that is, *rigens·rubens*) was intermediate between the parents for flower size (*Oe. muricata* had smaller flowers than *Oe. biennis*). The F_2 bred true for all characters except flower size which varied from "fast *muricata*-Grösse bis *biennis* ab. Diese Fluktuation (war) eine individuelle, die eine Pflanze (war) grossblumig an allen Tagen und auf allen Zweigen, die andere aber stets kleinblumig oder mittelblumig" (DE VRIES 1913, pp. 41–43). Similar results were obtained in the cross *Oe. muricata* × *Oe. Lamarckiana*, F_1 *velutina* (that is, *rigens·velans*) in which the F_2 segregated into two types "deren einer doppelt so grosse Blüten

[5] RUDLOFF'S cytological results are based on F_2 and backcross individuals. An extracted *ʰpurpurata·velans* had 12, 2, which must also have been the configuration of the F_1. An extracted *ʰpurpurata·gaudens* had 10, 2, 2, which means that the F_1 was either 10, 2, 2 or 10, 4. The genetic results suggest that *ʰpurpurata* carries chromosome 5–6; if this deduction is correct *ʰpurpurata·gaudens* is 10, 2, 2; and *ʰpurpurata·ʰHookeri* is also 10, 2, 2.

hat als der andere" (DE VRIES 1913, pp. 127–128). Similar conditions were found in other crosses.

Among the cases reported by DAVIS are the intercrosses between *Oe. franciscana* and *Oe. biennis*. Petal length in *Oe. franciscana* was 30 to 35

TABLE 1

Petal length (in mm) in crosses between Oe. biennis and Oe. Hookeri, data summarized from LANGENDORF *(1930) tables 1–28.*

TABLE	CROSS	10	11	12	13	14	15	16	17	18	19	20	21
1	*Oe. biennis*	..	..	..	1	2	6	4	7	5	2	..	..
	Oe. Hookeri	..	..	..	..	..	..	..	..	..	..	..	..
2	*biennis*×*Hookeri*	..	..	..	..	..	..	..	..	..	..	..	..
4	(B×H)F$_2$	..	1	8	12	17	18	25	41	17	6	2	1
5	F$_1$×*Hookeri*	..	1	2	..	5	10	15	7	6	9	3	2
6	*Hookeri*×F$_1$	..	..	..	..	1	2	2	5	3	2	1	..
7	F$_2$ large×self	..	..	..	..	..	..	..	..	..	..	..	..
8	F$_2$ large×self	..	..	..	..	..	..	..	..	..	..	..	..
9	F$_2$ large×self	..	..	..	..	..	..	..	..	..	..	..	..
10	F$_2$ small×self	..	..	..	..	3	1	5	4	5	4	..	..
11	F$_2$ small×self	..	..	..	..	..	..	2	..	9	14	4	..
12	F$_2$ small×self	..	3	4	9	10	15	11	7	1	..	..	..
13	F$_2$ small×*Hookeri*	..	..	..	..	..	1	3	12	11	6	2	..
14	(F$_1$×H) large×self	..	..	..	..	..	..	..	..	..	..	..	..
15	(F$_1$×H) large×self	..	..	..	..	..	..	..	..	..	..	..	..
16	(F$_1$×H) large×self	..	..	..	..	..	..	..	..	..	..	..	..
17	(F$_1$×H) small×self	1	3	2	4	3	5	8	6	5	1	..	..
18	(F$_1$×H) small×*Hookeri*	..	..	..	..	..	1	3	12	11	6	2	..
19	F$_2$ large×*flavens*	..	..	..	..	..	..	..	..	..	..	..	..
20	F$_2$ large×*flavens*	..	..	..	..	..	..	..	..	..	..	..	..
21	F$_2$ small×*flavens*	..	..	..	..	..	..	..	..	..	..	..	..
22	F$_2$ small×*flavens*	..	..	..	..	..	..	..	..	..	..	..	..
23	*flavens*×F$_2$ large	..	..	..	..	..	..	..	..	..	..	..	..
	albicans×F$_2$ large	..	..	..	..	..	..	..	..	..	..	..	..
24	*flavens*×F$_2$ small	..	..	..	..	..	..	..	..	..	..	..	..
	albicans×F$_2$ small	..	..	..	..	..	..	..	..	..	..	..	..
25	*flavens*×F$_2$ small	..	..	..	..	..	..	..	..	..	..	..	..
	albicans×F$_2$ small	..	..	..	..	..	..	..	..	..	..	..	..
26	F$_1$×*biennis*	..	..	..	1	..	..	..	7	16	15	17	2
27	(F$_1$×H) large×*biennis*	..	..	..	..	..	..	2	..	5	14	18	11
28	(F$_1$×H) small×*biennis*	..	..	1	..	..	2	3	3	3	10	14	3

mm and in *Oe. biennis* 20 to 23 mm. The *franciscana*×*biennis* F$_1$ (that is, *h franciscana·rubens*, probably with the configuration 10, 2, 2) had petals 21 to 24 mm long. The F$_2$ consisted of 64 plants of the F$_1$ constitution of which 7 had large flowers, 15 intermediate and 42 small; and 219 *francis-*

cana-like plants (that is, $^{h}franciscana \cdot {}^{h}franciscana$) of which 54 were large flowered, 38 intermediate and 127 small; the small flowered group in both types contained plants with smaller flowers than the *biennis* parent. The reciprocal F_1 (that is, $^{b}albicans \cdot {}^{h}franciscana$, with the probable configuration either 14, or 12, 2) had petals 23 to 25 mm in length and gave in F_2 20 plants of the F_1 type, of which 3 had large flowers, 5

TABLE 1 (continued)

22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	TABLE
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1
..	..	..	..	..	..	..	..	..	..	..	..	1	3	5	8	8	4	1	..	1
..	1	2	4	7	8	6	4	2	1	..	..	..	..	..	..	..	..	..	..	2
2	..	2	4	6	5	10	12	10	6	9	18	4	3	1	2	..	..	..	..	4
..	2	1	1	3	5	6	8	6	8	9	8	10	3	3	3	1	..	..	..	5
1	1	..	..	..	..	2	3	8	7	5	7	7	4	1	2	2	..	..	..	6
..	..	..	..	..	..	..	..	..	1	..	9	11	15	15	3	5	2	..	..	7
..	..	..	..	..	..	..	2	1	4	7	9	10	7	1	3	..	..	..	..	8
..	..	..	..	1	3	2	..	15	19	18	9	5	6	..	..	..	..	..	..	9
..	1	..	..	..	..	..	1	1	2	3	..	..	2	2	1	..	..	..	..	10
..	..	..	..	..	..	..	..	..	..	1	2	1	1	..	..	..	..	..	..	11
..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	12
..	..	..	..	..	..	..	1	2	3	7	8	3	6	2	..	1	..	..	..	13
..	..	..	..	..	..	..	2	4	9	8	8	10	7	3	1	1	..	..	..	14
..	..	..	..	..	..	1	2	6	11	24	52	38	39	18	8	5	1	..	1	15
..	..	..	..	..	..	1	..	..	2	7	6	19	17	8	7	..	3	..	..	16
..	..	..	2	..	..	2	1	2	1	3	2	..	..	1	..	..	..	..	..	17
..	..	..	..	..	1	..	..	..	2	3	8	6	3	3	1	..	..	..	..	18
..	..	2	13	11	10	8	10	4	2	..	1	..	..	..	..	..	..	..	..	19
..	..	..	1	1	..	2	6	12	18	7	1	1	..	..	..	..	1	..	..	20
..	1	..	10	21	18	8	2	..	..	1	1	..	..	..	..	..	..	..	..	21
1	..	5	8	8	14	9	5	2	4	..	..	..	..	..	..	..	..	..	..	22
..	2	2	5	12	18	18	21	20	9	3	1	..	..	..	..	..	..	..	..	23
..	..	1	..	6	6	3	2	1	1	..	..	..	..	..	..	..	..	..	..	23
..	2	1	11	14	13	10	10	3	..	..	..	..	..	..	..	..	..	..	..	24
..	..	2	6	6	1	4	..	1	3	..	..	..	..	..	..	..	..	..	..	24
..	..	..	4	7	3	6	10	6	1	2	..	..	..	..	..	..	..	..	..	25
1	1	2	4	4	6	4	..	3	2	..	..	..	..	..	..	..	..	..	..	25
4	3	2	1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	26
1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	27
1	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	28

intermediate and 12 small, and 96 *franciscana*-like plants of which 6 had large flowers, 28 intermediate and 62 small (DAVIS 1914, pp. 175, 189, 191; 1916, pp. 207, 215, 221–227). In the double reciprocal cross (*Oe. biennis* × *Oe. grandiflora*) × (*Oe. grandiflora* × *Oe. biennis*), there was segre-

gation for other characters as well as flower size, but "no correlations were discovered between flower size and any other features of morphology" (DAVIS 1917, p. 179).

GATES (1917) reported that flower size was intermediate between that of the parents in reciprocal F_1's in crosses between *Oe. rubricalyx* and *Oe. "biennis"* (a form collected from the wild in England), and that in the F_2 generations flower size was extremely variable. His observations on "somatic segregation" within individual plants are not germane to the present discussion since the variants were not tested genetically.

Among the cases reported by RENNER is the backcross *[b]albicans·curvans* × *rubens* (*[b]albicans·rubens* = *Oe. biennis*, petal length 28 mm; *curvans* from *Oe. muricata*, petal length 15 mm; F_1 *[b]albicans·curvans* had petal length 18 mm, probable configuration 6, 4, 2, 2) in which part of the plants had the flower size of *biennis*, the other being smaller (RENNER 1917, pp. 159–161, 167, 203). In the cross *Oe. biennis* × *Oe. Lamarckiana*, the three F_1 types (*[b]albicans·gaudens*, *[b]albicans·velans*, *rubens·velans*) had petals of about 28 mm in length (*Lamarckiana* had petals about 48 and *biennis* about 28 mm in length). The F_2 from the *rubens* F_1 segregated into three types for flower size (about 50, 40, and 30 mm). The backcross to *biennis* gave only small flowered plants (except for some difference between *velans* and *rubens* twins) while the backcross to *Lamarckiana* segregated for flower size much in the manner of the F_2 (RENNER 1917, pp. 159–161, 178, 197–199, 204–207). In *Oe. Hookeri* × *Oe. Cockerelli* F_1 *[h]Hookeri·elongans*, the petal length was 22 mm, and in the F_2 petal length varied from 21 to 40 mm. In the backcross *Oe. Hookeri* × *curtans·[h]Hookeri*, petal length varied from 23 to 43 mm (20 mm in the F_1) (RENNER 1925).

There is apparently a single locus responsible for such differences in flower size. RENNER (1925, p. 132) treats the various differences in flower size as due to a series of allelomorphs, C_o, C_{o1}, c_o, etc. The probable truth of this conclusion is evident when one compares the inheritance of flower size in such hybrids as *rigens·rubens*, *rigens·velans* and *[h]franciscana·rubens* in which three different flower sizes (small in *rigens*, intermediate in *rubens*, and large in *velans* and *[h]franciscana*) follow the same type of inheritance.

OTHER LOCI AFFECTING FLOWER SIZE

Not all inherited differences in flower size follow the scheme of inheritance described for C_o. In his description of the genes for flower size belonging to the C_o series of multiple allelomorphs, RENNER (1925, p. 132) states: "Dass die Blütengrösse auch durch andere Faktoren beeinflusst

wird, versteht sich von selbst. Als solche sind bekannt: $B>b$, $R>r$, p von *flavens* $>P$ von *velans*."

An indication of the influence of the p carrying chromosome of *flavens* on the expression of flower size was obtained in crosses between *Oe. "franciscana sulfurea"* (*sulfurens·s d hfranciscana*) and *Oe. suaveolens* (*albicans·flavens*). The F_1 *s d hfranciscana·flavens* had the configuration 4, 4, 2, 2, 2 (EMERSON 1931b). The rings of 4 involved chromosomes 1·2, 3·4 of *hfranciscana* with 1·4, 2·3 of *flavens*, and 7·10, 8·9 of *hfranciscana* with 7·8, 9·10 of *flavens*. The second ring was unmarked genetically, but the first could be followed by the genes *s* (sulfur flower color) and P^s (punctate stems, striped bud cones) in chromosome 3·4 of *hfranciscana* (EMERSON and STURTEVANT 1931). There was no great difference in flower size between *"franciscana sulfurea,"* homozygous *s d franciscana, Oe. suaveolens* and the various F_1 hybrids (petal length about 35 to 40 mm in each). The F_2 from *s d hfranciscana·flavens* (culture 2286 of 1931) gave the following frequencies:

24 P^s *S* large (22*D*, 2*d*)	petal length 35 to 40 mm
4 *p S* large (4*D*, 0*d*)	petal length 35 to 40 mm
3 P^s *s* large (3*D*, 0*d*)	petal length 35 to 40 mm
4 P^s *s* small (4*D*, 0*d*)	petal length 15 to 22.5 mm

In the backcross *s d hfranciscana·flavens* × *s d hfranciscana* (culture 2288 of 1931) the observed frequencies were:

12 *S* large (8*D*, 4*d*)	petal length 35 to 40 mm
9 *s* large (5*D*, 4*d*)	petal length 35 to 40 mm
8 *s* small (5*D*, 3*d*)	petal length 15 to 22.5 mm

Classification for homozygous *versus* heterozygous P^s was difficult because of the difference in size of the bud cones. Dwarf stature (*d*) segregated independently of flower color and flower size. In the backcross *s d hfranciscana·flavens* × *flavens* (culture 2287 of 1931) there were 11 P^s and 10 p, all of which had large flowers.

In this series of crosses, small flower size was confined to classes homozygous for chromosomes 1·2, 3·4 of *hfranciscana* (that is, homozygous for *s* carried in 3·4). The backcross to the large flowered *s d hfranciscana* showed that small flower size was dominant in plants homozygous for 1·2, 3·4. The gene responsible for small flower size (probably C_o) was independent of chromosomes 1·2, 3·4 since it was associated with them in just 50 percent of the gametes. There must therefore have been a dominant "suppressor" of small flower size carried in 1·4 or 2·3 of *flavens* which prevented

the appearance of small flowers in plants with yellow flowers. Since neither parent had small flowers and since small flower size was dominant when associated with the *hfranciscana* chromosomes, it is apparent that the gene for small flowers was introduced into the cross from *flavens*.

The F_1 *sulfurens·flavens* had the configuration 8, 4, 2 (EMERSON 1931b). The ring of 4 involves chromosomes 7·10, 8·9 of *sulfurens* with 7·8, 9·10 of *flavens*, and the pair was either 1·4 or 2·3, if the latter sulfur flowers should segregate independently since *S* is known to be in 2–3 of *flavens* (EMERSON and STURTEVANT 1931). In the F_2 (culture 2282 of 1931) there were 22 plants with large yellow flowers (2 of which had the configuration 8, 2, 2, 2), and there was one plant with large sulfur flowers (also 8, 2, 2, 2). In the backcross *sulfurens·flavens*×*flavens* (culture 2283 of 1931) there were 26 plants with large yellow flowers, 2 of which had the configuration 8, 2, 2, 2 (that is, *sulfurens·flavens*, but homozygous for chromosomes 7·8 and 9·10 of *flavens*). In the backcross *Oe. suaveolens* × *sulfurens·flavens* (culture 2284 of 1931) there were 19 plants (all presumably *albicans·flavens*) with large yellow flowers. In the backcross "*franciscana sulfurea*" × *sulfurens·flavens* (culture 2285 of 1931), 6 plants were of the constitution *s d hfranciscana·flavens* with striped buds (one plant had the configuration 4, 4, 2, 2, 2 and one had 4, 2, 2, 2, 2, 2; the extra pairs in the latter must have been 7·10, 8·9), and 6 plants were of the constitution *sulfurens·flavens* with green buds (3 plants had the configuration 8, 4, 2). All plants in this backcross had large yellow flowers.

The backcrosses to "*franciscana sulfurea*" and to *Oe. suaveolens* (*albicans*) were backcrosses for *s* and indicate that the factor pair *S s* was not independent of the ring of 8 in the F_1. The pollen lethal of *sulfurens* and the zygote lethal of *flavens* (in chromosome 5·6) were also in the ring of 8. The pair in *sulfurens·flavens* must have been 1·4 (known to be either 1·4 or 2·3 with *S* in 2·3 of *flavens*). The single sulfur-flowered plant in the F_2 must have arisen from a crossover bringing *s* into *flavens* (see discussion of crossing over for *s* in rings in EMERSON 1931a). Since no small flowered plants appeared in the F_2 or backcrosses, the flower size suppressor of *flavens* must have been in the ring of 8 chromosomes and consequently in chromosome 2·3 of *flavens* (known to be in either 1·4 or 2·3).

An analogous case is perhaps to be found in RENNER'S hybrid *flavens·velans*. As in *s d hfranciscana·flavens*, the P^s of *velans* is in chromosome 3·4 which together with 1·2 forms a ring of 4 with 1·4, 2·3 of *flavens* (EMERSON and STURTEVANT 1931). Concerning this hybrid RENNER says (1925, pp. 42–43): "Auffällig ist, dass *p-velans* grossere Blüte vererbt als *P-velans*, and entsprechend *P-flavens* kleinere Blüte als *p-flavens*. Mit *P* bezw. *p* sind

also Blütengrössefaktoren gekoppelt, die mit den oben erwähnten selbständig spaltenden (the independently inherited C_o) nichts zu tun haben, und der sehr grossblümige Komplex *velans* kann durch einen Anteil des kleinerblütigen Komplexes *flavens* die Blütengrösse, die er vererbt, noch steigern, und umgekehrt kann *flavens* durch eine Anleihe an *velans* etwas von seiner Blütengrösse einbüssen; durch Austauch der von *P* bezw. *p* nicht abhängig C_o Faktoren wird die Blütengrösse dagegen im umgekehrten Sinn abgeändert." It is almost certain that RENNER'S *p* velans had chromosomes 1·4 and 2·3 from *flavens*, and similarly *P flavens* must have had 1·2, 3·4 from *velans*, so the same "suppressor" of small flower size in chromosome 2·3 of *flavens* may have been responsible for the differences in flower size reported in this cross. One gathers from RENNER'S account that these flower size differences were obtained in out-crosses to *biennis* in which all plants should have had small flowers except those receiving the *flavens* "suppressor."

The same situation arises in the crosses of LANGENDORF, referred to in the preceding section. All backcrosses to plants of large flower size showed segregation for flower size except backcrosses to *flavens* (see summary of LANGENDORF'S data in table 1).

The linkage between flower size and *P* observed by GERHARD (1929) in *acuens* hybrids seems to be somewhat different and may represent the action of a different gene.

INHERITANCE OF *brevistylis*

The inheritance of the *brevistylis* character (b_r) is similar to that of flower size at the C_o locus. DE VRIES (1913) reported that b_r segregated independently of other characters in *Oe. biennis* × *Oe. Lamarckiana brevistylis* F_1 *velutina* (*that is*, ^{b}*albicans*·b_r *velans*). It has since been shown (CLELAND and OEHLKERS 1929) that *albicans*·*velans* had a ring of 14 chromosomes. If the original F_1 of DE VRIES had the same configuration, it appears that b_r was inherited independently of all the chromosomes of the *velans* complex. This appearance is supported by other crosses of DE VRIES: ^{b}*albicans*·b_r *gaudens*, *rigens*·b_r *gaudens*, *rigens*·b_r *velans*, *curtans*·b_r *gaudens*, *curtans*·b_r *velans*, and ^{h}*Hookeri*·b_r *velans*, in all of which b_r segregated independently. Similarly, SHULL (1926, 1928) has found b_r to be independent of all other characters studied by him.

Recent tests of the inheritance of *brevistylis* gave similar results. An F_1 plant from the cross *Oe. R Lamarckiana*×*Oe. Lamarckiana brevistylis* was found to have the configuration 12, 2 (STURTEVANT 1931), the same as in both parents. The gene *R* (red mid-ribs) was known to be in the pairing

chromosome 1·2 (EMERSON and STURTEVANT 1931). The F_2 (culture 14 of 1931) bred true for the characters carried in *velans* and *gaudens* but *R* and b_r segregated (2 *R* B_r, 3 *R* b_r, 2 *r* B_r), indicating that these two genes were independent of the *velans* and *gaudens* complexes (that is, independent of the ring of 12) which is of course in strict agreement with the data of DE VRIES (1900 and later), DAVIS and SHULL for independent segregation of b_r in inbred lines of *Oe.* B_r b_r *Lamarckiana*. The F_1 plant backcrossed to *Lamarckiana brevistylis* gave a progeny of which 88 plants flowered (culture 15 of 1931). All these were typical *Lamarckiana* (that is, *velans·gaudens*) but with *R* and b_r segregating independently. The observed frequencies were: 14 *R* B_r, 25 *R* b_r, 19 *r* B_r, and 30 *r* b_r, giving 44 of the parental types and 44 with new combinations. In these crosses b_r was independent of *R* in the pairing chromosome and of all genes in the ring of 12 (for example, P^s *p*, *N n*, the zygotic lethals, etc.).

The hybrid *jugens·*b_r *gaudens* (*Oe. Shulliana* × *Oe.* b_r *Lamarckiana*) was found to have a ring of 14 chromosomes (STURTEVANT 1931) and still b_r was found to segregate independently in F_2 (see discussion of this cross in the following section). It follows that b_r (like c_o) must either lie outside all the fourteen chromosomes or at such a distance from the translocation point in some chromosome as to give 50 percent crossing over with that point.

LINKAGE BETWEEN C_o AND b_r

One of the revolute-leaved mutations of *Oe. pratincola* (BARTLETT 1915) which had relatively small flowers and red mid-ribs (*R*?) was pollinated by *Oe. Lamarckiana brevistylis*, which had large flowers and white mid-ribs. An F_1 plant (*b*$_r$ *velans*) with the configuration 6, 4, 2, 2 gave the following frequencies in F_2 (culture 2314B of 1931):

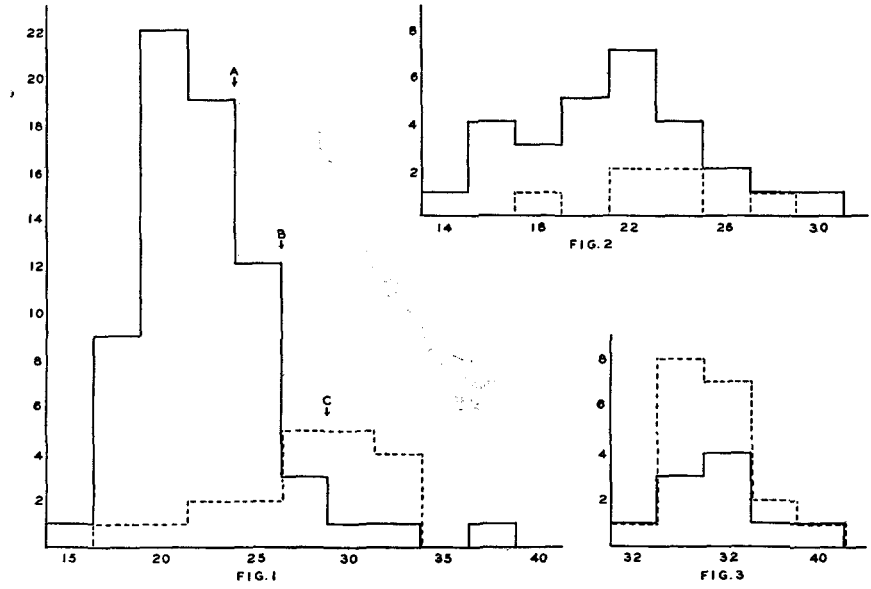
37 flat leaves, red mid-ribs, long styles
13 flat leaves, red mid-ribs, *brevistylis*
25 flat leaves, white mid-ribs, long styled
4 flat leaves, white mid-ribs, *brevistylis*
7 revolute, red mid-ribs, long styles
4 revolute, red mid-ribs, *brevistylis*

The data indicate that revolute leaves (*f*) and red mid-ribs (*R*?) were very closely linked while *brevistylis* (b_r) was completely independent of both.

Petal length varied between 15 and 37.5 mm. The population gave a bimodal curve, indicating a segregation into large and small flowered

types, but there was considerable intergrading between these types. The relation of flower size to *brevistylis* in the F_2 is shown graphically in figure 1.

The mean length of petals for long styled plants was 22.5 mm and for *brevistylis* plants 29.7. The coefficient of correlation between these two characters was 0.51 ± 0.05. The plants were arbitrarily divided into two classes for flower size at the petal lengths indicated in the graph as A, B, and C, and the following linkage values were obtained by use of the tables published by IMMER (1930): at A, 21 percent crossing over; at B 15 percent and at C 17 percent. The closest fit to a 3:1 ratio for flower size is at



FIGURES 1 to 3.—Distribution of flower size in *brevistylis* plants (broken lines) and in normal plants (entire lines) in certain crosses (see references in text). The frequencies (number of plants) are plotted as ordinates, the length of petals in mm as abscissas.

B, indicating that the most probable crossover value was in the neighborhood of 15 percent.

In another cross, however, there was no indication of linkage between flower size and the *brevistylis* character. This was a cross between *Oe. b_r Lamarckiana* and *Oe. Shulliana*. The F_1 (*jugens* · *b_r gaudens*) had a ring of 14 chromosomes (STURTEVANT 1931). In the F_2 (culture 41 of 1931) there were 28 long-styled plants (mean petal length 20.8 mm) and 6 *brevistylis* plants (mean petal length 22.2 mm). The relation of flower size to *brevistylis* in this cross is shown graphically in figure 2. These data, however, are not sufficient to show that no linkage existed in this cross.

The observed linkage with crossing over between flower size (C_o) and *brevistylis* (b_r) eliminates the possibility that these two genes lie outside the chromosomes. It is now almost certain that they are both near the end of one of the chromosomes with about 50 percent crossing over between the translocation point and the nearest gene. SHULL'S chromosome II and RENNER'S V become identical. Because of the high frequency of crossing over between these genes (C_o and b_r) and the translocation point it is not possible to determine which chromosome these genes are in. It is still possible that they are at the end of one of the established linkage groups.

A test of the direct effect of b_r on flower size was available in the cross between *R Lamarckiana* and b_r *Lamarckiana* reported in the preceding section. The *brevistylis* parent was of the Dutch strain which had slightly larger flowers than the Swedish strain carrying *R*. In the backcross to the larger flowered type (b_r), no difference was found in flower size between long-styled and *brevistylis* plants. Only 10 long-styled plants were measured; these had a mean petal length of 36 mm. Nineteen *brevistylis* plants were measured and found to have a mean petal length of 35.8 mm (figure 3).

SUMMARY

In Oenothera, most genes that were found to be independently inherited in hybrids with pairing chromosomes show nearly complete linkage in hybrids in which the chromosomes are in rings.

Red mid-ribs (*R*) and old-gold flower color (*v*) have been found to be linked and have been demonstrated to be in chromosome 1·2. Similarly, the linked genes *P* (punctate stems, various bud colors), *s* (sulfur flowers) and *n* (*nanella* stature) have been demonstrated to be in chromosome 3·4. In hybrids in which either or both 1·2 and 3·4 appeared as pairing chromosomes, the linkage group *R-v* was found to be inherited independently of the linkage group *P-s-n;* but, in hybrids in which both 1·2 and 3·4 were present in a common ring, these two linkage groups were not independent.

From the association of *d* (dwarf stature) with the ring chromosomes in certain hybrids, and from its independence of the ring chromosomes and of genes in 1·2 and 3·4 in other hybrids, it has been shown that *d* was inherited independently of all chromosomes of *franciscana* except 13·14, but there is no direct evidence placing *d* definitely in that chromosome.

Only two known genes have failed to show the variable linkage relations so universally found in Oenothera hybrids. The gene for small flower size (C_o) and the gene for *brevistylis* (b_r) have been found to be inherited

independently of all other genes, even in hybrids in which all 14 chromosomes were in a single ring. It has been suggested that C_o and b_r lie at such a distance from the translocation points in the chromosomes as to give 50 percent crossing over with these points.

Linkage between C_o and b_r with about 15 percent crossing over has been found, proving that these two genes are in the same chromosome but at a great distance from the translocation point.

The different type of flower size inheritance found in *flavens* hybrids has been accounted for on the basis of a dominant gene in chromosome 2·3 of *flavens* which "suppressed" the normally dominant C_o which was also carried by *flavens*.

LITERATURE CITED

BARTLETT, H. H., 1915 Mass mutation in *Oenothera pratincola*. Bot. Gaz. **60**: 425–456.

BLANCHARD, F. C., 1929 The genetic constitution of *Oenothera pratincola* and its revolute-leaved mutations. J. Washington Acad. Sci. **19**: 115–125.

CLELAND, R. E., and BLAKESLEE, A. F., 1930 Interaction between complexes as evidence of segmental interchange in Oenothera. Proc. Nat. Acad. Sci. Washington **16**: 183–189.

CLELAND, R. E., and OEHLKERS, F., 1929 New evidence bearing upon the problem of the cytological basis for genetical peculiarities in the Oenotheras. Amer. Nat. **63**: 497–510.

1930 Erblichkeit und Zytologie verschiedener Oenotheren und ihrer Kreuzungen. Jahrb. wiss. Bot. **73**: 1–124.

COBB, F., 1921 A case of Mendelian inheritance complicated by heterogametism in *Oenothera pratincola*. Genetics **6**: 1–42.

COBB, F., and BARTLETT, H. H., 1919 On Mendelian inheritance in crosses between mass-mutating and non-mass-mutating strains of *Oenothera pratincola*. J. Washington Acad. Sci. **9**: 462–483.

DAVIS, B. M., 1914 Genetical studies on Oenothera. V. Some reciprocal crosses in Oenothera. Z. indukt. Abstamm.- u. VererbLehre. **12**: 169–205.

1916 Hybrids of *Oenothera biennis* and *Oenothera franciscana* in the first and second generations. Genetics **1**: 197–251.

1917 Some inter- and backcrosses of F_1 Oenothera hybrids. Genetics **2**: 155–185.

EMERSON, S., 1930 The inheritance of rubricalyx bud color in crosses with *Oenothera Lamarckiana*. Proc. Nat. Acad. Sci. Washington **16**: 796–800.

1931a The inheritance of certain characters in Oenothera hybrids of different chromosome configurations. Genetics **16**: 325–348.

1931b Genetic and cytological studies on Oenothera. II. Certain crosses involving *Oe. rubricalyx* and *Oe. "franciscana sulfurea."* Z. indukt. Abstamm.-u. VererbLehre. **59**: 382–394.

EMERSON, S., and STURTEVANT, A. H., 1931 Genetic and cytological studies on Oenothera. III. The translocation interpretation. Z. indukt. Abstamm.-u. VererbLehre. **59**: 395–419.

GATES, R. R., 1917 Vegetative segregation in a hybrid race. J. Genet. **6**: 237–253.

GERHARD, K., 1929 Genetische und zytologische Untersuchungen an *Oenothera grandiflora* Ait. Jenaische Zeitschr. Naturwissenschaften **64**: 283–338.

HOEPPENER, E., and RENNER, O., 1929 Genetische und zytologische Oenotherenstudien. II. Zur Kenntnis von *Oenothera rubrinervis, deserens, Lamarckiana-gigas, biennis-gigas, franciscana, Hookeri, suaveolens, lutescens*. Botan. Abhandl. **15**: 1–86.

IMMER, F. R., 1930 Formulae and tables for calculating linkage intensities. Genetics **15**: 81–98.

KULKARNI, C. G., 1929 Meiosis in the pollen mother cells of strains of *Oenothera pratincola* Bartlett. Bot. Gaz. **87**: 218–259.

LANGENDORF, J., 1930 Zur Kenntnis der Genetik und Entwicklungsgeschichte von Oenothera fallax, rubririgida und Hookeri-albata. Bot. Arch. (Königsberg) **29**: 474–530.

RENNER, O., 1917 Versuche über die genetische Konstitution der Oenotheren. Z. indukt. Abstamm.-u. VererbLehre. **18**: 121–294.

1921 Heterogamie im weiblichen Geschlecht und Embryosackentwicklung bei den Oenotheren. Z. Bot. **13**: 609–621.

1925 Untersuchungen über die faktorielle Konstitution einiger Komplexheterozygotischer Oenotheren. Bibl. genet. **9**: 1–168.

1928 Über Koppelungswechsel bei *Oenothera*. Proceedings of the 5th International Congress, Supplementband of the Z. indukt. Abstamm.-u. VererbLehre. **2**: 1216–1220.

RUDLOFF, F., 1929 Zur Kenntnis der *Oenothera purpurata* Klebahn und *Oenothera rubricaulis* Klebahn. Z. indukt. Abstamm.-u. VererbLehre. **52**: 191–235.

SHULL, G. H., 1923a Linkage with lethal factors the solution of the Oenothera problem. Eugenics, Genetics and the Family **1**: 86–99.

1923b Further evidence of linkage with crossing over in Oenothera. Genetics **8**: 154–167.

1925 The third linkage group in Oenothera. Proc. Nat. Acad. Sci. Washington **11**: 715–718.

1926 "Old-gold" flower color, the second case of independent inheritance in Oenothera. Genetics **11**: 201–234.

1927 Crossing over in the third linkage group of Oenothera. Proc. Nat. Acad. Sci. Washington **13**: 21–24.

1928 A new gene mutation (mut. *bullata*) in *Oenothera Lamarckiana* and its linkage relations. Proceedings of the 5th International Congress of Genetics, Supplementband of the Z. indukt. Abstamm.-u. VererbLehre. **2**: 1322–1342.

STURTEVANT, A. H., 1931 Genetic and cytological studies on Oenothera. I. *Nobska, Oakesiana, Ostreae, Shulliana*, and the inheritance of old-gold flower color. Z. indukt. Abstamm.-u. VererbLehre. **59**: 365–380.

DE VRIES, H., 1900 Sur la loi de disjonction des hybrides. C. R. Acad. Sci. Paris. **130**: 845–847.

1913 Gruppenweise Artbildung unter spezieller Berücksichtigung der Gattung Oenothera. 365 pp. Berlin: Gebrüder Borntraeger.