The Trisomic Mutations of *Oenothera*.

BY

R. RUGGLES GATES, PH.D., F.L.S.,

Professor of Botany, University of London (King's College).

With Plate XI.

THE purpose of the present paper is to record the occurrence and cytological behaviour of a new mutation having 15 chromosomes, and to discuss various questions relating to trisomic mutations in *Oenothera*. The breeding experiments involved will be described elsewhere, but it is necessary to refer to them briefly in this connexion.

Reciprocal crosses were made between a pure homozygous race of *Oenothera rubricalyx* and *Oe. Hewettii*, Ckl., in 1915 at the Missouri Botanical Garden and the following year at the University of California. It should be pointed out that *Oe. Hewettii* has not bred entirely true in my cultures. There is a green-stemmed as well as a red-stemmed form, and a second generation culture of 73 red-stemmed plants includes one small dwarf. *Oe. Hewettii* differs throughout from *Oe. rubricalyx*, the most conspicuous differences being the narrower leaves, which are practically smooth (crinkled in *rubricalyx*) with midribs red on the upper surface and green below. The petals of *Oe. Hewettii* are also much narrower, so that gaps are left between them at the base where they fail to overlap. The buds are green and covered with soft pubescence, while the stems are free from the characteristic red papillae of the *Lamarckiana* forms. Four generations of hybrids have been grown from *Oe. Hewettii* $\times$ *rubricalyx*, and three generations of the reciprocal. With the exception of one culture these have been grown at the Royal Botanic Gardens, Regent's Park. The F_1 hybrids are intermediate between the parents, but in both cases more like the seed parent. They both have the red bud colour pattern of *rubricalyx*, but it is considerably diluted. In later generations these differences between the reciprocal hybrids are maintained. As regards bud colour in F_2 and later generations, there is a continuous range from full red to completely green buds,

and it was found impossible (contrary to the usual experience with this character in other hybrids) to classify the individuals with any certainty in the F_2 , and the usual ratios are not obtained. Nevertheless, there is segregation of this character in later generations, although the green-budded segregates usually retain a tinge of red on the hypanthium. Whether segregation actually occurs in the other characters need not be discussed in the present connexion, although the first impression is that of a blend which essentially retains its blended condition.

In the present strain of *Oe. Hewettii*, a native of New Mexico which was kindly sent me by its discoverer Dr. T. D. A. Cockerell (1913) in 1914, as well as in these hybrids, occasional aberrant forms appear, as already mentioned. Reference will here be made only to a type which appeared in 1920 in the F_1 of the cross *Oe. rubricalyx* $\times$ *Hewettii*. This culture (No. 54) numbered 53 plants, including two which were strikingly aberrant and precisely alike. The rosette leaves were very much broader and more crinkled than the typical F_1 hybrids. In this feature these mutants resembled *Oe. mut. lata*. The stem leaves were also more crinkled, but were pointed at the tip and a resemblance to the mutant *lata* was not at once suggested, although the plants were shorter than the type and the stem was slightly zigzag. These plants probably most resembled *Oe. mut. semilata*, Gates. For a discussion of the various occurrences of this mutation see Gates (1915, p. 111). Examination of the pollen in these plants showed that the grains were all three-angled. A flower of one of them was selfed and produced 33 seeds (as against the usual 100–300 in typical members from these crosses), but the seeds failed to germinate.

Descriptions and photographs of this type will be published elsewhere. Cytological material was collected from one of them and shows that this mutant had 15 chromosomes. I am indebted to Miss E. M. Rees, B.Sc., for making the microscopic preparations for this study, and to Mrs. N. Ferguson, B.Sc., for preparing the drawings. The remainder of this paper will be devoted to pointing out the main cytological peculiarities of this new 15-chromosome type. A large number of chromosome counts both in pollen mother-cells and in somatic tissues established beyond doubt that the chromosome number is 15, but in two somatic cells 16 chromosomes were clearly present. The explanation of such departures from the somatic number has been discussed elsewhere (Gates and Thomas, 1914).

In the first place, it may be pointed out that the occurrence of mutations with an extra chromosome in a pair of individuals in a culture is not uncommon, and it furnishes clear evidence as to how they have arisen. For it means that the irregular 8–6 distribution of chromosomes took place on the heterotypic spindle in a pollen mother-cell and resulted in the production of two pollen grains with eight chromosomes, both of which functioned in fertilization to produce mutants. If the irregular division had occurred in

a megaspore mother-cell, only one functional megaspore with eight chromosomes would have resulted. The occurrence of any aberrant form in a pair of individuals therefore suggests at once that they have probably arisen from an irregular chromatin distribution in the heterotypic mitosis of a pollen mother-cell of the previous generation. In this case the non-disjunction of a pair of chromosomes must then have occurred in a pollen mother-cell of *Oe. Hewettii*.

We may now consider briefly the main cytological features of this aberrant type, confining ourselves to diakinesis and the heterotypic mitosis. Figs. 1 and 2, Pl. XI, represent late stages in diakinesis. In the former 15 chromosomes can clearly be counted. It will be seen that nearly all of the chromosomes, but not all, are arranged in pairs, these pairs in many cases forming complete rings. It has long been known that in *Oenotheras* of the *Lamarckiana* and *biennis* group the formation of ring chromosomes seldom occurs (Gates, 1908; Davis, 1910), while Davis (1909) has described the constant formation of ring chromosomes during diakinesis in *Oe. grandiflora*, and Cleland (1922) has recently figured the regular occurrence in *Oe. franciscana* of five pairs of chromosomes in rings, the other four forming a single large ring. In Figs. 1 and 2, referred to above, there are five pairs of ring chromosomes in each case. In no case have more than five ring-pairs been found, although there are sometimes less, and usually not more than one ring persists on the heterotypic spindle. Unfortunately no material of the parent species *Oe. Hewettii* at this stage has been examined, so it is unknown whether this species is like *Oe. grandiflora* in having only ring chromosomes, but it appears more probable that it may be like *Oe. franciscana*, having five ring-pairs and four other chromosomes more loosely united into a single ring.

As previously pointed out by the author, the absence of a clear pairing of all the chromosomes during diakinesis and the heterotypic mitosis is an indication of a weak attraction between the chromosomes constituting a pair. This is the characteristic condition in *Oe. Lamarckiana* and its derivatives. Davis and Cleland have argued that the occurrence of ring chromosomes in *Oe. grandiflora* and *Oe. franciscana*¹ is a sign of a 'pure species'. In the present instance, however, we have as many as five ring-pairs of chromosomes in a 15-chromosome mutant occurring in an F_1 hybrid between forms belonging to quite distinct species. One of these rings might of course be descended from the pair which failed to separate in the *Hewettii* pollen mother-cell, but there is no evidence that such a pair will persist in this

¹ It should be pointed out that the writer made a study of the variability of *Oe. franciscana*, which Cleland stresses as a pure species. While in California in 1916 a study was made of large wild colonies growing near San Francisco, and also of the variations of this species in cultures. The wild variations were particularly conspicuous in size of flower, pigmentation, and the number of red papillae on the sepals. It was evidently a population of interbreeding forms and must have been heterozygous for a number of characters.

way. It appears probable that in *Oe. lata* (Gates and Thomas, 1914) the three chromosomes belonging to a particular pair ($A A_1 A_2$) may all undergo synapsis with each other equally according to chance. Bridges (1916) has shown that in $XY Y$ males of *Drosophila* the synapses of these three chromosomes are probably according to chance, while in $XX Y$ females homosynapsis occurs much oftener than heterosynapsis.

In this mutant from *Oe. rubricalyx* $\times$ *Hewettii* the unpaired chromosome is sometimes clearly indicated (see Fig. 5). Here we must suppose that four at least of the ring-pairs were made up of one chromosome from *rubricalyx* paired with the corresponding one from *Hewettii*. So far as can be judged from analogy, another pair might equally be made up from the descendants of the original non-disjoined *Hewettii* pair or from one of these and the corresponding *rubricalyx* chromosome. The odd chromosome is then likely to be a different one in different pollen mother-cell nuclei of this mutant according to how synapsis has taken place. But in any case it is clear that all these ring-pairs but one must be constituted from a union between a *rubricalyx* chromosome and a *Hewettii* chromosome, unless we make the very unlikely assumption that in this hybrid the pairing of homologous chromosomes does not take place. It is therefore impossible to regard the mere presence of ring chromosomes as evidence for a homozygous condition of the species. It is rather a useful indication of the strength of the attraction which produces ring-pairs, but it appears that that attraction may on occasion be quite as great between the chromosomes of forms belonging to distinct species as between the chromosomes of a homozygous species.

The chromosome rings may persist on the multipolar heterotypic spindle, although, as shown in Figs. 3 and 4, the number of rings is usually fewer at this time. Occasionally a ring is found persisting even in the heterotypic metaphase (Fig. 6), but this is unusual. That one or two ring-pairs of chromosomes are occasionally formed in diakinesis and may persist on the heterotypic spindle in *Oe. Lamarckiana* and *Oe. lata* is shown in an early paper (Gates, 1907, Figs. 17-20, 33, 34), although they were differently interpreted at the time. There appears to be no fixity in the number of such rings except in forms in which the attraction is so strong that all the pairs form rings.

One striking feature of this 15-chromosome mutant is the fact that the pollen is not conspicuously sterile, although the fact that only 33 seeds were produced from the self-pollination of a flower shows that a much higher percentage than usual of the pollen was non-functional. The irregularities in meiosis are much less numerous than in the various *lata* forms (cf. Gates and Thomas, 1914). They apparently begin in the heterotypic anaphase through chromosomes lagging behind, as in Fig. 7, where seven chromosomes are arriving at one pole, five at the other, and three are lagging behind. Fig. 8 is a heterotypic telophase in which apparently eight

chromosomes have reached one daughter nucleus, six the other, while the fifteenth is left out in the cytoplasm. As is usual, a number of these chromosomes already show the split for the homotypic mitosis.

DISCUSSION.

It has long been recognized that if the chromosomes of *Oenothera* are differentiated from each other in their hereditary qualities, as they clearly are in some organisms, then seven different types with 15 chromosomes might be expected. For a number of years *Oe. lata*, or the *lata*-like assemblage of forms, was the only mutation in which the chromosome count of 15 was clearly authenticated. The possibility remained either that *any* chromosome might constitute the extra one and give rise to a *lata*-like condition, or that the disturbance of duplicating one of the other chromosomes was so great that the result was non-viable. It seems highly probable that non-disjunction of any of the seven pairs of chromosomes may take place, but it was possible that only one of the seven simple trisomic types (to use Blakeslee's term) was viable. This possibility was perhaps strengthened by the discovery (Blakeslee, Belling, and Farnham, 1920) that *Datura*, which has twelve pairs of chromosomes, produces twelve trisomic mutations (i. e. forms with an extra chromosome), most of which have, like *Oe. lata*, high pollen sterility and transmit their characters almost entirely through the female sex. For since in *Datura* only one chromosome in twelve is duplicated, the germinal disturbance will be less than in *Oenothera*, where a chromosome constitutes one-seventh of the whole chromosome series.

In recent years, however, a long array of 15-chromosome mutants in *Oenothera* has been demonstrated. Indeed the number now far exceeds the seven types originally anticipated, and this raises a number of interesting questions regarding the relationship and manner of origin of these types. Blakeslee has also found two additional *Datura* mutants with 25 chromosomes, which he interprets as due to the presence of another genetic factor in certain trisomic forms. It may be pointed out here that Blackburn and Harrison (1921), in their studies of chromosomes in the roses, have found one plant of *Rosa pimpinellifolia* with sterile anthers and 15 instead of 14 chromosomes. But they apparently observed no other differences between this plant and the type. We may now enumerate the various *Oenothera* forms in which 15 chromosomes have been found. They are summarized in the following table. A (?) indicates either that the number of chromosomes is inferred from the genetic behaviour, or that it has not been determined with certainty.¹

¹ It may be pointed out that Lehmann (1922, pp. 366-99) has treated all these forms with an extra chromosome in a somewhat different way in his 'Oenotheraforschungen', and Tischler (1922, pp. 604 ff.) has also treated the subject from the cytological point of view.

TABLE I.

Mutants with 15 chromosomes.

<i>Mutation.</i>	<i>Parent form.</i>	<i>Author.¹</i>	<i>Remarks.</i>
<i>lata</i> , de Vries	<i>Oe. Lamarckiana</i>	Lutz, 1912 Gates, 1912 Gates and Thomas, 1914	
<i>semilata</i> , Gates	<i>Oe. lata</i> × <i>Lamarckiana</i>	Gates and Thomas, 1914	
<i>albida</i> , de Vries	<i>Oe. Lamarckiana</i>	Lutz, 1908, 1917	
<i>incurvata</i> , Gates	<i>Oe. Lamarckiana</i> , Swedish race	Gates, 1915	
<i>lata</i>	<i>Oe. biennis</i> race	Gates and Thomas, 1914	The conception of parallel mutations was based on this form.
<i>simplex lata</i>	<i>Oe. Lamarckiana</i> , mut. <i>simplex</i>	de Vries, 1919 Boedijn, 1920	<i>Oe. mut. simplex</i> differs from <i>Lamarckiana</i> in having lost a lethal factor. It has no empty seeds, no <i>velutina</i> gametes, and hence does not give twin types in <i>F</i> ₁ crosses. It produces <i>lata</i> , <i>oblonga</i> , <i>scintillans</i> , &c., as mutations.
<i>secunda lata</i>	<i>Oe. Lamarckiana</i> , mut. <i>secunda</i>	Boedijn, 1920	
<i>albinervis</i> , van Overeem	<i>Oe. biennis semigigas</i> × <i>biennis</i>	van Overeem, 1920	
<i>lata rubricalyx</i>	<i>Oe. rubricalyx</i> × <i>grandiflora</i> <i>F</i> ₂	Gates and Thomas, 1914	
<i>de Vriesii</i>	<i>Oe. Lamarckiana semigigas</i>	van Overeem, 1920, 1922	
<i>bipartita</i> , Lutz	<i>Oe. Lamarckiana</i>	Lutz, 1917	
type 5509 (modified <i>oblonga</i>)	"	"	
<i>subovata</i> , de Vries	<i>Oe. Lamarckiana</i> and <i>Oe. lata</i> × <i>Lamarckiana</i>	"	
type 2806	<i>Oe. Lamarckiana</i>	"	'Having many points in common with type 5509.'
type 4499	<i>Oe. lata</i> × <i>Lamarckiana</i> and <i>Oe. lata</i> selfed	"	
type 5365	<i>Oe. lata</i> selfed	"	
<i>exilis</i> , Lutz	<i>Oe. lata</i> selfed	"	
<i>exundans</i> , Lutz	<i>Oe. lata</i> selfed	"	
<i>superflua</i> , de Vries?	<i>Oe. lata</i> selfed	de Vries, 1916	'A mutant from <i>lata</i> ,' probably from <i>Oe. lata</i> × <i>Lamarckiana</i> .
<i>cana</i> , de Vries	<i>Oe. Lamarckiana</i> , &c.	van Overeem, 1922	
<i>pallescens</i> , de Vries	<i>Oe. Lamarckiana</i>	van Overeem, 1920	
<i>Lactuca</i> , "	"	"	
<i>liquida</i> , "	"	"	
<i>lata</i> , de Vries	<i>Oe. suaveolens</i> , Desf.	de Vries, 1918	Chromosomes counted by van Overeem.
<i>jaculatrix</i> , de Vries?	"	van Overeem, 1920	See below.
<i>scintillans</i> , de Vries	<i>Oe. Lamarckiana</i>	Hance, 1918	
<i>oblonga</i> , de Vries	"	Lutz, 1917 van Overeem, 1920, 1922	There are certain contradictory features in the record of ' <i>oblonga</i> ', but van Overeem (1922) has counted 15 chromosomes in 10 plants.
unnamed	<i>Oe. erythrina</i>	van Overeem, 1920	

¹ This refers to the author who determined the chromosome number.

Mutation.	Parent form.	Author.	Remarks.
<i>sublinearis</i> , de Vries ?	<i>Oe. Lamarckiana</i>	de Vries, 1909	This is based only on genetic behaviour.
<i>elliptica</i> , de Vries ?	"	"	"
<i>nanella lata</i>	<i>Oe. nanella</i>	Lutz, 1917	"
dwarf type 2256	"	"	"
<i>aberrans</i> , Lutz	<i>Oe. lata</i> × <i>Lamarckiana</i>	Lutz, 1916	14 ⁺¹ chromosomes.
<i>rubrinervis</i> , de Vries	<i>Oe. Lamarckiana</i> , &c.	"	14 ⁺¹ chromosomes. See remarks below.
<i>lasiopectala</i> , Bart. ?	<i>Oe. stenomeris</i> , Bart.	Bartlett, 1915	Chromosomes not counted.
<i>saligna</i> , de Vries	<i>Oe. biennis</i> , Chicago, de V.	de Vries, 1916	"
<i>lata</i>	<i>Oe. grandiflora</i> × <i>biennis</i>	Davis, 1913	"
unnamed	<i>Oe. rubricalyx</i> × <i>Hewettii</i>	Here recorded	"

For purposes of interpretation we may consider (1) the parallel mutations (*lata*) which have appeared in *Oe. Lamarckiana*, *biennis*, *suaveolens*, also as mutations from 14-chromosome mutants, and in various hybrids; (2) the various 15-chromosome types which have arisen directly from *Lamarckiana*. The now widely adopted conception of parallel mutations was based upon the fact (Gates, 1912a) that *Oe. Lamarckiana* mut. *lata* and *Oe. biennis* mut. *lata* were corresponding types resulting from the same kind of germinal change in different species. A partial list of parallel mutations in *Oenothera* has been published elsewhere (Gates, 1921). It has long been recognized that *lata* is in many respects intermediate between *Lamarckiana* and *gigas* although it has but one extra chromosome. Van Overeem (1922) shows that the papillary cells of its stigma are conspicuously larger than in *Lamarckiana*, and concludes that in *lata* there is a lack of balance between cell size and turgor, the lack of turgor accounting for the habit of the plant.

The question of the relationships between the various mutants with 15 chromosomes is a very difficult one. In the first place, we may eliminate from present consideration all such forms arising from different species than *Lamarckiana* or from hybrids between forms belonging to two distinct species. Such cases of course all arise through a chance irregular meiotic division during the distribution of the hybrid differences in the germ cells, as was originally explained in the case of *lata rubricalyx* (Gates, 1914). This leaves us to consider the various 15-chromosome forms arising from *Lamarckiana* and its mutants. In various combination mutations, such as *nanella lata* and *simplex lata*, the explanation is evidently similar to that given above. If we examine the 15-chromosome forms arising directly from *Lamarckiana*, we find in the first place the following from the experiments of de Vries: *lata*, *albida*, *scintillans*, *oblonga*, which are all widely different and have long been known, and *pallescent*, *Lactuca*, *liquida*, and *cana*, which are closely related, are more like *Lamarckiana* and have been discovered more recently (de Vries, 1916). The chromosome number in *cana* has apparently not been actually counted, but its genetic behaviour is exactly like that of the other forms with 15 chromosomes, leaving no doubt

that it must have the same unbalanced chromosome condition.¹ The genetic behaviour of all these forms will be referred to later. The mutant *incurvata* (see Table I) should probably not be included in this series, for, while it is evidently a distinct type, it appeared in the Swedish race of *Oe. Lamarckiana* and may owe its peculiarities to certain genetic differences which exist between it and the *Lamarckiana* of de Vries's cultures.

We now come to the various 15-chromosome forms described by Miss Lutz (1917). In the first place is *subovata*, de Vries, a sterile form which de Vries (1909) obtained not only from *Lamarckiana* and *lata* $\times$ *Lamarckiana*, but also from *sublinearis* and from *scintillans*. The latter has 15 chromosomes (Hance, 1918), and the genetic behaviour of *sublinearis* indicates that it also probably had 15. *Elliptica*, de Vries, also, from its genetic behaviour, is probably in the same condition. Miss Lutz describes a 15-chromosome form which she calls *bipartita* and which is much more like *Lamarckiana* than most of these types. It differs in that flowers with more than four stigma-lobes are much commoner than in *Lamarckiana*, and the petals frequently develop diagonal clefts owing to their not overlapping in regular order. Cleft petals, owing to conditions which are apparently somewhat different, have been observed in various other forms (van Overeem, 1920; Gates, 1917, 1923). The flowers are smaller and the leaves more finely crinkled than in *Lamarckiana*. Much of the pollen is obviously bad and it was very difficult to get seeds from self-pollination. There is apparently no genetic evidence to indicate the relation of *bipartita* to other 15-chromosome mutants, except that in one instance *Lamarckiana* $\times$ *lata* gave two *bipartita* (?) in addition to 63 *Lamarckiana*, one *lata*, and certain other forms. Miss Lutz also refers to two other mutations from *Lamarckiana* with 15 chromosomes, but they are not described. They are 'type 5509', which is said to be a modified *oblonga*, and 'type 2806', which is said to have 'many points in common with type 5509'. Both then appear to be nearest *oblonga*. In addition to the above 15-chromosome mutations from *Lamarckiana*, others have so far been obtained only from *lata* selfed or from *lata* $\times$ *Lamarckiana*. These will be referred to later.

For the purpose of further analysis it appears best to confine ourselves largely to the eight and more forms with an extra chromosome which have been identified by de Vries. The genetic relationships of these forms to one another renders the whole problem a very difficult one. The next evidence to be considered concerns the genetic behaviour of these forms when selfed or in crosses. In general they are more or less completely male sterile, and when pollinated from *Lamarckiana* give the two parental types with a greater or lesser preponderance of *Lamarckiana* offspring. Eight forms arising directly from the *Lamarckiana* of de Vries's cultures and

¹ Van Overeem (1922) has recently shown that the somatic cells of *cana* have 15 chromosomes.

showing this type of behaviour are known to have 15 chromosomes. Miss Lutz has shown that *subovata* also has 15 chromosomes, and the same may reasonably be inferred of *sublinearis* and *elliptica* from their genetic behaviour. In addition, we have *bipartita*, making a total of twelve forms. 'Type 5509' and 'type 2806' of Miss Lutz may be looked upon as modified oblongas, the modification being due, perhaps, to the presence of independent genetic factors, although in *Oenothera* so few factors of this kind have been demonstrated that great weight cannot be attached to this suggestion.

We may next consider the relationships of the trisomic forms as indicated by the offspring they produce when selfed or pollinated from *Oe. Lamarckiana*. As formerly pointed out (Gates and Thomas, 1914), *lata* and *semi-lata*, Gates, are peculiarly related, since the latter is essentially intermediate between *lata* and *Lamarckiana* and is only known to occur in the offspring of *lata* × *Lamarckiana*. Similarly mut. *superflua*, de Vries (1916), occurred as a mutant from *lata* (presumably pollinated by *Lamarckiana*) in 1914, and when selfed gave the usual dimorphic progeny characteristic of trisomic forms. It probably had 15 chromosomes. Then *cana*, *pallesces*, *Lactuca*, and *liquida* are found by de Vries (1916) to arise apparently with equal facility from *Lamarckiana* or from *lata* × *Lamarckiana*. Indeed, with far fewer seeds developed, owing to the sterility, they appear to arise with a much higher frequency from the latter source. Mut. *subovata* has also arisen both from *Lamarckiana* and from *lata* × *Lamarckiana*. Furthermore, the 'type 4499' of Miss Lutz has arisen from *lata* × *Lamarckiana* and from *lata* self-pollinated, while her *exilis*, *exundans*, and 'type 5365' are only known from the offspring of *Oe. lata* selfed. Hence there appears to be a peculiar relationship between *lata* and some at least of the other trisomic forms.

Oe. cana mutants have been obtained (de Vries, 1916) from *Lamarckiana*, *lata*, *pallesces*, *scintillans*, and *laevifolia*, but its frequency as a mutant from *Lamarckiana* is only 0.03 per cent., while from *lata* it may be as high as 9 per cent. When selfed, *cana* gives, in addition to *cana* and *Lamarckiana*, a significant frequency of *nanella*, as well as occasional stray mutations, including *albida*. *Pallesces*, which is said by de Vries to differ the least from *Lamarckiana*, was not discovered until 1911. It has since been obtained from some of the derivatives of *Lamarckiana*. When selfed it gives, in addition to the usual dimorphic progeny, *cana*, *liquida*, *scintillans*, *lata*, *albida*, and *rubrinervis* mutants, the mutants reaching as high as 4 per cent.¹ Mut. *Lactuca*, first observed in the offspring of *lata* × *Lamarckiana* in 1913, gave when selfed 39 *Lamarckiana*, four *Lactuca*, and one *nanella*. Mut. *liquida* most resembles *scintillans*. It was first observed in

¹ The question of *rubrinervis* will be discussed below.

1912, and has arisen once from *Lamarckiana*, four times from *lata* × *Lamarckiana*, and once from *pallenscens*. When selfed it yields *liquida* and *Lamarckiana* in nearly equal numbers, and also the mutants *scintillans*, *pallenscens*, *cana*, and *oblonga*. It thus appears that while these four simple trisomic forms arise more frequently from *lata* × *Lamarckiana* than from *Lamarckiana* itself, and frequently produce other trisomic forms as mutants in their offspring, yet they never give rise to *lata* itself. This fact appears to be significant as indicating that they are perhaps in some sense modified from *lata*, which appears as the basal form in the series. Thus the records show that *cana* can give rise to *pallenscens* and *pallenscens* to *cana*, also that the same interchangeable condition exists between *pallenscens* and *liquida*. But while any of these eight trisomic forms can apparently arise from *lata* × *Lamarckiana*, none of them except *pallenscens* apparently can give rise in turn to *lata*.

That *scintillans* can also give rise to *lata*, however, is shown by the following record (de Vries, 1913, p. 248). Eight *lata* mutants were derived from *scintillans* in a strain of *Oe. Lamarckiana* obtained from Messrs. Vilmorin, Andrieux & Cie, of Paris. *Lata* also appears (p. 257) in the offspring of *scintillans* in de Vries's strain of *Lamarckiana*. In addition, *scintillans* is said to have appeared 14 times as a mutant up to 1900, and to arise equally from *Lamarckiana* or *lata*. Hence this reciprocal relation exists between these two trisomic forms. Further, *lata* × *scintillans* (l. c., p. 257) produces only *lata* and *Lamarckiana* (736 plants) and *oblonga* × *scintillans* gave 61 *oblonga*, 13 *Lamarckiana*, and one *lata*. In another record (p. 265) *oblonga* × *scintillans* gave 81 per cent. *oblonga*, while *scintillans* × *oblonga* gave 18 per cent. *oblonga*. It has long been known (de Vries, 1909, i. 390) that a special relation exists between *oblonga* and *scintillans*, the latter producing a progeny which fluctuates widely but usually includes a high percentage (2–15 per cent.) of *oblonga* in addition to *scintillans*, *Lamarckiana*, and about one per cent. of *lata* and *nanella*. On the other hand, mut. *oblonga* when selfed is found to breed essentially true except that it gives occasional mutants, including *albida*, *elliptica*, and *rubrinervis*. It does not apparently produce *scintillans*, but it has arisen as a mutant both from *lata* and from *scintillans* × *nanella*.

By selfing certain *lata* plants, Miss Lutz (1917) has succeeded in getting 360 seeds from three individuals. Of these seeds 129 germinated and 126 developed. Three of the *lata* offspring were again selfed and yielded 259 seeds, of which 99 germinated. Of the 226 plants so produced 109 were *lata*, 8 *lata* (?), 57 *Lamarckiana*, 4 *Lamarckiana* (?), and 23 are said to have belonged to seven different 15-chromosome types (names unfortunately not given), 4 (belonging to three types) were 14-chromosome mutants, and one each had respectively 16, 21, and 22 chromosomes. The remaining 18 plants were apparently not classified. The offspring may be said to

have included approximately 50 per cent. of *lata* and 25 per cent. of *Lamarckiana*, the remainder being aberrant forms. Of the latter those known to have 15 chromosomes belonged to seven types. Only four mutants were known to have 14 chromosomes, and it is believed there were no others in this group. It appears from the rather involved account that the 18 unclassified forms were believed to have probably had more than 14 chromosomes. From *lata* × *Lamarckiana* Miss Lutz obtained 27 *lata*, 15 *Lamarckiana*, 1 *albida*, 1 *aberrans*, and one doubtful form. From *Lamarckiana* × *lata* she succeeded in getting 1 *lata*, 63 *Lamarckiana*, 2 *bipartita* (?), 1 *nanella*, and 9 of the *rubrinervis* type with 14 chromosomes which is probably *subrobusta* (see below).

From all these and many other rather jumbled facts, several significant points seem to emerge as regards these trisomic forms: (1) *scintillans* gives a large percentage of *oblonga* offspring and evidently stands in a peculiar relation to that type; (2) there is a reciprocal relationship between *lata* and *scintillans* in that each can give rise to the other; (3) *lata* can produce directly *albida*, *oblonga*, and *scintillans*, while *oblonga* can produce *albida* but apparently not *lata* or *scintillans*, and *scintillans* produces *oblonga* and *lata* with relatively high frequency but apparently not *albida*; (4) that *semi-lata*, Gates, stands in a peculiar relation to *lata* has already been pointed out.

We may next refer to the fact that *albida* and *oblonga* apparently breed true notwithstanding their unbalanced chromosome number. In the case of *albida* (de Vries, 1909) this involves only 122 offspring grown in 1897–8. At any rate no *Lamarckiana* appeared among them. For *oblonga* the evidence is better. Some 2,919 offspring were grown during 13 years, and were all *oblonga* except three *albida*, one *elliptica*, and seven *rubrinervis*. Miss Lutz (1917) suggests that such trisomic forms would breed true if all the gametes of one sex contain seven chromosomes and all those of the other sex eight chromosomes. In *lata* and other 15-chromosome forms it is clear that very few 8-chromosome pollen grains ever function in fertilization. In some cases, as I have previously suggested, the extra chromosome may be lost during the mitoses in pollen grain or pollen tube. It would therefore be necessary to assume that in *albida* and *oblonga* all the functional eggs contained eight chromosomes and all the functional pollen seven chromosomes. On the other hand, Bartlett (1915) probably overstates the case in assuming that all 8-chromosome pollen grains are eliminated, for various results indicate that trisomic forms do occasionally produce functional 8-chromosome pollen grains. As already pointed out in this paper, the frequent occurrence of trisomic mutants in pairs (de Vries, 1916, also notes such cases) shows that these have probably arisen from non-disjunction in a pollen mother-cell of the previous generation.

An effort has been made to systematize the many records of trisomic mutants in *Oenothera* as regards their origin, their offspring, and their

consequent relationships with each other, with the intention, if possible, of bringing order out of what appears to be chaos. But it seems that, with some exceptions, any trisomic form is capable of giving rise to any other. The experiments of de Vries with *cana* and other forms lead him to the conclusion that none of these trisomic mutants transmit their characters through the pollen. This is in accord with the cytological studies of *lata* (Gates and Thomas, 1914), in which it was shown that very few pollen grains can be formed having eight chromosomes. But in trisomic mutants such as the one described in this paper, where a larger percentage of functional pollen is produced and the pollen nuclei not infrequently receive eight chromosomes, it is probable that the extra chromosome may often be lost in the later nuclear divisions of the male gametophyte. When used as the female parent in crosses, these trisomic forms frequently appear in numbers approaching 50 per cent. of the offspring. From this fact it seems clear that in megaspore formation the chances are equal that the extra chromosome will pass to either pole, the defect in numbers of the trisomic form being the result of a lesser viability of gametes with the extra chromosome, or of the extra chromosome sometimes being left behind on the spindle. There is, on the contrary, some evidence of greater viability on the part of zygotes with an extra chromosome (at least in the case of *lata*).

We must now refer to certain other interesting forms in Table I (p. 548) which have not yet been mentioned. These are *aberrans*, Lutz, and *rubrinervis*, de Vries. Miss Lutz (1916) describes *aberrans* as a mutant from *lata* $\times$ *Lamarckiana*, two individuals occurring from this cross in 1908 and 1909. The type differs from *Lamarckiana* by no very marked characters except the almost complete pollen sterility. A moderate abundance of pollen was produced, but containing few good grains, and it was found almost impossible to obtain seed by self-pollination. The plants had more slender, tapering buds than *Lamarckiana*, but produced an abundance of flowers with slightly lighter yellow petals. Cytological examination of root tips showed the constant presence¹ in both plants of a small chromosome fragment in addition to the usual 14 (hence 14^{+1}). As Miss Lutz points out, this type no doubt arose through a fragment of a disintegrating chromosome becoming included in one of the daughter nuclei, a condition which was shown actually to occur (Gates and Thomas, 1914) in the meiotic pollen divisions of *Oe. lata* forms. The inclusion of such a fragment has been sufficient to alter appreciably the characters of the plant; the fragment has regularly divided in mitosis, but its presence during the meiotic division was a sufficient disturbance to cause almost complete pollen sterility.

The other fact recorded by Miss Lutz (1916) which is germane to the present discussion is that in a *rubrinervis* mutant arising from *lata* $\times$ *Lamarck-*

¹ Occasionally the small chromosome could not be found in cells in which it apparently could not have been concealed.

iana in the garden of de Vries and identified by him as typical *rubrinervis*, cytological examination of the root tips showed a small extra chromosome, somewhat larger than the small one in *aberrans*. It is significant that this mutant also arose from *lata* × *Lamarckiana*. While the origin of this chromosome fragment is therefore clear, its significance is less certain. Mut. *rubrinervis*, de Vries, is recorded as a form which breeds true and has no marked pollen sterility (i. e. the usual 50 per cent). It is therefore not clear whether this fragment will prove to be a constant feature of the type which de Vries calls *rubrinervis*. It has long been evident that the form identified in American cultures as *rubrinervis* differs in certain features from the type of de Vries. It is a taller, stronger plant without a zigzag stem but with the same red stripes on the sepals, and appears to be the same as the derivative from *rubrinervis* crosses which de Vries (1913, p. 192) has since called *subrobusta*. The latter may in turn give rise to *rubrinervis* (according to de Vries) when self-pollinated. The taller, stronger plant is the one which has been called *rubrinervis* in all of my experiments. It certainly has 14 chromosomes without any extra fragment (Gates, 1908). There would appear to be still some uncertainty regarding the unity of the forms which de Vries has called *rubrinervis*.

Finally, brief reference may be made to mut. *lasiopetala*, which originated from *Oe. stenomeris* in the cultures of Bartlett (1915). It has hairy petals and is very late in flowering, forming terminal rosettes on its branches. Less than half the pollen appears viable, and as its offspring are dimorphic, like those of other trisomic mutants, it probably also has 15 chromosomes. The hairy petals are a new character in the genus and it is totally different from any other trisomic form. The tetraploid mutant *gigas* from *Oe. stenomeris* also gave rise to a secondary mutation *lanosa* with hairy petals like *lasiopetala* and also the 'filaments of the stamens alternate with the petals were densely lanose'. It is therefore parallel with *lasiopetala* but more extreme. Possibly this form had 29 chromosomes.

We may next consider the occurrence of plants with 16 chromosomes, either as mutations or in the offspring of simple trisomic forms. Their appearance is rare, and this confirms the fact that 8-chromosome pollen grains rarely function or rarely retain their full chromosome complex in the male nuclei. Miss Lutz (1917) obtained two *lata*-like mutants from separate cultures of *Lamarckiana* in 1908 and 1910. Both had 16 chromosomes, but they were 'in no sense identical forms'. Like *lata*, they had crinkled leaves, one broad, the other narrower; both had yellow-green foliage, irregularly shaped buds, and were male sterile. A third form with 16 chromosomes was a dwarf arising from *lata* selfed and having broad leaves in the rosette stage. In the experiments of van Overeem (1920) several forms with 16 chromosomes (double trisomic) have appeared. In the offspring of *Oe. Lamarckiana semigigas* the chromosome number ranged from 14 to 28 and

included three plants with 16 chromosomes, one of which resembled *cana*. Also from *semigigas* and its crosses with *Lamarckiana* and *gigas* the following 15-chromosome forms were obtained: *lata*, *cana*, *pallescent*, and *liquida*. Similarly from *Oe. biennis semigigas* $\times$ *biennis* was obtained *albinervis* with 15 chromosomes and three rosettes with small blue-green leaves, one of which was shown to have 16 chromosomes.

Such forms may of course arise from $8 + 8$ chromosomes, or particularly in cases where the mother plant is triploid, from $9 \text{ ♀} + 7 \text{ ♂}$. That the condition is still an unbalanced one is shown by the male sterility of these forms.

We may now consider briefly the significance of these complicated facts, and it is well to point out in the first place a fact which has as yet been recognized by very few geneticists, namely, that the great majority of the known mutations in the *Oenotheras* involve altered chromosome numbers, chiefly simple trisomic. Indeed almost the only exceptions are (1) *brevistylis*, *rubricalyx*, and *gigas nanella*, which involve simple Mendelian differences, and (2) *rubrinervis*, *nanella*, perhaps *laevifolia*, and a few others which may possibly have arisen through crossing-over. Irregular chromosome distributions are then concerned in the great majority of *Oenothera* mutations.

It was first pointed out many years ago (Gates, 1908) that owing to the usually weak attraction between the chromosomes in *Oenothera* during meiosis, irregular chromosome distributions (now spoken of as non-disjunctions) may and do occur, giving rise to pollen grains (and probably also megaspores) with eight chromosomes. It was also pointed out that simultaneous non-disjunction of two pairs of chromosomes in opposite directions would lead to the formation of pollen grains all having seven chromosomes, but two of them lacking both members of one pair and two both members of another pair. Since then an attempt has often been made, by giving letters to the chromosomes, to work out the behaviour of the various mutations on a chromosome basis. Since no consistent scheme could be arrived at, the results were not published. Miss Lutz (1917) has made a similar attempt, but confesses failure. It is perhaps worth while to view the matter afresh in the light of our present knowledge. Let us apply this view first to mutations like *rubrinervis* and *nanella*. The striking facts in their genetic behaviour are (1) that they arise sporadically from *Lamarckiana*, (2) that they breed true except for occasional aberrant forms, (3) that in crosses with *Lamarckiana* they give the two parent types in various proportions, (4) that when crossed together they give (de Vries, 1913, p. 214) in F_1 *Lamarckiana* and *subrobusta* (which we have seen is closely related to *rubrinervis*). The *Lamarckiana* breeds true, while *subrobusta* in F_2 splits out dwarfs (*rubrinervis*, *nanella*) as a Mendelian recessive, and *rubrinervis*, both of which breed true. *Subrobusta* continues to split in the same manner in later generations. This is shown in diagram form on p. 557.

It may be worth while determining how many of these complicated facts of genetic behaviour can be explained by the simple hypothesis that in the origin of *nanella* and of *rubrinervis* there has been what we may call double non-disjunction in one or both parental germ cells, so that we have for *nanella* the formula $\frac{AACDEFG}{AACDEFG}$ (the *B* chromosome being absent), while

for *rubrinervis* we have $\frac{BBCDEFG}{ABCDEFG}$. *Oe. nanella* × *rubrinervis* will then

give an F_1 $\frac{AACDEFG}{BBCDEFG} + \frac{AACDEFG}{ABCDEFG}$. The former combination would be

Lamarckiana subrobusta.

expected to produce *Lamarckiana*, and in its pollen formation synapsis might be expected to take place between the *A* and *B* chromosomes instead of between the two *A*'s and the two *B*'s. It should therefore breed true, as it actually does. The other F_1 combination (*subrobusta*) might be said to be heterozygous for an *AB* pair of chromosomes. When selfed it would therefore be expected to give the following:

$$\frac{AACDEFG}{AACDEFG} + \frac{AACDEFG}{ABCDEFG} + \frac{ABCDEFG}{ABCDEFG}$$

nanella 2 *subrobusta* *Lamarckiana*.

But according to de Vries, we get in fact *rubrinervis* where we should expect to get *Lamarckiana*. In view of the fact that there is some confusion over the *rubrinervis* forms and that *subrobusta* was only recognized as a separate type in 1913, we might suppose that there was something incomplete in the analysis. But the hypothesis of double non-disjunction meets with other difficulties. It will explain the result of *Oe. rubrinervis* × *Lamarckiana* thus:

$$\frac{BBCDEFG}{ABCDEFG} \times \frac{ABCDEFG}{ABCDEFG} = \frac{BBCDEFG}{ABCDEFG} + \frac{ABCDEFG}{ABCDEFG}$$

rubrinervis *Lamarckiana* *rubrinervis* *Lamarckiana*.

But, as Miss Lutz pointed out, *nanella* × *Lamarckiana* introduces a fatal difficulty, for we have $\frac{AACDEFG}{AACDEFG} \times \frac{ABCDEFG}{ABCDEFG} = \frac{AACDEFG}{ABCDEFG}$, which is *subrobusta*, whereas we are supposed to obtain the two parent forms in the F_1 of this cross. It therefore appears to be impossible to explain the

behaviour of such 14-chromosome mutants as *nanella* and *rubrinervis* through double non-disjunction, although their origin and the fact that they breed true may be accounted for in this way. There are a few other forms whose origin could be explained by crossing-over, but this hypothesis equally fails to explain their later hereditary behaviour. Perhaps a critical repetition of some of the breeding experiments might throw light on these difficulties.

Let us now consider the situation as regards the trisomic forms. We have already seen that *lata* can apparently give rise to all the other trisomic forms, and that they usually arise with higher frequency from *lata* × *Lamarckiana* than from *Lamarckiana* itself. This must mean that when they arise from *lata* × *Lamarckiana* it is, usually at any rate, by the union of an 8-egg with a 7-male cell. The mutation giving a different trisomic form might then arise from a male gamete in which double non-disjunction has taken place. Thus if we suppose that *lata* is $\frac{AABCDEFGFG}{ABCDEFGG}$, its female gametes will be *AABCDEFGG* and *ABCDEFGG* in equal numbers unless some irregularity occurs. Double non-disjunction in a pollen mother-cell of *Lamarckiana* might produce a male gamete *ACCDEFG*. Hence a trisomic individual could arise which was $\frac{AABCDEFGG}{ACCDEFG}$. Let us suppose this is the formula for *scintillans*. Then the germ cells of this mutant could form various recombinations of chromosomes, such as (considering only the unbalanced pairs) $\frac{AABC}{ACC}$, $\frac{AACC}{ABC}$, $\frac{ABCC}{AAC}$, &c. In fertilization such recombinations could occur as $\frac{AABC}{ABC}$ (*lata*), $\frac{AABC}{ACC}$ (*scintillans*), $\frac{AACC}{ACC}$ (which might represent a different trisomic form), &c. Hence we can understand how *lata* could give rise to *scintillans* and vice versa, and also how *lata* might be the starting-point for a whole series of other trisomic forms arising through further irregular distributions of the chromosomes. Whether such a form as, e.g., $\frac{AACC}{ACC}$ is viable would depend on how far the chromosomes are differentiated from each other.

It has recently been found that a haploid mutant can arise in *Datura* (Blakeslee, Belling, Farnham, and Bergner, 1922). This number of chromosomes is then sufficient for the production of a complete sporophyte. If duplication and redistribution of chromosomes could go on indefinitely it might be possible to produce an organism with all *A* or all *C* chromosomes. Weismann's theory of the germ-plasm contemplated the view that each id contained all of the representative germinal material, each chromosome being made up of a number of ids. Speculation has since swung to the opposite extreme, and it has been rather tacitly assumed that the chromo-

somes, at least in the haploid series, all differed from each other throughout. This assumption is quite possibly too extreme, at least for plants. It appears probable that in animals, which are more highly integrated organisms than plants, the various chromosomes are differentiated from each other throughout their length. But even here there may be a common substratum for each chromosome which has remained undifferentiated in an evolutionary sense. It is reasonable to suppose that the amount of difference between chromosomes in one organism may be much greater than in another. We know this to be the case as regards sizes and shapes of chromosomes, since in some organisms the chromosomes are all visibly alike, while in others they show many constant differences. It is probable that there are equally great differences as regards chemical differentiation, which is presumably at the basis of mutations of the *Drosophila* type. On the other hand, it seems necessary to assume *some* difference between the chromosomes of every organism, for if there were no such difference it is difficult to see how they would maintain their identity, as they appear to do, while passing through the resting stage of the nucleus. But it does not necessarily follow that this difference is sufficiently great so that replacement of one or two chromosomes by duplicates of others would produce a non-viable result, or one which produced a new genus or family. It may be, for example, in *Oenothera* that its generic and family characteristics are equally represented in all the chromosomes, while minor differences may have arisen more recently through mutations of the type represented by *rubricalyx* and *brevistylis*.

An analogy may make this general position clearer. It seems evident that the differentiation of the sexes is much greater in some organisms than in others. Thus in *Hemiptera* the relation of sex differentiation to dimorphism of the *X* and *Y* chromosomes seems clear. On the other hand, Schaffer (1918) has given good reasons for the conclusion that in hermaphroditic flowering plants sex differentiation has 'absolutely nothing to do with segregation or association of chromosomes or allosomes'. In a similar way I believe that there is evidence in the *Oenotheras* that the chromosomes are much less differentiated than in animals and some plants, i. e. the undifferentiated substratum occupies a greater portion of the whole chromosome. And the occurrence of such a large number of trisomic mutants in *Oenothera*, a number of which have interchangeable relationships with each other, seems to find its explanation in further assortments of non-homologous chromosomes. It seems unlikely that this process could go further than the production of forms with four members of one chromosome and none of another.

The almost complete sterility of trisomic forms in *Oenothera* renders the solution of these problems almost impossible, but it is to be hoped that in *Datura*, where there is greater viability and where there are also more

Mendelian characters whose inheritance can be used as a check, a further analysis of the situation will be possible. There is apparently, however, no evidence at present that any of the trisomic mutants in *Datura* are interchangeable, so the conditions in the two genera differ in some respects. The further study of the offspring of triploid *Oenothera* mutants and hybrids will also throw further light on these questions.

One question which remains to be discussed is the possible visible differentiation of the seven pairs of chromosomes in *Oenothera*. Hance (1918) claims that the chromosome pairs of *Oenothera scintillans* form a graded series in length, but it must be said that his treatment of the subject is not entirely convincing. The difficulties of obtaining all the chromosomes of a large number of equatorial plates exactly in the plane of section are very great, and the frequent bendings of the chromosomes render accurate measurements still more precarious where small differences in length are involved. Van Overeem (1922), in an important paper, has, however, reached a similar conclusion. He identifies the extra chromosome in *lata* (which we have called *A*) as belonging to a trio which are long and strongly bent. He calls this chromosome No. 1 (see his Pl. II, Figs. 9–12). In *cana* he identifies the extra chromosome as belonging to No. 5 pair, a pair which he believes is probably of medium length and is bent near the end and often somewhat constricted (Pl. II, Figs. 1–8). If these differences can be proved to be constant this will help to substantiate the views expressed in the present paper. But more critical and extensive measurements of these chromosomes must be made before one can regard it as proved that the chromosomes of *Oenothera* form a series which are constantly differentiated in size and shape. The facts, as far as they go, are entirely in accord with the views here expressed, and it is to be hoped that with further evidence it may be possible to identify the chromosome composition of each form. The possibility should be kept in view that some forms with an extra chromosome may at the same time be lacking both members of a different pair.

It may be pointed out here that van Overeem (1922) concludes from the genetic data that the extra chromosome in *lata* belongs to the *gaudens* complex (since in crosses it gives, like *Lamarckiana*, the twin types *laeta* and *velutina*) and that the same is true of *scintillans* and *oblonga*, although the extra chromosome is a different one in all three. In a paper now in the press I have shown reasons for believing that the difference between *gaudens* and *velans* resides in a single pair of *Lamarckiana* chromosomes. How these two views are to be harmonized can only be determined by further breeding experiments with various trisomic forms. There seems no reason for assuming that in any of these mutants the *gaudens-velans* pair of chromosomes is the extra one. There should however, on my view, be one trisomic mutant in which this was the case, and this should distort the

ratios of *laeta* and *velutina* obtained by pollination from, e.g., *Oe. Hookeri* or *Oe. strigosa*, according to whether the extra chromosome in the mutant was carrying *laeta* or *velutina*.

SUMMARY.

This paper records the occurrence in the F_1 of *Oenothera rubricalyx* $\times$ *Oe. Hewettii* of two mutants having 15 chromosomes, but of a type different from *Oe. lata* and having viable pollen. It probably most nearly resembles some of the *semilata* mutations, which also have 15 chromosomes. The occurrence of a pair in such cases is significant, indicating that non-disjunction of a pair of chromosomes in the heterotypic division of a pollen mother-cell of the male parent (in this case *Oe. Hewettii*) led to the formation of two pollen grains having eight chromosomes, both of which afterwards functioned in fertilizing eggs.

In diakinesis in the pollen mother-cells of this mutant as many as five ring-pairs of chromosomes are found. One of these ring-pairs may perhaps be descended from the original pair of chromosomes which underwent non-disjunction in a pollen mother-cell of *Oe. Hewettii*. The others must be formed by the union of homologous chromosomes from *rubricalyx* and *Hewettii*. The presence of chromosome rings, while an indication of strong attraction between synaptic mates, cannot therefore be regarded as evidence that the species is homozygous.

Some of the chromosome-rings persist on the heterotypic spindle even until metaphase. The later irregularities in the chromosome behaviour of this mutant are not so great as in *Oe. lata*, but chromosomes are frequently left behind in the cytoplasm.

This is followed by a discussion of all the trisomic forms of *Oenothera* (having 15 or 16 chromosomes). The origin of mutations with 14 chromosomes such as *nanella* could be accounted for by double non-disjunction as well as through crossing-over, but neither theory explains the later genetic behaviour of these forms.

The evidence now indicates that forms with aberrant chromosome numbers make up the great majority of *Oenothera* mutations. There is an older group of 15-chromosome mutants from *Oenothera Lamarckiana* which includes *lata*, *scintillans*, *albida*, *oblonga*, *subovata*, and probably several others. More recently a series of others more like *Oe. Lamarckiana* has been recognized, including *cana*, *pallescent*, *Lactuca*, and *liquida*. Apparently *lata* $\times$ *Lamarckiana* can give rise to any of these.

Trisomic mutants appear much more frequently in the offspring of *lata* than in the offspring of *Lamarckiana*. Again, several at least of the simple trisomic mutants are interchangeable. Thus *lata* gives rise to *scintillans* and *scintillans* to *lata*. The view is developed that this results from secondary irregular chromosome distributions.

This leads to the question how far the chromosomes of *Oenothera* may be differentiated from each other. The conclusion is reached that the degree of differentiation probably varies in different organisms, being generally greater in animals than in plants. Such differentiation may be increased by the occurrence of Mendelian mutations, but in *Oenothera* mutations of this type are relatively infrequent.

In conclusion, I wish to record my thanks to the Royal Society and the British Association for grants in connexion with this work, and also to the Royal Botanic Gardens, Regent's Park, for the facilities afforded.

LITERATURE CITED.

- BARTLETT, H. H. (1915): The Mutations of *Oenothera stenomerus*. Amer. Journ. Bot., ii. 100-109, Figs. 4.
- BLACKBURN, K. B., and HARRISON, J. W. H. (1921): The Status of the British Rose Forms as determined by their Cytological Behaviour. Ann. Bot., xxvii. 511-32, Pls. 2.
- BLAKESLEE, A. F., BELLING, JOHN, and FARNHAM, M. E. (1920): Chromosomal Duplication and Mendelian Phenomena in *Datura* Mutants. Science, N. S., lii. 388-90.
- BLAKESLEE, A. F., BELLING, JOHN, FARNHAM, M. E., and BERGNER, A. D. (1922): A Haploid Mutant in the Jimson Weed *Datura stramonium*. Ibid., lv. 646-7.
- BOEDIJN, K. (1920): Die Chromosomen von *Oenothera Lamarckiana*, mut. *simplex*. Zeitsch. f. Abst. u. Vererb., xxiv. 71-6, Pl. I.
- BRIDGES, CALVIN B. (1916): Non-disjunction as Proof of the Chromosome Theory of Heredity. Genetics, i. 1-52, 107-63, Figs. 9, Pl. I.
- CLELAND, R. E. (1922): The Reduction Divisions in the Pollen Mother-cells of *Oenothera franciscana*. Amer. Journ. Bot., ix. 391-413, Pls. XXV-XXVII.
- COCKERELL, T. D. (1913): Some Plants from New Mexico. Proc. Biol. Soc., Washington, xxvi. 203-4.
- DAVIS, B. M. (1909): Pollen Development of *Oenothera grandiflora*. Ann. Bot., xxiii. 551-71, Pls. XLI, XLII.
- (1910): The Reduction Divisions of *Oenothera biennis*. Ibid, xxiv. 631-51, Pls. LII, LIII.
- (1913): The Behaviour of Hybrids between *Oenothera biennis* and *Oe. grandiflora* in the Second and Third Generations. Amer. Nat., xlvii. 449-76, 547-71, Figs. 17.
- GATES, R. R. (1907): Pollen Development in Hybrids of *Oenothera lata* × *Oe. Lamarckiana*, and its Relation to Mutation. Bot. Gaz., xliii. 81-115, Pls. II-IV.
- (1908): A Study of Reduction in *Oenothera rubrinervis*. Bot. Gaz., xlvi. 1-34, Pls. I-III.
- (1912 a): Parallel Mutations in *Oenothera biennis*. Nature, lxxxix. 659-60.
- (1912 b): Somatic Mitoses in *Oenothera*. Ann. Bot., xxvi. 993-1010, Pl. I.
- (1914): Breeding Experiments which show that Hybridization and Mutation are Independent Phenomena. Zeitsch. f. Abst. u. Vererb., xi. 209-79, Figs. 25.
- (1915): The Mutation Factor in Evolution, with Particular Reference to *Oenothera*. London: Macmillan, pp. 353, Figs. 114.
- (1917): Vegetative Segregation in a Hybrid Race. Journ. Genet., vi. 237-53, Pl. 9.
- (1921): Mutations and Evolution. London: Wesley, pp. 118, Figs. 2. New Phytol. Reprint No. 12.

- GATES, R. R. (1922): Some Points on the Relation of Cytology and Genetics. *Journ. of Heredity*, xiii. 75-6.
- (1923): A Peculiar Type of Variability in Plants. *Journ. Genet.*, xiii. 13-45, Figs. 24.
- and THOMAS, NESTA (1914): A Cytological Study of *Oenothera* mut. *lata* and *Oe.* mut. *semilata* in Relation to Mutation. *Quart. Journ. Micro. Sci.*, lix. 523-71, Pls. 35-7, Figs. 4.
- HANCE, ROBERT T. (1918): Variations in the Number of Somatic Chromosomes in *Oenothera scintillans*, de Vries. *Genetics*, iii. 225-75, Pls. 7, Figs. 5.
- LEHMANN, ERNST (1922): Die Theorien der *Oenothera*-forschung. Jena: Fischer, pp. 526, Figs. 207.
- LUTZ, A. M. (1908): Chromosomes of the Somatic Cells of the *Oenotheras*. *Science*, N. S., xxvii. 335.
- (1912): Triploid Mutants in *Oenothera*. *Biol. Centralbl.*, xxxii. 385-435, Figs. 7.
- (1916): The Production of 14+ -chromosome Mutants by 14-chromosome *Oenothera Lamarckiana*. *Science*, N.S. xliii. 291-2.
- (1916): *Oenothera* Mutants with Diminutive Chromosomes. *Amer. Journ. Bot.*, iii. 502-26, Pl. 24, Figs. 7.
- (1917): Fifteen- and Sixteen-chromosome *Oenothera* Mutants. *Ibid.*, iv. 53-111, Figs. 9.
- MACDOUGAL, D. T., VAIL, A. M., SHULL, G. H., and SMALL, J. K. (1905): Mutants and Hybrids of the *Oenotheras*. *Carnegie Publ.*, No. 24, pp. 57, Figs. 13, Pls. 22.
- VAN OVEREEM, CASPAR (1920): Über Formen mit abweichender Chromosomenzahl bei *Oenothera*. Dissertation. *Beih. z. Bot. Centralbl.*, xxxviii, pp. 47, Pls. 6.
- (1922): Same title. *Ibid.*, xxxix, pp. 1-80, Pls. 15.
- SCHAFFNER, J. H. (1918): The Expression of Sexual Dimorphism in Heterosporous Sporophytes. *Ohio Journ. Sci.*, xviii. 101-25.
- TISCHLER, G. (1921-1922): Allgemeine Pflanzenkaryologie. Berlin: Bornträger, pp. 899, Figs. 406.
- DE VRIES, HUGO (1909): The Mutation Theory, vol. i, pp. 582, Figs. 119. *Trans. Farmer and Darbishire*.
- (1913): Gruppenweise Artbildung, unter spezieller Berücksichtigung der Gattung *Oenothera*. Gebrüder Bornträger, Berlin, pp. 365, Figs. 121.
- (1916): New Dimorphic Mutants of the *Oenotheras*. *Bot. Gaz.*, lxii. 249-80, Figs. 5.
- (1918): Mutations of *Oenothera suaveolens*, Desf. *Genetics*, iii. 1-26, Figs. 4.
- (1919): *Oenothera Lamarckiana* mut. *simplex*. *Per. Dent. Bot. Gesellsch.*, xxxvii. 65-73.

EXPLANATION OF PLATE XI.

Illustrating Professor Gates's paper on the Trisomic Mutations of *Oenothera*.

All figures were drawn with a $\frac{1}{12}$ -inch Koristka immersion lens N.A. 1.30 and compensating ocular 12, and reduced one-fourth in reproduction, giving a magnification of 2,250 diameters.

Fig. 1. Pollen mother-cell in diakinesis, showing five ring-pairs of chromosomes and five single chromosomes.

Fig. 2. Another cell at the same stage, showing five rings.

Fig. 3. Multipolar spindle stage, showing 15 chromosomes, including a looped ring.

Fig. 4. Another cell at the same stage, showing a looped ring.

Fig. 5. Heterotypic spindle in early anaphase, showing the odd chromosome *e*.

Fig. 6. Heterotypic bipolar spindle, showing a persistent ring chromosome.

Fig. 7. Heterotypic anaphase, showing 15 chromosomes, seven of them approaching one pole, five the other, and three lagging behind.

Fig. 8. Heterotypic telophase with probably eight chromosomes in one daughter nucleus, six in the other, and one left behind in the cytoplasm. Most of the chromosomes show their split character at this time.

Gates, R. Ruggles. 1923. "The trisomic mutations of *Oenothera*." *Annals of botany* 37, 543–563. <https://doi.org/10.1093/oxfordjournals.aob.a089866>.

View This Item Online: <https://www.biodiversitylibrary.org/item/270686>

DOI: <https://doi.org/10.1093/oxfordjournals.aob.a089866>

Permalink: <https://www.biodiversitylibrary.org/partpdf/319102>

Holding Institution

New York Botanical Garden, LuEsther T. Mertz Library

Sponsored by

BHL-SIL-FEDLINK

Copyright & Reuse

Copyright Status: Public domain. The BHL considers that this work is no longer under copyright protection.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.