

THE
BOTANICAL GAZETTE

JANUARY 1919

OENOTHERA RUBRINERVIS; A HALF MUTANT

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In the spring of 1913 in a culture of *Oenothera rubrinervis* I noticed some young plants, the leaves of which were a little broader than those of the other rosettes. Although the difference was very small, I planted them separately and saw that the deviation did not increase until the time of flowering. The spikes, however, gave proof that the aberrant specimens constituted a type of their own, since the bracts repeated the marks of the primordial leaves, being broader and more flattened than in ordinary *rubrinervis*. There were 7 specimens of the new form among a culture of 25 plants, all of which flowered in August. This indicates a percentage of about 30. In the following year the seeds of the new form gave a uniform progeny, whereas those of the normal specimens repeated the splitting. Thereupon I studied their seeds and found that about one-fourth of those of *O. rubrinervis* were empty, but almost every seed of the new type contained a living embryo. On account of this very small but constant difference the new form was designated as mut. *deserens*.¹ Evidently it might have escaped observation in previous years, the individuals simply being taken for weaker specimens of the type. I studied the progeny of as many self-fertilized specimens of *O. rubrinervis* as were available, therefore, and found the new type among all of them, and as a rule in correspondingly high numbers. Different strains of *rubrinervis* yielded the same result.

¹ Zeitschr. f. Ind. Abst. 16: 262. 1916.

If we should apply the principle of BARTLETT concerning mass mutation, and that of MORGAN concerning lethal factors to this case, as I have made use of them in explaining the secondary mutability of *O. grandiflora* and *O. Lamarckiana*,² we would conclude that *O. deserens* is a mass mutation of *O. rubrinervis*, and as such is a repetition of the initial mutation which produced the *O. rubrinervis* from *O. Lamarckiana* in my garden. This initial mutation must have occurred in a sexual cell, which, after copulation with a normal gamete of *O. Lamarckiana*, gave rise to a half mutant, *O. rubrinervis*. In other words, *O. rubrinervis* arose as a half mutant between potential *O. deserens* and normal *O. Lamarckiana*. This half mutant, after artificial self-fertilization, must have produced a splitting into three types, exactly in the same way as this splitting can be observed in the half mutants of *O. gigas nanella*. Of these types two must be constant, but the third must repeat the splitting. *O. deserens* is one of the constant ones, whereas the other is assumed to be hidden in the empty seeds, containing a lethal factor just as in *O. grandiflora* and *O. Lamarckiana*. The third type is the continuance of *O. rubrinervis*, and repeats the splitting in every generation.

According to my view *O. Lamarckiana* produces yearly two kinds of gametes in consequence of a secondary mutability into *velutina*. These *velutina* are linked to a lethal factor, which kills them in the young seeds. If we assume that the mutation into *deserens* took place in the typical gametes, leaving the *velutina* unchanged, we would conclude that *O. rubrinervis* consists of two types of gametes, even as *O. Lamarckiana*, but that both of them are in a mutated condition. One is the new *deserens*, without lethal factor; the other is the old *velutina*, linked to a lethal factor. The result of self-fertilization is now easily explained; the copulation of *deserens* gametes among themselves must produce this form, that of *velutina* must give empty seeds, and the combination of the two types must repeat the *rubrinervis* with its splitting capacity.

On the same basis the occurrence of twin hybrids may be explained, the *deserens* gametes giving the *laeta* hybrids; but here we have a considerable advantage over other instances of twin

² Mass mutation and twin hybrids of *Oenothera grandiflora* Ait. BOT. GAZ. 65: 377-422. 1918.

hybrids, since both the constituents are available in pure condition for controlling crosses. Any cross which gives twins with *rubrinervis* may be repeated with *O. deserens* and with my *O. mut. velutina* (*O. blandina*). In the first case the result must be hybrids of the type *laeta*, in the second case hybrids of the form *velutina*, and the addition of these must simply duplicate the split progeny of the corresponding cross of *O. rubrinervis*. I have made these crosses in a number of cases and found this deduction verified.

Apart from the described secondary mutability into viable *deserens* and dead *velutina* germs, *O. rubrinervis* is not known to possess any noticeable degree of mutability; it has, especially, never produced those mutants which are of so common occurrence in allied mutating forms. Thus we see that secondary mutability is not, in itself, to be considered as a cause of further mutations, and this seems to me to be a fact of paramount interest in the discussion concerning the probable causes of this phenomenon.

The details of the following experiments will give proof of the proposed conception. I shall first give those relating to self-fertilizations and afterward deal with the crosses.

Oenothera rubrinervis originated in my garden from *O. Lamarckiana* quite regularly in a percentage of about 0.1. Every time the visible characters were exactly the same. Between 1890 and 1900 the mutation was repeated 66 times among 66,000 plants.³ In 1905 I introduced new rosettes of *O. Lamarckiana* from the original locality near Hilversum into my garden, and among their offspring I observed also repeated mutations into *rubrinervis*. The characters were always the same, namely, a pale reddish tinge, narrow and longitudinally folded leaves, a hairy epidermis, cup-shaped flowers, but above all the brittleness of the stems, branches, and petioles, due to the incomplete development of the cell walls in the fibers of the bark and wood. Until now I cultivated mainly two strains, derived from two different mutants of 1895. One of them has given the material for all my crosses, and I shall designate it as the main line. The second line of 1895 was originally destined for control experiments only, but in 1913 it produced the first observed

³ The mutation theory, English ed. 1: 331. 1909.

case of *O. deserens*, as previously mentioned, and since then it has been studied carefully in this respect.

After repeated cultures of pure *O. deserens* had been made and compared with *O. rubrinervis*, the characteristic marks of the two forms became quite clear and reliable, although very small. In mixed cultures the types may even be separated when very young, but some dubious specimens may remain. At the time of flowering these have almost always been shown to belong to the new type. Among the very young rosettes, with only 3-5 leaves, those of *deserens* are broader and more flattened and of a deeper and purer green, resembling therein young plants of *O. Lamarckiana*. These differences increase slowly until the time when the rosettes must be planted out from the boxes into the garden, about the middle of April. The leaves of *O. deserens* have now a broader base and a less pointed top than those of *O. rubrinervis*, besides the marks already given. In July the differences remain very small, the two types reaching the same height at the same period, but the *rubrinervis* begin to flower one or two weeks earlier than the *deserens*. Seen from above, the spikes show narrow, folded bracts in the first type and flat, broad ones in the second type. This character is easily appreciated and wholly reliable; no dubious cases trouble the counting in mixed cultures. The beginning of August, when the *deserens* have opened only a few of their first flowers, is the best time to separate them. A difference in the color has now become clear, the red tinge of the parent type failing in the *deserens*. Here the leaves, bracts, and flower buds are green, and the flowers are also of a purer yellow. A number of smaller marks, which are helpful in the distinction, almost escape description, as, for example, the form of the flowers, their grouping at the top of the spike, and the more erect position of the buds before opening.

The main character of *O. rubrinervis* is the brittleness of all its parts, as already mentioned. It is exactly the same in *O. deserens*. I have broken the stems of all the plants to be mentioned in this article at the time of sorting them out in August or after harvesting their seeds, but no exception has been found to this rule.⁴ Hybrids

⁴ I have, moreover, injected all the seeds for the sowings of the later years under a pressure of 8 atmospheres during 48 hours, this being the only reliable means of making the germination as complete as possible.

which possess the other characters of *rubrinervis*, but lack the brittleness, are easily recognizable as rosettes of radical leaves as well as during the growth of the stems. They will be designated as *subrobusta*.⁵

The determination of the percentage of mutants in self-fertilized seeds was made in 1916 in the following manner. The specimens were counted in the boxes at the time of planting out in April and the most undoubtful specimens of *rubrinervis* were counted and destroyed. All the others were planted out and tried at the time of flowering in August. By this means the space required for the cultures was reduced to about one-half of what would have been necessary if all the plants had been set out. Some losses were unavoidable and the percentage figures may be a little too small in ordinary cases. Only under favorable conditions do they come up to the amount of the theoretical expectation, namely, one-third of all the individuals. Since my question, however, was mainly to decide whether all specimens of *rubrinervis* split into this form and *deserens*, or whether there are also plants with a uniform progeny, I shall give the figures as I found them.

PERCENTAGE OF *O. deserens* AMONG CULTURES OF *O. rubrinervis*

Seeds of	Parent number	Number of specimens	Percentage of <i>deserens</i>	Mean	
Third generation in	1910....	1	60	10	19
	1913....	2	59	20	
	1913....	3	60	22	
	1914....	4	59	19	
	1914....	5	60	25	
	1914....	6	59	19	
	1914....	7	60	15	
Fourth generation in	1915....	1	89	16	18
	1915....	2	60	25	
	1915....	3	79	13	
	1915....	4	89	19	

In the first place, I shall now describe the main line of *O. rubrinervis*. Part of the seeds of the original mutant of 1895 had been preserved until 1905; they germinated sufficiently and gave the second generation. From this a third generation was derived in 1910, 1913, and 1914, and a fourth in 1913, 1914, and 1915. All the parents of these generations have been artificially fertilized by

⁵ Gruppenweise Artbildung, p. 143. 1913.

myself. In 1914 I observed for the first time a specimen of *deserens* among these cultures, and this in a third generation. Thereupon I sowed in 1916 the self-fertilized seeds of 11 specimens in order to decide whether all of them would repeat the splitting and to determine roughly the percentage of the new type. The results are given on page 5. From these figures we see that all the specimens tried show the same splitting, and that this is always a mass mutation.

The countings for this table were partly made in the stadium of the young rosettes and partly at the time of flowering. In order to prove the correctness of this process, I repeated the sowings in 1917 for those of the parents of which sufficient seed had been preserved, planted out all of their seedlings, and counted them in August, when they were ripening their first fruits. The results are as follows:

Seeds of	Parent number	Number of specimens	Percentage of <i>deserens</i>	Mean
Third generation in 1913....	2	48	15	16
1914....	4	55	24	
1914....	6	59	13	
1914....	7	53	13	
Fourth generation in 1915....	1	58	14	
1915....	4	57	19	

Although the cultures were but small, they show that the deviations from the theoretically expected result (25 per cent) do not depend upon the method of counting as used in 1916.

In this race I self-fertilized the first mutant *deserens* observed in 1914 and derived from it a second and a third generation in 1915 and 1916. The second generation consisted of 95 plants, of which 50 flowered; the third was derived from two parents and embraced 77 and 140 specimens, among which 60 and 60 were left to flower. All of these cultures were wholly uniform at the time of planting out as well as during the flowering period. No *rubrinervis* and no new mutants occurred among them. Thus *O. deserens* is seen to constitute a pure and uniform race.

The percentage of empty grains among the seeds has been given elsewhere for this race of *O. rubrinervis*.⁶ The determination was made in the harvest of 5 plants of the third generation grown in

⁶ Zeitschr. f. Ind. Abst. 16:262. 1916.

1910 and 1915, and in that of two specimens of the fourth generation of 1915. I found 53–68 per cent of germs, with a mean of 60 per cent. Among the specimens of *deserens*, quoted in the same table, 5 belonged to this race; their seeds contained 96, 99, 94, 83, and 58 per cent of good germs. Thus we see that the empty grains, which are a character of *O. rubrinervis*, have disappeared almost wholly in the new mutant.

My second strain of *O. rubrinervis* was derived from another mutant of 1895. It has not been used for any crosses except those mentioned in this article, and which served as control for the experiments in the main line. Part of the seeds of 1895 were sowed in 1907 and yielded a second generation from which a third has been derived in 1913 and a fourth in 1914. I counted the *deserens* for three parent plants as previously described and found the percentages as follows:

PERCENTAGE OF *O. deserens* IN CULTURES OF *O. rubrinervis*

Seeds of	Culture	Number of specimens	Percentage of <i>deserens</i>	Mean
Second generation in 1910....	1913	25	28	19
Third generation in 1913....	1914 (A)	70	14	
Third generation in 1913....	1914 (B)	70	16	

The results agree exactly with those deduced from the previous table. The suspicion, however, that in the two last cases the percentage figures were found too low, on account of losses of specimens of *deserens* at the time of planting out, induced me to repeat these sowings in 1916 from preserved seeds, giving them all the care which the previous cultures and the first ones of 1916 had shown to be necessary. Moreover, in 1913 I had self-fertilized a third plant, besides the two mentioned in the table, and also sowed its seeds. In this way I got in 1916 the following percentages for the seeds of the three self-fertilized plants of 1913:

PERCENTAGES OF *O. deserens* IN CULTURES OF *O. rubrinervis*, STRAIN B

Seeds of third generation	Number of specimens	Number of <i>deserens</i>	Percentage of <i>deserens</i>	Mean
Plant A.....	84	32	38	30
B.....	90	25	28	
C.....	98	22	25	

The result confirms the expectation and shows that the figures given in the former table, although they give proof of the occurrence of mass mutation among the offspring of every plant of *rubrinervis*, are too low for the appreciation of the exact percentage of *deserens*. This must be estimated at about 30 per cent, or almost one-third of the whole progeny. In this race I self-fertilized three mutants in 1913 and two specimens of *deserens* among their offspring in 1915. I cultivated 150+84+180 specimens of the first group and left about one-half of them to flower, and 70+89 plants of the second group, all of which flowered in 1916. I had 573 plants in all, among which 319 bore flowers and fruits. They were all uniformly *deserens*, showing the marks of the type as previously described. No specimens of *rubrinervis* and no new mutants were observed among them. For one mutant of 1913 and for two plants of the second generation in 1915 I determined the amount of germs in the seeds and found 97-96 and 98 per cent, or an almost total absence of empty grains.

Besides the two described families of *O. rubrinervis* I have controlled the seeds of some mutants in order to know whether all of them contained specimens of *O. deserens* and in percentages pointing to mass mutation. I found the following figures:

PERCENTAGE OF *deserens* AMONG THE OFFSPRING OF
MUTANTS

Mutant <i>rubrinervis</i> from	Number of offspring	Percentage of <i>deserens</i>
<i>O. Lamarckiana</i> , 1910.....	25	12
<i>O. Lamarckiana</i> , 1910.....	60	15
<i>O. pallescens</i> , 1911.....	25	16

The strain of *O. Lamarckiana* was derived from a rosette found in the original station near Hilversum in 1905, and the *pallescens* had been a mutant from this same strain.⁷ Although the cultures were small, they prove the existence of mass mutation. I sowed the seeds of a specimen of *deserens* from the first culture in 1914, cultivated 25 flowering plants, and found these uniform with the type of their parent.

⁷ New dimorphic mutants of the *Oenotheras*. BOT. GAZ. 62:262. 1916.

Summing up the results of all the tables, we may conclude that all specimens of *O. rubrinervis*, derived from various sources, and the mutants as well as their offspring, show mass mutation into *O. deserens*, besides a considerable number of empty seeds. Taking into consideration the unavoidable losses in the numerical estimations, we may further conclude that *O. rubrinervis* produces about one-fourth empty seeds, and among the living offspring about one-third *O. deserens*, which are constant in their progeny and have no empty grains, or almost none. This points to a relation of 1:2:1 for the whole harvest. The phenomenon is thus shown to be parallel to the splitting of the hybrid mutant of *O. gigas nanella* and to the mass mutability of *O. grandiflora* and of *O. Lamarckiana* itself.

CROSSES BETWEEN *O. RUBRINERVIS* AND *O. DESERENS*.—If this explanation is true, it may be confirmed by means of crossing *O. rubrinervis* with its mass mutant. The sexual cells of the first are about one-half *deserens* without a lethal factor, and the rest *velutina* provided with such a factor; those of *O. deserens*, however, are uniformly so. We must expect, therefore, a splitting into almost equal parts of $deserens \times deserens = O. deserens$, and of $velutina \times deserens = O. rubrinervis$. I made both the reciprocal crosses in 1915, cultivated 58 and 50 specimens of their offspring in 1916, and counted them at the beginning of the flowering period in July, finding as follows:

	Percentage of <i>rubrinervis</i>	Percentage of <i>deserens</i>
<i>O. rubrinervis</i> × <i>O. deserens</i> . .	48	52
<i>O. deserens</i> × <i>O. rubrinervis</i> . .	78	22

The two types of hybrids resembled their parents exactly, and the figures point to numerical equality of the two groups, although the cultures were only small. Thus we see that the expectation from our formula is confirmed by the experiment.

TWIN HYBRIDS OF *O. RUBRINERVIS*.—The twin hybrids of *O. Lamarckiana* and *O. grandiflora* are now explained as the result of the mass mutation of these species, but the experimental proof is not complete as yet because neither of these species is known to occur without that form of mutation. In this respect the case of

O. rubrinervis is far stronger, since its two constituents are both represented in my cultures. This fact makes a complete analysis possible, as I have already pointed out. If *O. rubrinervis* is split by some cross into *laeta* and *velutina* on account of its composition of gametes of *deserens* and *velutina*, then the corresponding cross with *O. deserens* must evidently give the same *laeta* and that with *O. Lamarckiana* mut. *velutina* the same *velutina*. Thus the split progeny can be duplicated by the addition of its components.

I have described the splitting crosses in *Gruppenweise Artbildung* (pp. 122, 196-200, 1913) and repeated some of them so as to have the dimorphic progeny together with the cultures of the presumed constituents, in order to be able to identify their characters during the whole time of their development. The percentage figures given in my book are as follows:

TWIN HYBRIDS OF *O. rubrinervis*

Cross	Percentage of <i>laeta</i>	Percentage of <i>velutina</i>
<i>O. biennis</i> × <i>rubrinervis</i>	30-49	51-70
<i>O. rubrinervis</i> × <i>O. biennis</i> Chicago . .	39-44	56-61
<i>O. rubrinervis</i> × <i>O. Cockerelli</i>	49	51
Mean	42	58

In the second and third generation of the two latter crosses the *laeta* have split off brittle *rubrinervis* in about one-third of the cultures, whereas the *velutina* remained constant.

I repeated the two first named crosses in 1915, but not the third one. On the other hand, I have repeated the cross with *O. Hookeri*, in the progeny of which I had previously not been able to distinguish the twin types. I had the following cultures in 1916. Most of these plants flowered in August.

TWIN HYBRIDS OF *O. rubrinervis*; CULTURES OF 1916

Cross	Number of specimens	Percentage of <i>laeta</i>	Percentage of <i>velutina</i>
<i>O. biennis</i> × <i>rubrinervis</i>	59	46	54
<i>O. rubrinervis</i> × <i>O. biennis</i> Chicago	60	53	47
<i>O. Hookeri</i> × <i>rubrinervis</i>	60	20	80
Mean	40	60

The results coincide with the previous ones as nearly as might be expected. The types of the twins were the same as those in the older cultures.

For these twins I have determined the amount of empty grains, self-fertilizing two specimens of each of them in August 1916 and counting out 100 seeds for each parent.

PERCENTAGE OF GERMS IN SEEDS OF *laeta* AND *velutina*

Cross	Parent number	<i>laeta</i>	<i>velutina</i>
<i>O. biennis</i> × <i>rubrinervis</i>	1	93	3
	2	96	4
<i>O. rubrinervis</i> × Chicago	1	94	28
	2	95	31
<i>O. Hookeri</i> × <i>rubrinervis</i>	1	94	59
	2	95	71

As in other cases, the seeds of the *laeta* hardly contain any empty grains, whereas those of the *velutina* are often badly developed.

My task was now to repeat these crosses, substituting *O. mut. deserens* and *O. mut. velutina* for *O. rubrinervis*. The latter group of crosses have already been described elsewhere;⁸ they yielded pure cultures of *velutina* which in every case were exactly like the *velutina* of the corresponding cross with *O. Lamarckiana*. The crosses with *O. deserens* were made in 1915 and their progeny studied in 1916; it was in every case wholly uniform.

CROSSES OF *O. MUT. deserens*

Cross	Number of specimens	Type
<i>O. biennis</i> × <i>deserens</i>	60	<i>O. (bien. × Lam.) laeta</i>
<i>O. syrticola</i> × <i>deserens</i>	70	<i>O. (syrtic. × Lam.) laeta</i>
<i>O. Hookeri</i> × <i>deserens</i>	60	<i>O. (Hook. × Lam.) laeta</i>
<i>O. deserens</i> × <i>biennis</i> Chicago	70	<i>O. (Lam. × Chic.) laeta</i>

About one-half of each culture flowered and developed their fruits. For each culture a control parcel was cultivated with the *laeta* from the corresponding cross with *O. Lamarckiana*, and they were compared during all the time of their development. I could

⁸ Kreuzungen von *Oenothera Lamarckiana* mut. *velutina*. Zeitschr. f. Ind. Abst. 17:1917.

not find any differences. The descriptions for the *deserens laeta* are exactly the same as those given previously for the *Lamarckiana laeta*. Although I have not made the cross *O. syrticola* × *O. rubrinervis*, I have added the second experiment of the table. From this and the result of *O. syrticola* × *O. blandina* (mut. *velutina*) described in my former article the result of the cross *O. syrticola* × *rubrinervis* may be predicted, and so it would be in other cases also.

Summing up the results of these experiments, we see that in producing twin hybrids *O. rubrinervis* is split in exactly the same way as an artificial mixture of about equal parts of gametes of *O. deserens* and *O. mut. velutina* would be. The conclusion that its gametes really possess this dimorphy is thereby as clearly proven as might be expected.

CROSSES OF *O. RUBRINERVIS* WITH *O. LAMARCKIANA* AND ITS DERIVATIVES.—In *Gruppenweise Artbildung* I have described the first generation of these crosses as consisting of two types, *O. Lamarckiana* and *O. hybr. subrobusta*. The latter is a *rubrinervis* in which the brittleness fails, and thereby very similar to our new mut. *erythrina*,⁹ but this similarity is only an external one, since after self-fertilization the hybrid *subrobusta* splits off, as a rule, brittle *rubrinervis* plants, whereas the *erythrina* produces the *decipiens*, which is not brittle. Shortly after publishing my book, however, I discovered in the summer of 1913, among the progeny of a cross of *O. rubrinervis* and *O. Lamarckiana*, a slight difference among the *Lamarckiana*-like plants. Some of them were stouter and had broader and less crinkled leaves than the others. I self-fertilized them and got a culture, which, although not uniform, repeated the deviating marks of the parental type in the majority of the individuals. I shall call this hybrid type *lucida*. Moreover, in making a large number of crosses of individuals of the same family of *rubrinervis* with *Lamarckiana* plants from various sources, as well as different mutant strains, I discovered that the second hybrid type is not always the solid *subrobusta*, but sometimes the brittle *rubrinervis*. I have not as yet discovered why this should be so. We should expect the brittleness to be recessive to the production of

⁹ Zeitschr. f. Ind. Abst. 16:262. 1916.

strong fibers, and as a rule it is so, but not always. The two contrasting cases have occurred mainly in strains derived from different initial plants, and some hidden mutation might be responsible for the dominance of the brittleness. This seems to be the case at least in *O. nanella*, but the number of crosses in each of my different families of dwarfs is too small to decide whether this is the real cause. Crosses of *O. rubrinervis* with other mutants than the dwarfs have also given sometimes the brittle form and sometimes the *subrobusta* for the second hybrid.

If we keep in mind that the hybrid *rubrinervis* is only a brittle form of the hybrid *subrobusta*, and that the one may be substituted for the other for unknown reasons, the following descriptions will easily be understood. I might add, however, that from a single cross between two individual parents both types never arise simultaneously in the first generation. In the succeeding generations the *rubrinervis* as a rule are constant, whereas the *subrobusta* may split off the brittle form.

If we assume the gametes of *O. Lamarckiana* to consist of equal parts of typical ones and of *velutina*, and those of *O. rubrinervis* to consist of *deserens* and *velutina*, *O. Lamarckiana* × *O. rubrinervis* must yield 25 per cent *typica* × *deserens*, 25 per cent *typica* × *velutina*, 25 per cent *velutina* × *deserens*, and 25 per cent *velutina* × *velutina*. The last combination will produce empty grains, since the same lethal factor comes in from both sides; on the other hand, the three first named combinations must give viable seeds. *Typica* × *velutina* is the formula for *O. Lamarckiana*, and *velutina* × *deserens* that for *O. rubrinervis* and *subrobusta*, and so the occurrence of these hybrid types is easily explained. The remaining combination *typica* × *deserens* must then be assumed to give the new hybrid *lucida*, and this can be verified by crossing *O. deserens* with *O. Lamarckiana*. All these deductions are, of course, the same for the reciprocal crosses. If these deductions are reliable, they show that the polymorphy of the first generation of hybrids between the two older forms is due to the combination of their capacities to produce twins in other crosses. In other words, it is a natural sequence of their secondary mutability. I shall now describe the experiments which seem to me to justify these deductions.

O. Lamarckiana × *O. rubrinervis*.—According to the deductions just given the expectation for this cross is

$$\begin{aligned}
 &O. \textit{Lamarckiana} \times O. \textit{rubrinervis} = \\
 &(\textit{typica} + \textit{velutina}) \times (\textit{deserens} + \textit{velutina}) = \\
 &\textit{typ.} \times \textit{des.} + \textit{vel.} \times \textit{des.} + \textit{typ.} \times \textit{vel.} + \textit{vel.} \times \textit{vel.} = \\
 &\textit{lucida subrobusta Lamarckiana empty grains} \\
 &\quad \text{or} \\
 &\quad \textit{rubrinervis}
 \end{aligned}$$

In the first place, I determined the amount of empty grains, using the same method as in previous cases.

Cross	Parent number	Cross	Percentage of germs
<i>O. Lamarckiana</i> × <i>rubrinervis</i>	1	1913	21
	2		29
	3		33
<i>O. rubrinervis</i> × <i>Lamarckiana</i>	1	1913	48
	2		60

The presence of empty grains is thereby proven, although the percentages of germs are much smaller than would be expected; but this may be due to quite different causes, as has been shown elsewhere.

In the second place, I studied the living progeny for the fourth cross of this table and for a cross made in 1907 with another strain of *O. Lamarckiana*. Each of these cultures was trimorphous, containing the types *Lamarckiana* and *lucida*, and besides these either *subrobusta* or *rubrinervis* (that is, tough or brittle).

CROSS	NUMBER OF SPECIMENS	PERCENTAGE OF		
		<i>Lamarckiana</i>	<i>lucida</i>	<i>subrobusta</i> or <i>rubrinervis</i>
<i>O. rubrinervis</i> × <i>Lamarckiana</i>	1913	32	20	48 <i>rubrinervis</i>
	1907	40	6	54 <i>subrobusta</i>
Mean.....	36	13	51

The expectation would be for equal parts, but for some unknown reason the *lucida* almost always fall short of this. Apart from this difficulty the results of these cultures coincide with the theoretical

deductions from our formula. I have made quite a number of further crosses between these two forms, partly in 1905 and partly in 1913, using always the same family of *rubrinervis*, and taking the combinations in both reciprocal directions. Six of them have given for the third hybrid type *rubrinervis* and three of them *subrobusta*; but since I have not determined the amount of *lucida* among them, it is of no use to give the percentage figures.

The exactness of the identification of the types in the formula can be controlled by direct crosses with the constituents mut. *deserens* and mut. *velutina*. The latter has been described under the synonym *O. blandina*. I made the following combinations:

CROSS	YEAR	NUMBER OF PLANTS	PERCENTAGE OF		
			<i>lucida</i>	<i>subrobusta</i>	<i>velutina</i>
<i>O. deserens</i> × <i>Lamarckiana</i>	1915	49	18	82	0
<i>O. rubrinervis</i> × <i>blandina</i>	1915	70	0	50	50
<i>O. blandina</i> × <i>rubrinervis</i>	1913	70	0	53	47
<i>O. deserens</i> × <i>blandina</i>	1915	70	0	100	0
<i>O. blandina</i> × <i>deserens</i>	1915	49	0	100	0

The expectation for these crosses was:

- O. deserens* × *Lamarckiana* = *O. deserens* × (typ. + *velutina*) = *lucida* + *subrobusta*
O. blandina × *rubrinervis* = *O. blandina* × (*deserens* + *velutina*) = *subrobusta* + *velutina*
O. blandina × *deserens* = *O. blandina* × (*deserens*) = *subrobusta*

Apart from the figure for *lucida*, which is too small, the results of the experiments directly confirm the expectation. I have determined the amount of empty seeds for the four last named crosses, and found almost none:

Cross	Percentage of germs in seeds
<i>O. rubrinervis</i> × <i>blandina</i>	97
<i>O. blandina</i> × <i>rubrinervis</i>	91
<i>O. deserens</i> × <i>blandina</i>	100
<i>O. blandina</i> × <i>deserens</i>	90

Moreover, I made the same determinations for the hybrids from the two first named of these crosses, self-fertilizing them in 1916. For the two latter crosses it was evident that the hybrids would

hardly have any empty grains, and I did not think it necessary to control this.

CROSS	PARENT NUMBER	PERCENTAGE OF GERMS IN SEEDS OF	
		<i>subrobusta</i>	<i>velutina</i>
O. rubrinervis × blandina.....	1	96	70
	2	97	75
	3	99	76
	4	97	68
O. blandina × rubrinervis.....	1	96	75
	2	96	80
	3	96

The *laeta* have hardly any empty grains, but the figures for *velutina* fall short of this, even as in other instances. In the last place, I counted the germs in the hybrids of the crosses with *Lamarckiana*, self-fertilizing their specimens of each of the types:

CROSS	PARENT NUMBER	PERCENTAGE OF GERMS IN SEEDS OF		
		<i>lucida</i>	<i>Lamarckiana</i>	<i>rubrinervis</i>
O. rubrinervis × Lamarckiana.....	1	87	25	53
	2	91	34	59
	3	94	93	65
O. deserens × Lamarckiana.....	1	85
	2	86

The *lucida* have almost no empty grains; the figures for hybr. *rubrinervis* are the same as those for the mutant of that name, but those for the *Lamarckiana* type give an unexpected result. In two cases they are the same as for the species, but in the third the empty grains have almost wholly disappeared. This latter specimen has lost all the external marks of *O. deserens* and *O. rubrinervis*, but kept the absence of the lethal factors. Its progeny splits into *Lamarckiana*, *lucida*, and *rubrinervis*, and the first of these forms repeats the splitting in the following generation.

O. LAMARCKIANA NANELLA × RUBRINERVIS.—As in so many other cases, the crosses with dwarfs can give a verification of those with the species itself. In *Gruppenweise Artbildung* (p. 215) I have

described the pedigrees of two reciprocal crosses, both of which produced as a second hybrid the *subrobusta*. This was seen to split off, after self-fertilization, brittle plants and dwarfs. In 1915 I sowed some seeds of the *subrobusta* plants of 1907 mentioned in those tables, in order to compare their progeny with my newer cultures. I found for two specimens of *O. (nanella × rubrinervis) subrobusta* 38 and 45 per cent of dwarfs among 82 and 60 plants, and for two parents *O. (rubrinervis × nanella) subrobusta* 20 and 13 per cent of dwarfs among 60 and 46 individuals. The number of brittle plants, however, was very small, being two specimens for the first and one for the reciprocal group. It is possible that the germs of this type are weaker, and that some of them had died during the 7 years of their preservation. I self-fertilized one brittle specimen in each of the two main groups and had in 1916 two lots of 45 and 60 flowering plants, all of which were brittle and like their parents. They contained 9 and 8 per cent of dwarfs, the stems of which were likewise brittle at the time of flowering.¹⁰

Other races of *O. nanella* or other conditions may produce in the corresponding crosses brittle hybrids instead of *subrobusta*. I made the cross *O. rubrinervis × nanella* in 1905 with a dwarf mutant race of 1895 and the reciprocal one with the progeny of a dwarf which had arisen in 1911 from *Lamarckiana*, using in both cases the same family of *rubrinervis* as in all previous crosses. The first named cross gave 35 per cent *Lamarckiana*, 3 per cent *lucida*, and 62 per cent brittle *rubrinervis* among 68 specimens in 1913. The second cross yielded the same three types, but the percentage figures deviated widely. I had only 6 per cent *Lamarckiana* and 2 per cent *lucida*, but 92 per cent brittle *rubrinervis* among 140 plants, most of which flowered in August. The main result, however, is clear, namely, that the crosses between *O. rubrinervis* and *O. nanella* give three types of viable hybrids, one of which carries the visible marks of *O. rubrinervis*, but may be either brittle or tough.

I have made only one cross between *O. deserens* and a dwarf, taking this latter from the first of the two last mentioned families.

¹⁰ By means of this the gap left in the second pedigree of p. 215 of my book is filled up, and both pedigrees are completed by the production of dwarfs from the *rubrinervis* specimens.

I crossed them in 1915 and had in 1916 a culture of 60 plants, among which 3 per cent were *lucida* and 97 per cent brittle *rubrinervis*. Other types failed, as was to be expected. The seeds of the two *lucida* plants contained 89 and 95 per cent of good germs.

Summing up the results of the crosses between *O. rubrinervis* and *O. nanella*, we see that they yield exactly the same hybrid types as those with *O. Lamarckiana* and in corresponding percentages.

CROSSES OF *O. RUBRINERVIS* WITH HETEROGAMIC MUTANTS.— Crosses with the pollen of these forms must simply confirm those with *O. Lamarckiana*, since their pollen carries mainly the same hereditary qualities as that of the parent species. I fertilized in 1913 two plants of my main race of *O. rubrinervis* with *O. cana*, two with the pollen of the *Lamarckiana*-like offspring of self-fertilized *scintillans*, and added the reciprocal cross of the latter combination. In the following table I shall call these offspring *scintillans-Lamarckiana*.

CROSSES OF *O. rubrinervis* WITH HETEROGAMIC MUTANTS

CROSS	NUMBER OF SPECIMENS	PERCENTAGE OF		
		<i>Lamarckiana</i>	<i>lucida</i>	<i>subrobusta</i>
<i>O. rubrinervis</i> × <i>cana</i>	60	32	38	30
<i>O. rubrinervis</i> × <i>cana</i>	57	53	32	15
<i>O. rubrinervis</i> × <i>scintillans-Lamarckiana</i>	60	13	3	84
<i>O. rubrinervis</i> × <i>scintillans-Lamarckiana</i>	60	7	10	83
<i>O. scintillans-Lamarckiana</i> × <i>rubrinervis</i>	84	7	4	89
<i>O. scintillans-Lamarckiana</i> × <i>rubrinervis</i>	34	15	9	76

About one-half of each group flowered in August. No brittle specimens occurred. The types were exactly the same as those derived from the cross between *O. rubrinervis* and *O. Lamarckiana*.

If the heterogamic types are used as female parents, the splitting of course will be more complicated. I fertilized a strong biennial specimen of *O. scintillans* with the pollen of a plant of *O. rubrinervis* and had in 1916 a culture of only 23 plants, all of which flowered in August. There were 5 types: 11 *Lamarckiana*, 2 *lucida*, 1 *sub-*

robusta, 9 *scintillans*, and 8 *oblonga*. The first three were the same as in previous crosses and confirm their result; the last two named types are the same as are always seen in the first generation of crosses of *O. scintillans* when this is used as the seed parent.

Moreover, in 1915 I fertilized 4 plants of my race of *O. lata* with *O. rubrinervis*, counted the *lata* and *albida* in their progeny in May 1916, and for want of space planted out only a part of the others, in order to distinguish the types, but without trying to determine percentage figures. Altogether I had 434 seedlings, among which 7 per cent were *lata* and 6 per cent *albida*. At the time of flowering I counted 23 *Lamarckiana*, 1 *lucida*, 20 brittle *rubrinervis*, besides 11 mutants (5 *oblonga*, 5 *obovata*, and 1 *scintillans*). No *subrobusta* occurred in these cultures. These results confirm those previously given.

SECOND AND LATER GENERATIONS.—Brittleness and dwarfish stature are recessive characters, and as such may be expected to be split off in the succeeding generations. For the crosses between *O. rubrinervis* and *O. nanella* this splitting has already been dealt with. For the other crosses our analytical formula for *O. Lamarckiana* × *rubrinervis* shows that the types *lucida* and *subrobusta* may be expected to produce a splitting, whereas the *Lamarckiana*-like hybrids cannot contain the necessary factors. The production of brittle plants from *subrobusta* had been observed in the case of the dwarfs, and so I studied in 1916 the progeny of three specimens of *lucida* from previous crosses.

SPLITTING PROGENY OF *O.* HYBR. *lucida*; CULTURES OF 1916

LUCIDA FROM	NUMBER OF SPECIMENS	PERCENTAGE OF	
		Tall plants	<i>deserens</i>
<i>O. rubrinervis</i> × <i>scintillans</i>	67	52	48
<i>O. rubrinervis</i> × <i>scintillans</i>	56	80	20
<i>O. rubrinervis</i> × <i>Lamarckiana</i>	106	53	47
Mean.....	62	38

Moreover, in 1916 I self-fertilized some specimens of *lucida* taken in the first generations of the crosses mentioned, sowed their seeds in 1917, cultivated all the seedlings until the time of ripening their first fruits, and counted them repeatedly during the summer. The

difference between the *deserens* and the *lucida* was very striking, the first reaching only half the height of the latter. I have broken the stems of all the plants in August, at the time of the last counting, and found all the *deserens* brittle and all the tall ones tough. The first were evidently *deserens* and not *rubrinervis*, as seen by the characters described for these two types. Among the tall ones, however, I have not succeeded in finding any difference, the type of *lucida* prevailing to the apparent exclusion of that of *O. Lamarckiana*. For each of the crosses mentioned in the following table I had 58-60 flowering specimens in August.

SPLITTING PROGENY OF HYBRID *lucida*; CULTURE OF 1917

LUCIDA FROM	PARENT NUMBER	PERCENTAGE OF	
		Tall plants	<i>deserens</i>
<i>O. rubrinervis</i> × <i>O. Lamarckiana</i>	1	50	50
	2	60	40
	3	48	52
<i>O. deserens</i> × <i>O. Lamarckiana</i>	1	55	45
	2	39	61
<i>O. deserens</i> × <i>O. nanella</i>	1	51	49
	2	41	59
Mean	49	51

Oenothera Lamarckiana* mut. *oblonga* and mut. *nanella

Our conception of *Oenothera rubrinervis* as a half mutant may be applied to *O. oblonga*, and explain its behavior in crosses in an analogous way. The main difference, as I have pointed out in *Gruppenweise Artbildung*, is that some types of hybrids, as we might expect, are constantly absent or suppressed, as I called it. If we assume this suppression to take place in the pollen before fecundation, the remaining phenomena are easily explained on this basis. It will be sufficient to review the facts given in my book, and to combine them with the results of some determinations of the amount of barren grains in the seeds of self-fertilized and crossed individuals.

The amount of empty seeds is about the same in *O. oblonga* as in *O. Lamarckiana*. For the cultures of 1911, mentioned in my book, I found among the seeds of two self-fertilized individuals 25 and 33 per cent of germs. Seeds of biennial plants collected in 1913 contained 30-18 and 17 per cent of germs; but seeds of annual

plants, saved in 1914 on two new mutants from *O. Lamarckiana* and on one from *O. cana*, gave only 6-5 and 6 per cent of germs. Annual specimens are always much weaker than biennial ones, and their fruits are often thin instead of club-shaped. These figures evidently point to a complete analogy with *O. Lamarckiana*.

The question whether the lethal factors are the same as in *O. Lamarckiana* may be answered by crosses with this species. I tried the seeds of a cross *O. oblonga* × *Lamarckiana*, of one of *O. oblonga* × *nanella*, both made in 1911, and of a cross of 1913 of *O. oblonga* × *O. cana*. I found 53-40 and 34 per cent of good germs. The figures do not essentially differ from those found for self-fertilized *Lamarckiana*, and thereby show that the lethal factors must be the same and simply inherited by *O. oblonga* from its parent species without change.

The ovules which produce empty grains after self-fertilization may develop into normal seeds after crosses with other species, even as in the case of *O. Lamarckiana* itself. *O. oblonga* × *biennis* gave 92 per cent of germs, *O. oblonga* × *atrovirens (cruciata)* 87 per cent, *O. oblonga* × *Hookeri* 90 per cent, and *O. syriicola (muricata)* × *oblonga* 90 per cent. Thus we see that in this respect also the lethal factors are the same as in *O. Lamarckiana*.

Our assumption is that *O. oblonga* arises by means of a mutation in the *Lamarckiana* gametes of our species, leaving the *velutina* gametes unchanged. The formula for self-fertilization, assuming the *oblonga* gametes to be suppressed in the pollen before fecundation, is as follows: (obl. + velu.) × velu. = obl. × velu. + velu. × velu. This explains the constancy of the mutant, since the *velutina* × *velutina* germs contain the same lethal factor on both sides and thus produce the empty grains. If we compare this formula with the results of the crosses described in my book (pp. 266-267), we find a complete harmony, as I shall now try to show.

Fertilized by *O. Lamarckiana* and analogous mutants, *O. oblonga* must give (obl. + velu.) × (Lam. + velu.) = obl. × Lam. + obl. × velu. + velu. × Lam. + velu. × velu. = 25 per cent empty grains + 25 per cent *oblonga* + 25 per cent *Lamarckiana* + 25 per cent empty grains. The expectation is therefore for two types and these in equal proportions. The two types always appeared, and no others besides

them, but the percentage figures are very variable. I found them as follows:

CROSS	PARENT NUMBER	PERCENTAGE OF	
		<i>oblonga</i>	<i>Lamarckiana</i>
<i>O. oblonga</i> × <i>Lamarckiana</i>	1	4	93
<i>O. oblonga</i> × <i>Lamarckiana</i>	2	4	96
<i>O. oblonga</i> × <i>Lamarckiana</i>	3	14	85
<i>O. oblonga</i> × <i>nanella</i>	1	15	80
<i>O. oblonga</i> × <i>nanella</i>	2	46	14
<i>O. oblonga</i> × <i>scintillans</i>	1	81	17

The reciprocal crosses cannot produce any *oblonga*, since this is assumed to be suppressed in the pollen. The only exception is *O. scintillans*, which gives rise to a high amount of *oblonga* after self-fertilization, and therefore may produce the same mutant after a cross. I found as follows:

CROSS	PERCENTAGE OF	
	<i>oblonga</i>	<i>Lamarckiana</i>
<i>O. Lamarckiana</i> × <i>oblonga</i> ...	0	100
<i>O. nanella</i> × <i>oblonga</i>	0	100
<i>O. lata</i> × <i>oblonga</i>	0	100
<i>O. scintillans</i> × <i>oblonga</i>	18	82

The pollen of *O. oblonga* must produce, after crosses with different species, only *velutina*, as is easily seen from our formula. No *oblonga* and no *laeta* are to be expected. *O. biennis*, *O. syrticola*, *O. Cockerelli*, and *O. Hookeri* fecundated with *O. oblonga* uniformly gave this result. The reciprocal crosses, however, must give a splitting, the *laeta* hybrids assuming the characters of *O. oblonga*. The percentages should be about 50, but in my experiments there was much fluctuation in this respect. I found as follows:

CROSS	PARENT NUMBER	PERCENTAGE OF	
		<i>oblonga</i>	<i>velutina</i>
<i>O. oblonga</i> × <i>biennis</i> Chicago.....	1	8	92
<i>O. oblonga</i> × <i>biennis</i> Chicago.....	2	16	84
<i>O. oblonga</i> × <i>biennis</i> Chicago.....	3	38	62
<i>O. oblonga</i> × <i>Cockerelli</i>	1	41	59
<i>O. oblonga</i> × <i>Hookeri</i>	1	11	89
<i>O. oblonga</i> × <i>Hookeri</i>	2	24	75

Crosses with *O. rubrinervis* also yield the expected result. This would be in one direction (obl. + velu.) \times (deserens + velu.) = obl. \times des. + obl. \times velu. + velu. \times deserens + velu. \times velu. = 25 per cent (obl. \times des.) + 25 per cent *oblonga* + 25 per cent *rubrinervis* + 25 per cent empty grains. I have not as yet tried the cross between *O. oblonga* and *O. deserens*, however, and thus must leave undecided the question as to which characters will dominate in this hybrid. As a matter of fact, I found 20 per cent *oblonga* and 80 per cent *rubrinervis* and no other types. The reciprocal cross must give (des. + velu.) \times *velutina* = des. \times velu. + velu. \times velu. = 50 per cent *rubrinervis* + 50 per cent empty grains. Only *rubrinervis* have been observed in this culture.

Crosses with the pollen of *O. biennis* must give *oblonga* \times *biennis* + *velutina* \times *biennis*. The former is intermediate between the parents, whereas the second is the same as the hybrid type *Lamarckiana* \times *biennis*. I found in one cross 65 per cent *oblonga* (partly dwarfish) and 35 per cent hybrids of the second type. In another instance, however, the *oblonga* failed from some unknown reason.

With those species which ordinarily produce the twins *densa* and *laxa* the pollen of *O. oblonga* must evidently give only the latter type. This has been the case in three trials with *O. biennis* *Chicago* and in one with *O. atrovirens* (*cruciata*).

For further details and for the constancy or splitting in the second generation I must refer the reader to the pages of my book already quoted. These results, however, show clearly that all the facts hitherto ascertained confirm the formula assumed for the self-fertilization, and thereby the analogy with the phenomena observed in *O. rubrinervis*.

Summing up this discussion we may say, therefore, that *O. oblonga* arises through a mutation of the typical sexual cells of *O. Lamarckiana*, leaving the *velutina* gametes and also the lethal factors unchanged, but producing, besides the externally visible marks of the mutant, a suppression of the mutated pollen grains.

On the other hand, *O. mut. nanella* seems to arise through mutations in the *velutina* gametes of *O. Lamarckiana*, as is shown by the fact that the *laeta* do not split off dwarfs, whereas the *velutina* regularly do so. The figures given in my book for the crosses with *O. nanella* may be calculated in the same way, and

will be found to comply with the views proposed in this article. It would lead us too far, however, to reproduce these calculations here.

In all these cases the conception that mass mutation is the chief cause of the production of twin hybrids evidently makes the supposition of a labile condition of the factor for *laeta* superfluous. It seems desirable, therefore, to lay stress on the fact that this supposition does not rest on the phenomena observed in the production of these twins. It is mainly derived from other observations, and some of them may be briefly repeated here in order to make this point clear. They refer to the brittleness of *O. rubrinervis* and *O. deserens* and to the dwarfish stature of *O. nanella*.

In crosses brittleness behaves in three different ways. With *O. biennis* Chicago and *O. Cockerelli* it is recessive to the tough structure of the fibers, since it fails in the first generation and reappears in the second in ratios corresponding to Mendel's law. In crosses with *O. Lamarckiana* it is sometimes dominant and sometimes recessive, as has been shown. In *O. rubrinervis* and *O. deserens* the toughness is wholly absent. From these and other facts it is clear that at least three conditions of this factor are possible. I call them active, labile, and inactive. Whether the labile condition is due to linkage or to some other cause is as yet an open question, which, however, has no influence upon the main contention. The combination "active \times inactive" is assumed to be responsible for Mendelian crosses, but the combination "labile \times inactive" may cause a splitting in the first generation and produces, as a rule, constant hybrids. The two types of first generation hybrids appear in variable numerical proportions according to different circumstances. If one of the groups is so small as not to be represented in every 100 specimens, the splitting may seem to fail, and such extremes are of common occurrence. This would explain the dominance of an evidently recessive character.

The case is exactly the same for the dwarfish stature. The factor for tallness must be in the inactive condition in the dwarfs, but in the active condition in *O. rubrinervis*, since the crosses between these two types follow Mendel's law. In *O. Lamarckiana*,

however, it is labile, since tall and low specimens appear in the first generation of its cross with *O. nanella*. In many ternary crosses of hybrids of this mutant the dwarfish stature dominates over the tall condition, but the dominance is not always absolute and sometimes 3–5 per cent of tall specimens appear among the dwarfs, as I have shown in *Gruppenweise Artbildung*. This fact evidently supports our conception.

The conclusion from this discussion is that since brittleness and dwarfish stature are in some cases recessive to and in other cases dominant over their antagonists, these latter must be sometimes in the active and in other instances in the labile condition.

Summary

1. *Oenothera rubrinervis* is a half mutant, produced by the copulation of a mutated gamete with a normal *velutina* gamete of *O. Lamarckiana*.

2. In consequence, it produces about one-fourth empty grains, a mass mutation of about one-fourth pure or double mutants, and one-half specimens of *O. rubrinervis*, which will repeat the splitting.

3. The pure or double mutant is called *O. mut. deserens*. It is very similar to *O. rubrinervis*, but the leaves of its young rosettes and the bracts of its flower spike are broader and more even.

4. *O. mut. deserens* is constant from seed. It has no hereditary empty grains.

5. The formula for the self-fertilization of *O. rubrinervis* is therefore $O. (deserens + velutina) = des. \times des. + velu. \times velu. + des. \times velu.$ The first combination gives the mass mutation, the second the empty grains, the third the normal plants of *O. rubrinervis*.

6. In crossing with other species the two kinds of gametes will produce twin hybrids, as, for example, *laeta* and *velutina*. This assertion has been controlled by making the corresponding crosses of *O. mut. deserens* and *O. mut. velutina*. The first produce the *laeta* and the second the hybrid *velutina*. The result of a cross of *O. rubrinervis* is equal to the sum of these two crosses.

7. Outside of the mass mutability into *O. deserens*, *O. rubrinervis* is not known to mutate to any noticeable degree. This shows that

the internal constitution, which causes the mass mutation, is not in itself a cause for further mutability.

8. The constitution of the gametes of *O. rubrinervis* can directly be proven by a cross with *O. deserens*, since $O. rubrinervis = (deserens + velutina) \times O. deserens$ produces *O. deserens* and $(O. deserens \times velutina)$ or *rubrinervis*.

9. Crosses of *O. rubrinervis* with *O. Lamarckiana* give three types of hybrids, besides about one-fourth empty seeds. One type exactly resembles *O. Lamarckiana* and is constant in its progeny. A second type called *lucida* has broader and more shiny leaves, and after self-fertilization splits off brittle specimens. The third type is either *subrobusta* or *rubrinervis*, and in the first case may produce the brittle form in the second generation. All these phenomena are easily explained by the proposed formula for the constitution of *O. rubrinervis* as a half mutant. They were confirmed by means of crosses with *O. nanella* and some other mutants.

10. *O. oblonga* is quite analogous to *O. rubrinervis*, since it must arise through a mutation of the typical sexual cells of *O. Lamarckiana*, leaving the *velutina* gametes unchanged. Contrary to *O. rubrinervis*, however, the two lethal factors remain in their condition, and moreover the mutated gametes must be assumed to become suppressed in the pollen of the mutant.

11. *O. nanella* seems to arise through mutations in the *velutina* gametes of *O. Lamarckiana*, since after crosses with other species or mutants it is not split off by the *laeta* hybrids, but only by those of the type *velutina*.

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