MISCELLANEOUS PAPERS ON OENOTHERA

By

Hugo de Vries, H. H. Bartlett,
B. M. Davis, and R. R. Gates

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On atavistic Variation in Oenothera cruciata

By HUGO DE VRIES

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On atavistic Variation in Oenothera cruciata

By Hugo de Vries

After *Oenothera Lamarckiana* had shown itself to be a very proper material for the study of the mutations by which new species suddenly arise from old ones, I was naturally led to investigate whether in other plants similar mutations might not be met with. For it is clear that the phenomena shown by Lamarck's evening primrose are of prevailing interest only if they may be taken as an instance of a general rule. The other species of the same genus were of course the first to receive attention. Most of these showed no signs of being fit for a study along the same lines, while on the other hand one, *Oenothera cruciata*, was found to be inconstant in the very character to which it owes its name. At least the plant which is cultivated under this name in European botanical gardens is variable in this regard.

In proposing to bring the results of my experimental cultures of this plant before the readers of this journal, my aim is principally to direct their attention to any deviations which the species of the above-named genus might show in their native localities. For it is of undoubted interest to the study of mutability to know whether the variability which *Oenothera cruciata* displays with us is also met with in America, in those parts where the plant grows wild. The allied forms such as *O. biennis* and *O. muricata*, should be tested in the same direction. Any deviations from the original types should be carefully observed and if possible perpetuated by seeds. Wherever such deviations are found the question would have to be answered whether the general type of the locality possesses the power of again producing this deviation, and perhaps others too, in succeeding years.

Oenothera cruciata Nutt. or *Onagra cruciata* (Nutt.) Small, as it is also called, has been described and figured in Britton and Brown's "Illustrated Flora of the Northern United States, Canada and the British Possessions" (2 : 485. 1897). It is a rare plant, found wild from Vermont to New York and Massachusetts, and ascends to 2,000 feet in the Adirondacks. It is described as being annual and flowering from August to October. It may readily be recognized, even without flowers, by the narrowly oblong or oblanceolate leaves and the purple color of the nerves and the stem. The flowers are as small as those of *O. muricata*, but the spikes are much more slender and the fruits are less broad. In all these characters the European plants correspond exactly with the description given by Britton and Brown. The petals of the American type are linear instead of being broad and obcordate as in the allied species.

As yet I have not had an opportunity to cultivate the original wild species, but I hope to be able to do so next year, as I have obtained seeds from the Adirondacks through the kindness of Dr. D. T. MacDougal, of New York, and Dr. B. L. Robinson, of Cambridge, Mass.*

Dr. MacDougal had also the kindness to ask Dr. Britton about an eventual variability of the petals, but the celebrated author of the Illustrated Flora informed him that *Oenothera cruciata does not make broad petals* in America.

This is the essential point. For in all the cultures I have as yet been able to make from seeds of this species, sent to me from different botanical gardens in Europe, I found the form of the petals to be varying in a high degree, so as to reach, in many individuals, the same outline as is presented by the petals of the allied species, *O. biennis*, *O. muricata* and others.

For this reason, I presume that our plants are not the typical *O. cruciata* of Nuttall, but a variety, which perhaps has been produced from it in Europe. Therefore I have called my plants *O. cruciata varia*, merely in order to distinguish them from the pure species. How this variety may have originated of course I do not know. Two possibilities present themselves. The one is by mu-

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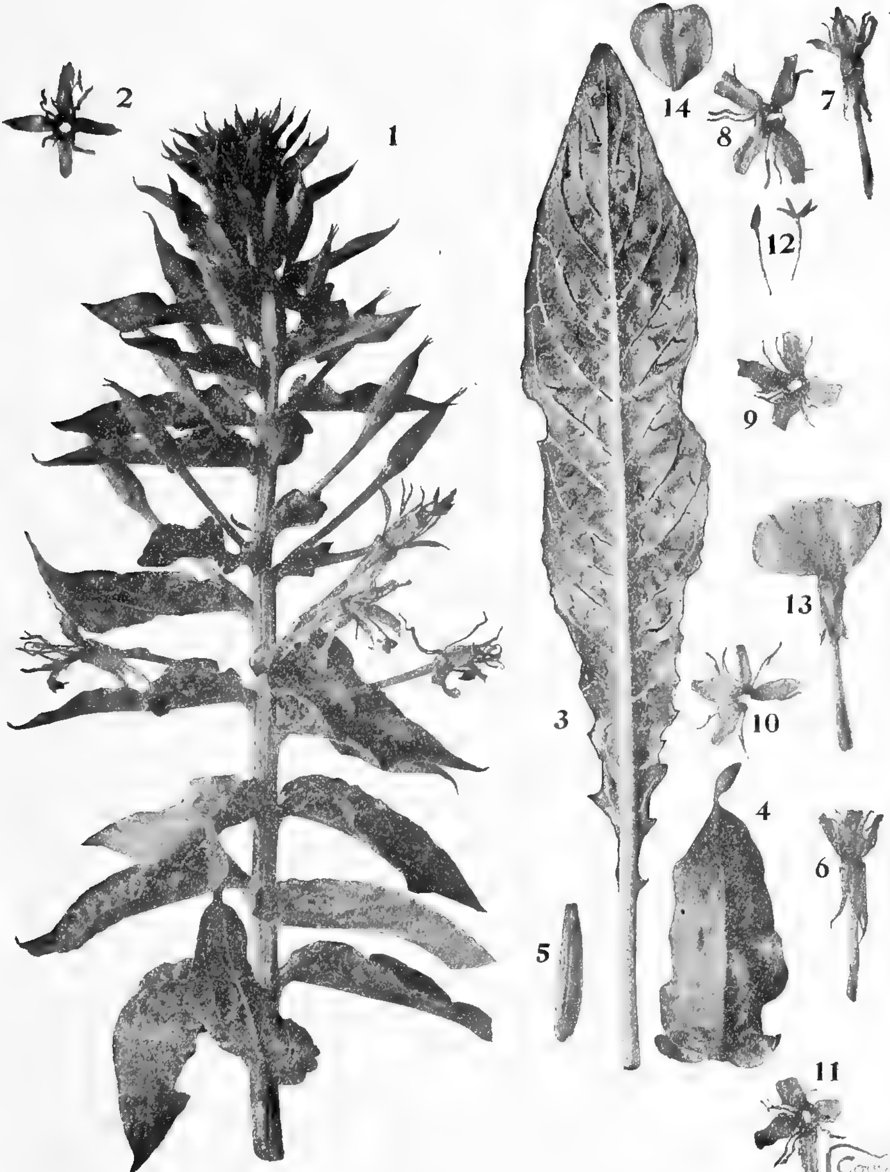
* Seeds from different localities would be always very welcome to me, as the plant may be in a mutable state in some districts, while it is not so in others.



Figs. 1, 2. *Oenothera cruciata* Nutt.
Figs. 3–14. *Oenothera cruciata varia* De Vries.

tation, in the same way as many of our ordinary varieties of garden plants have been produced, the other is by crossing, which is perhaps a still more common source of new garden varieties.

Both possibilities seem to me to be of some interest, since they bear directly on the great question of the internal causes of inconstancy in general. For in my variety the petals do not vary according to Quetelet's law, about a mean, which lies somewhere between the obcordate and the linear form, producing petals of which the majority do not essentially differ from this mean, whilst the extremes are very rare. Quite on the contrary, the obcordate and the linear petals seem to be two alternating types only united by rare intermediate steps.

In case my variety originated by a mutation, we would therefore have an imperfect one, producing the new type only in part of the individuals and remaining true or returning to the pure form of *Oenothera cruciata* in the others. In many points this case would be analogous to that of *Oenothera scintillans*, which originated in my garden from *O. Lamarckiana*, but which, though artificially pollinated with its own pollen, returns in each generation in often a relatively large part of the individuals to the original type.

In case my variety originated by a cross, it should first be remarked that the supposed hybrid is not intermediate between *O. cruciata* and some allied species, but that it has, as far as I can judge, all the characters of the former, the constancy in the form of the petals excepted. I have endeavored to show in my "Mutations-theorie" (Part II., p. 100) that *O. muricata* is probably the only species which could have given such a hybrid with the *O. cruciata*. Now it is clear that having once obtained seeds from the original and constant *O. cruciata*, I possess the materials to bring about this crossing and also those with other allied species, and to try whether it will be possible to get an inconstant hybrid in this way. I propose to do so, but from what I know of my *O. cruciata varia* and of the hybrids I have made of it with more than one other species, it is very improbable that the hybrid *O. cruciata* × *O. muricata* will be as a rule inconstant. It is far more probable that it will exhibit the dominant character, which must be the broad petals, and either give a constant progeny with this feature or split up according to Mendel's laws. I take the broad petals to be phylogenetically older than the linear ones, because they are the rule in the whole genus. But some authors suppose that from time to time there arise exceptions to the ordinary laws governing hybrids, and that such exceptions might be the source of many inconstant varieties and even of inconstancy in general. In this case the chance of getting such an exception by crossing would scarcely be greater than that of getting a mutation from the pure type.

However slight these chances may be, I propose to try both ways and to see whether it would be possible to repeat the as yet doubtful and unknown original production of my *O. cruciata varia.* For there are not a great many cases in which the starting-points are to be had in so pure and so thoroughly controlled a state as in this instance. As to the question of the rule of the constancy of *O. cruciata* under cultivation, and of the hybrids, I hope to solve this in some years; but as to the chances of getting exceptions, it is evident that these are only small and that it would be preferable if the same experiments were made by a number of investigators.

The aim of such experiments would be to repeat artificially the production of *O. cruciata varia* and by this means to throw some light on its origin in particular and on the origin of inconstant varieties in general. With a view to the possible repetition of this cross I will now give a description of the inheritance of the broad and linear petals in this variety. In so doing I limit myself to the detailed exposition of a single experiment carried on with the descendants of one original specimen of my variety.

In the year 1897 this plant was raised from seed obtained in the usual way of exchange between botanical gardens. I obtained but a single specimen, which bore all the characteristics of the typical *O. cruciata.* The spike, before the opening of the flowers, was placed in a bag of prepared parchment paper to prevent any visits from bees. The anthers touch the stigmas when opening, and the flowers fertilize themselves without any aid. In the same way I always took care to collect each year purely pollinated seeds only,

This original plant bore but a few seeds, from which during the next year I obtained only sixteen flowering individuals. But this number was sufficient to show the whole range of the variability of the race. Nine plants bore typical cruciate flowers with linear petals, two specimens had broad obcordate petals like those of *O. muricata*, and the five remaining had an intermediate breadth, varying in all degrees between these two extremes. Even on the same spike the petals of the different flowers were in this regard unlike each other, and sometimes of the four petals of one flower some were narrow and others broad. I also found petals large on one side of the median nerve and small on the other side.

I obtained pure seed of some of the narrow-petalled ones and of some of the intermediate specimens, separately for each plant, and the next year (1899) had four groups flowering. Two of them from two typically cruciate mothers repeated this type only, each group in thirty plants. One group, also from a cruciate mother, produced twenty-two typical and eight atavistic individuals, meaning thereby those with broad obcordate petals. Intermediate types were wanting. So it was with the fourth group, the children of an intermediate mother, of which only four were purely cruciate, the remaining fifty-eight being atavistic.

Afterwards I continued these four strains, sowing from the two last named in 1900, from the first named in 1901. The atavistic mothers gave only children which were in this regard like them. The purely cruciate strains on the other hand continued to produce atavistic and intermediate types, and these last were also inconstant as far as I observed them.

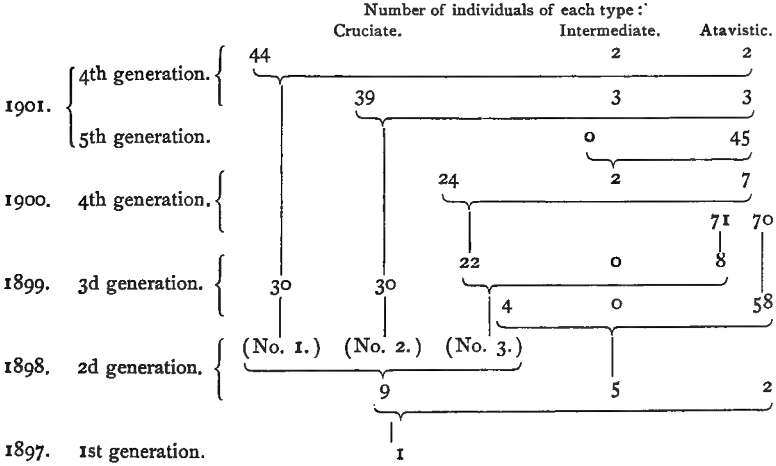
Taking the five generations together, I had 232 children from cruciate mothers, 103 from intermediate and 141 from atavistic parents. The first group consisted of 85 per cent. cruciate, 5 per cent. intermediate and 10 per cent. atavistic individuals. The second, of 4 per cent. cruciate, no intermediate and 96 per cent. atavistic specimens. The third was nearly constant, all individuals bearing the broad obcordate petals.

I say nearly constant, for among those atavists I observed some cases of bud-variation, by which they returned to the cruciate type. This rare phenomenon occasionally presents itself without apparent reason, but it may be induced to appear oftener in the following manner. Around the main stem the plants produce a circle of smaller stems growing upwards from the axils of the root leaves. In my cultures these side-stems do not ordinarily become tall enough to bear flowers. But by cutting out the main stem at an early period I could induce the others to a more vigorous growth. I repeatedly made this experiment; but will only cite here observations made on a single plant in the summer of 1901, grown from seed of a purely cruciate parent. It made six side-stems, out of which three bore only atavistic or broad-petalled flowers. The three other stems likewise produced obcordate petals, but not exclusively, bearing on one side of the spike flowers with the narrow and variable petals of the above-named intermediate types.

Such cases prove that the atavistic individuals are not, or at least are not always, so constant as could be deduced from the figures above given. Analogous instances of sectorial variation, one sector of the spike bearing other flowers than the remaining sectors, were from time to time observed on atavistic individuals and also on intermediate ones, the sport giving flowers with obcordate petals. As yet I have found no such sports on plants of the purely cruciate type nor purely cruciate flowers on those of the two other types. But I have no doubt that this is only due to the small extent of my cultures.

Pedigree of

Oenothera cruciata varia



I give, above, the description of my whole race in the form of a pedigree, omitting the sectorial and bud-variations, again reminding the reader that in every case the seed-bearing plants were fertilized only with their own pollen after enclosure in bags of prepared parchment-paper.

Though the figures of this experiment are but small, they seem to be sufficient to prove the presence of a very curious case of variability, the alternation between the typical cruciate flowers of the species and the atavistic petals of the group to which the species belongs, and to justify the provisional name chosen for my race : *Oenothera* or *Onagra cruciata varia.*

AMSTERDAM.

Überreicht vom Verfasser.

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Über die Dauer der Mutationsperiode bei Oenothera Lamarckiana.

Von

Hugo de Vries.

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56. Hugo de Vries: Über die Dauer der Mutationsperiode bei Oenothera Lamarckiana.

Eingegangen am 12. Oktober 1905.

Auf einem verlassenen Felde zwischen 's Graveland und Hilversum, unweit Amsterdam, zeigt die *Oenothera Lamarckiana* einen Grad der Mutabilität, wie ihn bis jetzt keine andere Pflanze aufgewiesen hat. Man findet auf diesem Felde teils konstante, sich selbst fortpflanzende Nebenarten, teils solche, welche von Zeit zu Zeit aus den Samen der normalen Individuen hervorgehen, ohne selbst an Ort und Stelle ihre Samen auszubilden.

Zu den ersteren gehören die *Oenothera laevifolia* und *O. brevistylis*. Beide fand ich zuerst im Jahre 1886 und seitdem nahezu alljährlich. Die *Oenothera laevifolia* findet sich stets ungefähr an derselben Stelle des Feldes, wo sie zuerst erschien. Im Sommer 1905 fand ich dort mehrere Exemplare, welche namentlich an den eigentümlichen, oft eirunden, oft zugespitzten Blumenblättern leicht kenntlich waren.[3]) Die *Oenothera brevistylis* hat im Laufe der Jahre, wegen der Ausdehnung der Bepflanzung mit Eichen, ihren Platz gewechselt, ohne jemals zu verschwinden; ich sammelte im Frühling dieses Jahres eine Rosette, welche seitdem in meinem Garten geblüht hat.

Die sich wiederholenden Mutationen beobachtet man teils auf dem Felde selbst, teils wenn man dort Samen einsammelt und diese im Garten aussät. So beobachtete ich z. B. daselbst im September 1902

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3) Für die Beschreibung und für die Abbildungen dieser und der übrigen neuen Arten verweise ich auf: Die Mutationstheorie, Bd. I, 1901, S. 212ff.

die *Oenothera lata* in Blüte, und erhielt ich sie ebenfalls in meinem Garten aus im Herbst 1901 im Freien gereiften Samen.

Diese Fähigkeit zu mutieren hat sich in den Kulturen meines Gartens erhalten und zeigte sich ebenfalls in anderen botanischen Gärten, denen ich meine Samen zugesandt habe. Sie wurde namentlich im botanischen Garten zu New York von Dr. D. T. MAC DOUGAL, Miss A. M. VAIL, Dr. G. H. SHULL und Dr. J. K. SMALL ausführlich studiert. Die von diesen Forschern bis dahin erzogenen Mutanten stimmen genau mit den in Amsterdam beobachteten überein,[1]) während der Wert der unterscheidenden Merkmale und die Berechtigung, die neuen Formen als Arten von der *Oenothera Lamarckiana* zu trennen, durch die statistischen Ermittelungen von Dr. SHULL in ein klares Licht gestellt wurden.[2]).

In meiner Mutationstheorie musste ich es unentschieden lassen, ob diese Mutabilität an Ort und Stelle entstanden sei, oder ob sie vielleicht bereits zu Anfang in den ausgesäten Samen vorhanden war.[3])

Um diese Frage zu beantworten, habe ich schon damals Samen aus dem Grosshandel bezogen, hatte aber erst neuerlich die Gelegenheit, diese in befriedigender Weise auf ihren etwaigen Gehalt an Mutanten zu prüfen. Um jeder Gefahr vorzubeugen, kaufte ich diese Samen kurze Zeit bevor ich diejenigen meiner eigenen Kulturen dem Tauschhandel der botanischen Gärten übergab.

Die eine Probe wurde im Winter 1901—1902 von den Herren HAAGE und SCHMIDT in Erfurt bezogen. Ihr Studium war namentlich deshalb wichtig, weil auch die Pflanzen des oben erwähnten Fundortes aus einer Erfurter Gärtnerei stammten. Aus diesen Samen erzog ich über 2000 Keimlinge und erhielt darunter eine Rosette von *Oenothera rubrinervis*, eine von *Oenothera oblonga* und drei Pflanzen von *Oenothera nanella*, von denen eine reichlich geblüht hat. Dazu

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[1]) D. T. MAC DOUGAL, assisted by A. M. VAIL, G. H. SHULL and J. K. SMALL, Mutants and Hybrids of the Oenotheras, Carnegie Institution of Washington, Publication 24, Exp. Evol. Station, Cold Spring Harbor No. 2. 1905. Ferner MAC DOUGAL, Mutations in plants. Contrib. N. Y. Bot. Garden No. 48. 1903.

[2]) Dr. G. H. SHULL, ebendaselbst S. 36—55.

[3]) Vergl. Die Mutationstheorie Bd. I, S. 217, und Species and Varieties: their Origin by Mutation, Chicago 1905, Chapter XVIII. Die in diesen beiden Werken entwickelten Ansichten wurden namentlich in der Sitzung der American Society of Naturalists im Dezember 1904 zu Philadelphia einer vielseitigen Kritik unterzogen. Vergl. die Vorträge von CASTLE, CONKLIN, DWIGHT, BAILEY, WHEELER und MAC DOUGAL in Science N. S. Vol. XXI. No. 536. S. 521—543. Von sonstigen Kritiken hebe ich hier nur hervor L. PLATE, Die Mutationstheorie im Lichte zoologischer Tatsachen. Cps. rs. 6e Congrès intern. de Zoologie, Berne 1904, S. 203 und G. H. SHULL, Species and Varieties, Torreya Vol. 5. Mai 1905, S. 89. Die Beziehungen zwischen Selektion und Mutation sind namentlich von T. H. MORGAN auseinandergesetzt worden in The Popular Science Monthly, Mai 1905, S. 54.

kamen noch ein Dutzend Keimpflanzen, welche deutlich abweichende Merkmale zeigten, welche es mir aber nicht gelang, soweit zu kultivieren, dass eine sichere Bestimmung möglich geworden wäre. Die *Oenothera rubrinervis* und *O. nanella* sind bekanntlich bereits in jungen, wenigblättrigen Rosetten leicht und sicher zu erkennen, während das Exemplar der *Oenothera oblonga* eine kräftige Rosette von 30 bis 40 Wurzelblättern von über 20 *cm* Länge bildete und bis in den Winter die Merkmale ihrer Art deutlich zeigte.

Die andere Probe erhielt ich von den Herren VILMORIN, ANDRIEUX & CO. zu Paris im Winter 1898—1899. Einen Teil dieser Samen säte ich im Jahre 1899 aus und befruchtete die Blüten mit ihrem eigenen Blütenstaub unter Ausschluss des Insektenbesuches. Die davon geernteten Samen dienten mir zur Ermittelung der Mutabilität. Ein Versuch ergab auf 3500 Keimlinge 14 *Oenothera nanella*, 3 *O. lata*, 3 *O. scintillans*, 1 *O. albida*, 1 *O. oblonga* und einige sonst abweichende Formen. Also im ganzen etwa 0,7 pCt. Mutanten. Eine zweite Probe gab auf 600 Keimlinge 3 *Oenothera lata*, 1 *O. nanella* und eine Pflanze, welche anfänglich die Merkmale der *Oenothera rubrinervis* zeigte, aber durch einen Zufall zu früh verloren ging.

Aus diesen Kulturen geht somit hervor, dass auch die im Handel befindlichen Samen Mutationserscheinungen zeigen und dabei dieselben Formen hervorbringen, welche auf dem erwähnten Felde und in meinen Kulturen die häufigsten sind. Es ist daher klar, dass die Mutationsperiode nicht auf jenem Felde entstanden ist, wo die Verbreitung der *Oenothera Lamarckiana* etwa 1875 angefangen hat, sondern dass ihr Anfang wenigstens bis auf den gemeinschaftlichen Ausgangspunkt der besprochenen Kulturlinien zurückzuführen ist.

Dieser Ausgangspunkt fällt, allem Anscheine nach, mit der Einfuhr der Pflanze aus Amerika in die europäischen Gärtnereien zusammen. Die Handelsfirmen HAAGE und SCHMIDT und VILMORIN haben die *Oenothera Lamarckiana* zum ersten Male in ihren Samenkatalogen von 1862 bezw. 1863 angeboten, nachdem sie selbst ihre Samen von einer anderen Handelsgärtnerei bezogen hatten.[1])

Die Samenhandlung von ERNST BENARY zu Erfurt, aus deren Kulturen die jetzt bei Hilversum wild wachsenden Oenotheren stammen, hat die *Oenothera Lamarckiana* zum ersten Male im Jahre 1861 in ihrem Katalog aufgeführt, und zwar infolge einer Empfehlung

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1) Diese Angaben verdanke ich der Freundlichkeit der Herren HAAGE und SCHMIDT in Erfurt und des Herrn JACQUES L. DE VILMORIN in Paris. Es sei mir gestattet, ihnen dafür an dieser Stelle meinen besten Dank auszusprechen. Die Firma HAAGE und SCHMIDT hat die Samen direkt aus England, die Herren VILMORIN haben die ihrigen ein Jahr später von einem anderen Samenhändler bezogen.

der Royal Horticultural Society in London.[1]). In der Illustration Horticole von 1862 (Tafel 318) teilt der Herausgeber, CH. LEMAIRE, mit, dass Herr AMBROISE VERSCHAFFELT, der bekannte Handelsgärtner in Gent (Belgien), gleichfalls um dieselbe Zeit zuerst die Kultur dieser Pflanze eingeführt hat. Er bezog seine Samen von den Herren CARTER & CO., Handelsgärtnern zu High Holborn bei London, welche sie damals dem Grosshandel darboten. Diese hatten die Pflanze aus Samen erzogen, welche sie drei oder vier Jahre vorher aus Texas bekommen hatten. Die Samen waren ohne Namen eingeführt; die Pflanze wurde von LINDLEY bestimmt [2])

Diese gleichzeitige Einfuhr durch die hervorragendsten Gärtnereien deutet auf eine gemeinsame Quelle hin, und so darf man annehmen, dass die jetzt in den europäischen Gärten verbreiteten Oenotheren von LAMARCK wohl alle von jenen aus Texas eingeführten Samen abstammen. Über die Herkunft und das fernere Loos der Pflanzen, welche LAMARCK das Material zu seiner Beschreibung lieferten, scheint dagegen nichts bekannt zu sein.[3])

Verbindet man nun die oben mitgeteilten Ergebnisse meiner Kultur mit diesen historischen Angaben, so gelangt man zu der Schlussfolgerung, dass die jetzige Mutationsperiode der *Oenothera Lamarckiana* wenigstens ungefähr ebenso alt ist, wie ihre Einfuhr aus Texas in Europa.

Zwei Punkte bleiben dabei vorläufig noch unentschieden. Sie betreffen die Frage, ob die Fähigkeit, neue Formen hervorzubringen, mit einem Male oder für jede Form getrennt bzw. gruppenweise entstanden ist. Die *Oenothera laevifolia* und *O. brevistylis* wurden bis jetzt nur auf dem Felde zu Hilversum gefunden, und die sehr seltene *Oenothera gigas* ist nur in meinen Kulturen entstanden. Vielleicht ist die Fähigkeit, sie hervorzubringen, nicht nur eine beschränkte, sondern auch eine jüngere.

Der andere Punkt betrifft die Frage, ob die Mutationsperiode nach der Einfuhr und vielleicht als Folge von dieser eingetreten ist, oder ob den aus Texas eingeführten Samen bereits die betreffenden Fähigkeiten innewohnten. Um diese Frage zu entscheiden, müsste man Samen von den wilden Standorten der *Oenothera Lamarckiana*

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1) Auch Herrn BENARY gestatte ich mir für die freundliche Mitteilung obiger Daten meinen Dank auszusprechen.

2) Floral Magazine 1862 und namentlich L'Illustration Horticole 1862, Tafel 318 und Beischrift. Vergl. auch MAC DOUGAL, Hybrids and Mutants, S. 5..

3) In seinen berühmten Katalogen des Jardin des Plantes zu Paris führt DESFONTAINES die *Oenothera Lamarckiana* bzw. die *Oenothera grandiflora* Lam. nicht auf in den Ausgaben von 1804 und 1815, wohl aber in derjenigen von 1829. (Tableau de l'école de botanique 1804 und 1815 und Illustration Horticole 1862, IX, Mars 1862, 4.

prüfen können, diese aber hat man in neuerer Zeit noch nicht wieder gefunden.

Um die Heimat unserer Pflanze zu ermitteln, habe ich im vorigen Jahre an verschiedenen Universitäten und botanischen Gärten in Amerika das Herbarmaterial der Untergattung *Onagra*, zu der unsere Art gehört, verglichen. Ich untersuchte zehn verschiedene Herbare und fand sie nur in drei vertreten und folgere daraus, dass die Pflanze wenigstens nicht stark verbreitet ist. Die betreffenden Exemplare wurden unter dem Sammelnamen *Oenothera biennis*, ohne nähere Bezeichnung, aufbewahrt. In Verbindung mit Dr. N. L. BRITTON, Direktor und Dr. D. T. MAC DOUGAL, Unter-Direktor des botanischen Gartens zu New York, fand ich in dem dortigen Herbar ein Exemplar, welches von A. W. CHAPMAN in Florida gesammelt war (vor 1860).[1]) Von demselben Sammler wird ein zweites, gleichfalls aus Florida stammendes Exemplar im Herbar der Missouri Botanical Gardens in St. Louis aufbewahrt, wo ich es durch die Gefälligkeit des Herrn Direktors Dr. W. TRELEASE auffinden konnte. Ferner fand ich unter der freundlichen Leitung von Dr. JOHN W. HARSHBERGER im Herbar der Akademie der Wissenschaften in Philadelphia ein Exemplar, welches von C. W. SHORT unweit Lexington in Kentucky gesammelt war[2]). An den betreffenden Stellen hat man aber seitdem die *Oenothera Lamarckiana* nicht mehr beobachtet, was wohl zum Teil dem Mangel an genauen Angaben über die betreffenden Standorte zugeschrieben werden muss. Die wahrscheinliche Heimat unserer Pflanze ist also im südlichen Teile der Vereinigten Staaten zu suchen, aber bis es gelingt, sie dort wieder zu sammeln, muss die Frage, ob sie bereits im wilden Zustande mutiert, unentschieden bleiben.

In meiner Mutationstheorie habe ich die Vermutung ausgesprochen, dass die *Oenothera Lamarckiana* die Fähigkeit, Zwerge hervorzubringen, vielleicht von ihren Vorfahren geerbt hat.[3]) Ich gründete diese Ansicht damals auf das Verhalten der *Oenothera nanella* bei Kreuzungen mit *Oenothera biennis*. Seitdem habe ich aber eine Beobachtung gemacht, welche ein mehr direktes Argument für diese Meinung bietet. Eine Unterart der *Oenothera biennis* hat in meinem Garten durch Mutation eine *Nanella*-Pflanze hervorgebracht.

In meinem Buche habe ich (Bd. II S. 599) eine von meinem Sohne ERNST im Jahre 1900 unweit Santpoort in Holland im Freien aufgefundene Mutation von *Oenothera biennis* als *Oenothera biennis cruciata* beschrieben. Sie unterscheidet sich von der gewöhn-

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1) Vergl. MAC DOUGAL, Hybrids and Mutants, S. 6.

2) Vergl. HARSHBERGER, Torreya Vol. 5, Aug. 1905, S. 147.

3) Mutationstheorie II, S. 459.

lichen Form durch kleine linealische Blumenblätter, ein Merkmal, welches bei *Oenothera cruciata* Nutt. (aus den Staaten Vermont und New York) spezifischen Wert hat. Diese neue Form habe ich im Jahre 1901 zuerst und seitdem alljährlich in vielen Hunderten von Exemplaren kultiviert. Die einzige Abweichung, welche sich dabei zeigte, war eine Zwergpflanze, welche im Jahre 1903 plötzlich und unvermittelt auftrat. Sie hatte die Blätter der *Oenothera biennis*, aber eine dicht gedrungene Rosette, ähnlich wie die *Oenothera nanella*, und kleine linealische Blumenblätter, wie ihre Mutter. Sie erreichte nur eine Höhe von etwa 30 *cm*, fing erst Mitte September zu blühen an und brachte demzufolge nur zwei keimfähige Samen. Aus diesen erzog ich im Sommer 1905 zwei kräftige Pflanzen, von denen die eine mit cruciaten Blüten blühte, die andere aber eine grosse Rosette von Wurzelblättern hervorbrachte. Beide wiederholten genau die Merkmale ihrer Mutter. Die neue Form scheint somit konstant zu sein, was aber erst durch fortgesetzte Kultur endgültig festgestellt werden kann.

Die Fähigkeit der *Oenothera biennis cruciata,* Zwerge hervorzubringen, mag vielleicht unabhängig von der entsprechenden Fähigkeit der *Oenothera Lamarckiana* entstanden sein. Wahrscheinlicher erscheint es mir aber, dass beide auf einen gemeinschaftlichen Ursprung zurückzuführen sind und dass diese übrigens im Pflanzenreich sehr verbreitete Mutabilität von den gemeinschaftlichen Vorfahren herrührt.

Nach dem Mitgeteilten darf es als feststehend betrachtet werden, dass die jetzige Mutationsperiode der *Oenothera Lamarckiana* in ihren Hauptzügen vor oder sofort nach ihrer Einfuhr aus Texas in Europa (etwa 1860) angefangen und seitdem sich im Wesentlichen erhalten hat.

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THE PROBABLE ORIGIN OF OENOTHERA LAMARCKIANA SER.

(WITH PLATES XVII–XIX)

HUGO DE VRIES

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THE PROBABLE ORIGIN OF OENOTHERA LAMARCKIANA SER.

HUGO DE VRIES

(WITH PLATES XVII–XIX)

In a series of most interesting articles, B. M. DAVIS has recently tried to prove that mutability might be a result of previous crosses. This view was first proposed by BATESON and SAUNDERS, and applies especially to the phenomena which *Oenothera Lamarckiana* shows when seeds from the pure strain, and even from pure lines within this strain, are sown, as in the experiments I conducted in my experimental garden. DAVIS expected to be able to offer the desired proof by showing that *O. Lamarckiana* might be duplicated by crossing two other species of the same group. Up to this time, as a matter of fact, he has not succeeded in producing any form which comes sufficiently near *O. Lamarckiana* to be compared with it.[1] But if he had succeeded in doing so, evidently it would not have been a proof for his assertion, unless his hybrid should show the same degree of mutability as does *O. Lamarckiana*, since we have as yet no means of judging from the morphological characters of a given plant whether its hereditary characters are in a stable or in an unstable condition.

In starting his experiments to produce a duplication of LAMARCK's evening primrose, DAVIS was unfortunate in the choice of the species for his combination. He chose *O. biennis* L. and a

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[1] For a successful duplication of an elementary species by means of crossing, see *Oenothera biennis* × *O. cruciata* Nutt. in Gruppenweise Artbildung, p. 311.

form which he assumed to be *O. grandiflora* Aiton. It is evident that the first condition of success in such work consists in the purity and the immutability of the species which are to produce the hybrid. If they are already in a mutable condition, it is to be expected that their hybrids, or at least some of them, may combine the different lines of mutability of their parents; and at all events, the mutability of such a hybrid would be no proof that this phenomenon may be produced by means of crossing. On the other hand, if the species to be crossed, or even only one of them, were not pure, the hybrid might inherit this impurity and show phenomena which might easily be mistaken for mutations.

It so happens that *O. biennis* is in a condition of mutability analogous to that of *O. Lamarckiana*, although not developed to the same high degree. From time to time it produces dwarfs, which are distinguished from it by exactly the same two characters which differentiate the dwarfs of *O. Lamarckiana* from their mother species, namely, low stature and sensitiveness to the attacks of some species of soil bacteria.[2] Moreover, STOMPS has shown that *O. biennis* may, although very rarely, double the number of chromosomes in its sexual cells, which in *O. Lamarckiana* produces the two mutants *O. gigas* and *O. semigigas*.[3] As is now generally admitted, *O. gigas* results from the pairing of two mutated sexual cells, each of which had a double number of chromosomes. *O. semigigas*, on the other hand, is produced by the pairing of a sexual cell mutated in the same way, with a normal gamete; therefore it possesses only 21 chromosomes (14+7), while the number in *O. gigas* is 28. As yet, only *semigigas* mutants have been observed coming from *O. biennis*, and it is obvious that the double combination must be much rarer. As a proof of this special kind of mutability in *O. biennis*, however, the observations of STOMPS are wholly sufficient.

In quoting these facts, DAVIS says that if it can be shown "that tested strains of this *biennis* are able to produce new forms of specific

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[2] STOMPS, TH. J., Mutation von *Oenothera biennis* L. Biol. Centralbl. 32:521–535. 1912; also ZEYLSTRA, H. H., *Oenothera nanella* De Vries, eine krankhafte Pflanzenart. Biol. Centralbl. 31:129–138. 1911. Vergl. ferner: Gruppenweise Artbildung 1913:296–304.

[3] STOMPS, TH. J., *op. cit.* p. 533.

rank or even marked varieties, the mutationists would have much stronger evidence in support of the mutation theory than that based on the behavior of *O. Lamarckiana*."[4] After conceding this strong position to his adversaries, DAVIS subjects the results of STOMPS to a rather sharp criticism, which, unfortunately, is based upon a confusion of two wholly distinct types, namely, *O. biennis* L. var. *cruciata*[5] and *O. cruciata* Nutt. He says: "It should be made clear that the form (*O. biennis cruciata*) is recognized in the more recent taxonomic treatments as a true species sharply distinguished from types of *biennis* by its floral characters," and "a cross between these types must certainly be regarded as a cross between two very distinct evolutionary lines and its product as a hybrid in which marked modifications of germinal constitution are to be expected."[6] But, as a matter of fact, the Dutch *O. biennis cruciata* differs from *O. biennis* only in the characters of the petals; in all other respects it is wholly the same, and therefore evidently only a subordinate variety of this species. It has not been dealt with in recent taxonomic treatments, since it occurs almost exclusively in the sand dunes of Holland, where it is produced from time to time by mutation from the mother form (first observed in 1900), without having been able until recently to multiply in the field so as to produce a persistent local variety.[7]

On the other hand, *O. cruciata* Nutt. is quite a different species, with narrow, brownish green leaves, and a different type of branching, of spikes, and of fruits. It grows wild in New York and Vermont, and is well known to all students of the American flora. By some authors it has been considered a variety of *O. biennis*, and this probably is the chief cause of DAVIS' confusion. The character and the behavior of its hybrids with *O. biennis* have been amply dealt with in my *Gruppenweise Artbildung*.

In the experiment of STOMPS, the dwarf and *semigigas* mutations were produced by hybrid strains of *O. biennis* and *O. biennis*

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[4] DAVIS, B. M., Mutations in *Oenothera biennis* L.? Amer. Nat. 47:116–121 (especially p. 116). 1913; see also *op. cit.* 47:540–596 (especially p. 567). 1913.

[5] Die Mutations-Theorie 2:599. 1903.

[6] Amer. Nat. 47:117. 1913.

[7] Die Mutations-Theorie 2:599. 1903.

cruciata, and it was assumed that such strains would behave as true species in all characters not related to the differentiating marks of the petals. It must be conceded, therefore, that the cross of these two forms may be treated "as though it were the combination of forms within the same species, which have similar germinal constitutions" (DAVIS, *op. cit.* p. 117).

But the most clear and simple way of obviating this whole objection is evidently to sow seeds of *O. biennis* of pure descent upon the same large scale as in the former experiment. This has been done, and a dwarf and a *semigigas* form have been produced by this pure line, besides some other mutations.[8] They had the same characters as the former ones, and now provide us with the "strong support" asked for by DAVIS. Moreover, they show that his choice of *O. biennis* for a proof of the assertion that mutability might be produced by crossing immutable species was a most unhappy one.

The second condition for success in this kind of work is, as has been stated, the purity of the types to be crossed. As already quoted, DAVIS assumes that a cross between two very distinct evolutionary lines may give a hybrid with marked modifications of germinal constitution. This may be applied to his choice of the type which he calls *O. grandiflora*, and which he has made the other parent of his initial cross. He got his seeds from Dixie Landing, Alabama, a locality where BARTRAM had discovered *O. grandiflora* about a century ago. He assumed them to be of the pure species, but a culture which I made in my garden from seeds kindly supplied to me by Mr. DAVIS proved to be a mixture, and thereby threw a distinct doubt upon the purity of the station. For this reason I visited Dixie Landing in September 1912, and had the good fortune to be accompanied by Mr. H. H. BARTLETT, of Washington, well known for his systematic researches among the wild species of this group. We found the station in a most desolate condition. A small-flowered species, *O. Tracyi*, in almost all respects different from *O. grandiflora*, had migrated into the same old cotton fields and mixed everywhere with the species of BAR-

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[8] STOMPS, TH. J., Parallele Mutationen bei den Oenotheren. Ber. Deutsch. Bot. Gesells. 30:Heft 3, 1914.

TRAM.[9] On no single field was the original form pure; it was always mixed to such a degree with *O. Tracyi* and with their hybrids that we found it impossible to collect undoubtedly pure *grandiflora* seed from this locality. Moreover, the intermediate types were so numerous (over a dozen) that it was difficult to regard all of them as normal hybrids between only two parents. To produce such a diversity of forms, either one or both of the parents must have been in a mutating condition, or more than two species must have combined in the crosses. In both cases, the material can hardly be considered as a fit starting-point for experiments bearing upon the causal relations of crossing and mutability.

Recently I have shown that besides *O. biennis* some other species of *Oenothera* are actually in a state of mutability, and especially has one of the most common American types thrown off marked mutants in my experiment garden.[10] The degrees of development of this condition, however, are very different in different species. In some of them mutations occur rarely, but they serve to throw a doubt upon the stability of those forms for which no positive results have as yet been won. In other words, we may say that almost all the nearest allies of *O. Lamarckiana* are open to the suspicion of sharing at least some degree of the mutability of this species. There is no use, therefore, in trying to produce mutability by crosses of species of the same subgenus (*Onagra*) in order to show that this phenomenon is only a result of crossing, as is asserted by DAVIS.

Moreover, I might point out that the question should be dealt with from a general standpoint and not be limited to the evening primroses. If it should be true that phenomena like those of *O. Lamarckiana* could be produced by crossing immutable species, it would, of course, be of much higher scientific value to produce them in other families or genera, or at least in the other subgenera of the evening primroses. The chance of finding immutable parents for a cross would be far greater and the proof could be given as easily and in many cases with less amount of mechanical work

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[9] DE VRIES, HUGO, and BARTLETT, H. H., The evening primroses of Dixie Landing, Alabama. Science N.S. 35:599–601. 1912.

[10] Gruppenweise Artbildung, pp. 296–312. 1913.

and space in the garden. The line of work chosen by DAVIS seems to me to be necessarily without any chance of success.

Besides his experimental work, DAVIS has made some historical researches to discover the origin of *O. Lamarckiana*.[11] Unfortunately, he has neglected to visit the Museum d'Histoire Naturelle at Paris, where the herbarium of LAMARCK is preserved, and where other valuable documents concerning the first appearance of our species are to be found. For myself I visited these collections in 1895 and reported on the results of my investigations in my *Mutation theory* (vol. I. pp. 437–444 of the English edition). In October 1913 I repeated my visit and compared the authentic specimens with the remarks made upon them by DAVIS. I regret to say that, through his ignorance of the available evidence, DAVIS has been led to conclusions which are fully contradicted by the herbarium material, both of the "Herbier de Lamarck" and of the "Herbier général" of the Museum. As we shall see, the origin of *O. Lamarckiana* is the same as I have pointed out in my book.

In the herbarium of LAMARCK, *O. grandiflora* (Lam.), which later was renamed by SERINGE and called *O. Lamarckiana*, the name it still bears, is represented by two large flowering specimens. When I studied them in 1895, they were loose on their sheets and bore together the no. 12, indicating that they corresponded with no. 12 *O. grandiflora* of the *Encyclopédie méthodique*, *Botanique*, by LAMARCK.[12] About 1900 they were fastened on new sheets and the numbers have been lost.[13] For convenience, I shall call these specimens *A* and *B*, the former being represented by our pl. XVII, while a photograph of *B* has been published by DAVIS.[14]

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[11] DAVIS, B. M., Was LAMARCK's evening primrose (*Oenothera Lamarckiana* Seringe) a form of *Oenothera grandiflora* Solander? Bull. Torr. Bot. Club **39**:519–533. *pls. 37–39.* 1912; A much desired *Oenothera.* Plant World **16**:145–153. 1913; The problem of the origin of *Oenothera Lamarckiana.* New. Phytol. **12**:233–241. 1913.

[12] The Mutation Theory **1**:442. 1901.

[13] The herbarium of LAMARCK was acquired by the Museum d'Histoire Naturelle in 1886. Vergl. BONNET, ED., L'herbier de LAMARCK, son histoire, ses vicissitudes, son état actuel. Jour. Botanique **16**:129–138. 1902.

[14] DAVIS, B. M., Was LAMARCK's evening primrose (*Oenothera Lamarckiana* Seringe) a form of *Oenothera grandiflora* Solander? Bull. Torr. Bot. Club **39**:519–533. 1912. See *pl. 37*.

Unfortunately, these two specimens do not belong to the same elementary species, but the question as to which of them is to be considered as the authentic specimen has been answered by all authors in the same way, with the exception of DAVIS. According to the general agreement, *A* (pl. XVII) is the type of the species. DAVIS has not seen this specimen, and has based his judgment upon the communications of botanists concerned with systematic rather than with elementary species.

The plant *A* corresponds exactly with *O. Lamarckiana* Ser. as it is now universally cultivated and as I know it from my own cultures. The specimen is evidently a side branch, picked in the autumn, and the flowers, although very large, are not quite so large as may be seen in July and August. It bears no fruits, but the sexual organs of the flowers and the form of the flower buds do not leave the least doubt concerning its identity. The stigma lobes are widely spread and raised by the long style high above the tops of the anthers, and this is one of the best characters of *O. Lamarckiana*. The buds are conical and thick, and not thin as in *O. grandiflora* Ait. For comparison, I have given a group of flower buds (pl. XVII), picked in the autumn also, from my pure cultures. All the other marks correspond to those of the present species, although of course not all of them distinguish it from allied forms.

This sheet bears the label, "d'Amérique sept., tige rameuse, haute de 3 à 4 pieds," in the handwriting of LAMARCK. The description in the *Encyclopédie* says of the origin of the species: "Cette espèce est originaire de l'Amérique septentrionale. On la cultive au jardin du Muséum d'Histoire Naturelle (V.S.)."[15] The description, however, quotes some points which are not visible on the herbarium specimen, nor on specimen *B*. It is therefore clear that the author knew his plants from another source still, probably from the living material of the Jardin des Plantes. The most interesting point for us is the description of the fruits: "Le fruit est une capsule courte, cylindrique, glabre, tronquée légèrement, quadrangulaire, n'ayant environ que le tiers de la longueur

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[15] V.S. ("vidi siccum") means that the diagnosis is based on herbarium material.

du tube calicinal."[16] This description wholly agrees with the fruits of the present species, especially if we remember that LAMARCK based his description on a comparison with the only other large-flowered form he knew, *O. longiflora.* The short fruits at once distinguish our species from the allied types, such as *O. suaveolens* Desf. and *O. grandiflora* Ait., which have thin and proportionally long fruits.[17]

This character of the fruits shows that the description of the *Encyclopédie* has been based upon specimen *A* and not upon the other one. For, although *B* lacks fruits also, it belongs to an elementary species which has long and narrow fruits, as we shall soon see. Here I might point out that in systematic researches of this kind, more value is to be attached to published diagnoses and descriptions than to the material preserved in a herbarium. The older systematists, as a rule, did not take much care of their material, even if they were very careful of their descriptions.[18] The herbarium specimens are often found without their names and without any indication concerning their origin. The rule "descriptio praestat herbario" applies in our special case, even as it does in many others. In our case, the description is relatively complete and clear, while in the dried specimen only part of the characters are represented.

For all these reasons I cannot agree with DAVIS, who says (p. 519) that I made an incorrect determination of the material of my cultures, when I identified it with LAMARCK's plant of 1796. The authentic specimen of LAMARCK and the description in the

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[16] Encyclopédie méthodique, Botanique par LAMARCK, Tome IV, 1796. pp. 550–554, "Onagraire." Twelve species of this genus are enumerated, *O. longiflora* being no. 4, *O. corymbosa* no. 11, and *O. grandiflora* no. 12. A copy of the diagnosis of this last one may be found in my *Mutation theory* (p. 441) and in the article of DAVIS. The article in the *Encyclopédie* is not signed and was probably written by POIRET, who prepared many articles in vol. IV, and wrote the whole of the later volumes. In the herbarium of Paris some of the specimens may be seen quoted with the authority of POIRET, as, for example, on the sheet of *O. suaveolens* Desf., where above that name is written *Oenothera grandiflora* Poiret Encyclopédie. (Cf. *pl. 39* of the article of DAVIS.)

[17] L'*Oenothera grandiflora* de l'herbier de LAMARCK. Rev. Gén. Botanique **25**: 1914.

[18] Cf. BONNETT, *op. cit.* p. 138.

Encyclopédie correspond as closely with the characters of my plants as dried specimens and descriptions expressed in words ever can do.

On the contrary, the specimen *B* is surrounded with doubts. DAVIS has given a very elaborate description of this branch, comparing it with my *Lamarckiana*. The sheet bears the label: "*Oenothera* . . . . [*grandiflora*] . . . . nova spec. flores magni lutei, odore grato, caulis 3 pedalis." The fact that the name *grandiflora* is placed in brackets shows that LAMARCK did not wholly trust his identification of this plant with the other one. Perhaps the words "nova species" indicate that he took it to be possibly a different species. Later, POIRET discovered the identity of this specimen with *O. grandiflora* Aiton Hort. Kew,[19] as has been indicated by DAVIS. And in DE CANDOLLE'S *Prodromus* (3:47. 1828), SERINGE separated the two types, describing *O. grandiflora* Ait. and *O. Lamarckiana* (SER. MSS) as different species.

The words "odore grato" point to *O. grandiflora* Ait., which has fragrant flowers, while the flowers of *O. Lamarckiana* Ser. are almost without odor. In the original description no mention is made of the odor, and this shows once more that the specimen *B* was not the authentic one for this description.

DAVIS has compared the branch *B* with some of his hybrid strains from Dixie Landing[20] and finds a close resemblance. Perhaps the plant of LAMARCK was a chance hybrid found in the Jardin des Plantes, and in this case, as DAVIS says, "we can have no certainty as to the characters of an individual plant unless its seeds have been grown in large cultures.[21] At all events, it is not backed by other herbarium material in the Museum d'Histoire Naturelle, so far as I know. If POIRET'S opinion that it belongs to *O. grandiflora* Ait. is correct, then it has evidently not served as a basis for the description of *O. grandiflora* Lam. (*O. Lamarckiana* Ser.). In *O. grandiflora* the fruits are thin and relatively large, for example,

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[19] Encyclopédie méthodique. Suppl. IV, p. 141. 1816. See DAVIS, p. 522.

[20] At Dixie Landing, Alabama, only hybrid strains of *O. grandiflora* and *O. Tracyi*, perhaps mixed with other species too, are to be found. See Science *op. cit.* p. 399. 1912.

[21] DAVIS, B. M., A much desired *Oenothera*. Plant World **16**:148. 1913.

3 cm. long and 3 mm. wide; while those of *O. Lamarckiana* may measure 2.5 cm. in length and 6 mm. in width, making a ratio of $\frac{10}{1}$ in the one case and $\frac{4}{1}$ in the other.[22] The description of the fruits as short, as given by LAMARCK, evidently points to the second and not to the first case.[23]

Summing up the main results of this discussion, we find that specimen *A* of the herbarium of LAMARCK closely corresponds to the *O. Lamarckiana* Ser. of the present time, and has been taken by almost all authors for its prototype. The specimen *B* differs from it in its general aspect, in the words "odore grato" on its label, and in the opinion of POIRET that it belongs to *O. grandiflora* Ait., this opinion pointing to long and narrow fruits. Personally, it impressed me as having been brought into the herbarium of LAMARCK only later on, and as having been placed in the cover of *O. grandiflora* Lam. with a doubt shown by the placing of the name in brackets.

The best proof for the fact that *A* and not *B* is the authentic specimen of *O. grandiflora* Lam. is perhaps given by the specimen in the herbarium of Father POURRET, which was given to the Muséum d'Histoire Naturelle by Dr. BARBIER in 1847.[24] It bears the name *Oenothera grandiflora* Lam. written in the clear and beautiful handwriting of the clerk of POURRET. In the same cover there is another sheet of POURRET's collection, on which the same clerk wrote *Oenothera biennis*. Unfortunately, DAVIS, who did not visit the Museum, has mistaken this one for the one studied by me,[25] and has accordingly published a photograph (*pl. 38*) and a description of it. It is easily seen that this specimen really comes nearer to our present *O. biennis* L. than to anything else.

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[22] L'*Oenothera grandiflora* de l'herbier de LAMARCK, *op. cit. fig. 1*, *b* and *c*.

[23] DAVIS (*op. cit.* p. 523) lays great stress on the tips of the sepals, but I cannot find a well defined difference between the two species in this character. He calls attention to the word "sétacé" in LAMARCK's description of the sepal tips: "this has been translated by DE VRIES (*Mutations-Theorie*, p. 317. 1901) as "dicke." The French, however, is from the late Latin word *setaceus*, derived from "seta," a stiff hair or bristle. The meaning, therefore, is exactly the opposite of that given by DE VRIES." If the reader will kindly look up my book at the page quoted by DAVIS, he will find that I have translated "sétacé" by "fadenförmig."

[24] The Mutation Theory, Engl. ed. 1:442, note 2.

[25] Bull. Torr. Bot. Club *op. cit.* p. 527.

The plant which POURRET called *O. grandiflora* Lam. is represented on our pl. XVIII. It agrees wholly with the present *O. Lamarckiana* Ser., and in all respects. It was fastened on its sheet by the clerk of POURRET and consists of two flowering spikes and two separate flowers. The stigma lobes are seen spread above the anthers in the normal way. The specimens were picked at the beginning of the flowering period and bear no fruits; obviously they were main spikes. They will be recognized at once as *O. Lamarckiana* by anyone who has seen living cultures of this species. As I have quoted in my *Mutation theory* (*loc. cit.*), SPACH has written on this sheet "*Onagra vulgaris grandiflora* Spach," which remark also proves the identity with *O. Lamarckiana* Ser. The printed label says "Collection de l'Abbé POURRET, extraite de l'herbier légué par M. le Dr. BARBIER en 1847." The main spike measures about 40 cm., the smaller one about 20 cm.

In my book I have also referred to a specimen of *O. suaveolens* Desf. At that time I did not know the Alabama species and believed that *O. suaveolens* Desf. and *O. grandiflora* Ait. were synonyms, as almost all authors did. Therefore I used the two names promiscuously. Last summer, however, I cultivated, side by side, *O. suaveolens* Desf. from Fontainebleau, collected by Dr. BLARINGHEM, and *O. grandiflora* Ait. from Castleberry, Alabama, collected by myself with Mr. BARTLETT. They proved to be wholly different species.[26] So far as I know, the large-flowered Oenotheras, which are now relatively common in the western departments of France, all belong to *O. suaveolens* Desf., at least all the specimens and cultures on which I based my opinion in 1901 did. The specimen of the Muséum d'Histoire Naturelle, which I referred to especially, has been described by DAVIS from a photograph which is reproduced on *pl. 39* of his paper. DAVIS, who did not know the *O. suaveolens* as a separate species, called it the flotsam of the herbarium (p. 529); it is, on the contrary, the authentic specimen of DESFONTAINES, bearing on the label the name *suaveolens* written by DESFONTAINES himself. The smaller plant, fastened on the same sheet, has another label, saying only *O. grandiflora*, and seems to me to have been fastened on this sheet subsequently. The

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[26] L'*Oenothera grandiflora* de l'herbier de LAMARCK, *loc. cit.*

larger one, however, corresponds exactly with the species which is now growing in many thousands of specimens near Samois on the eastern limit of the Forêt de Fontainebleau, where I visited the different stations with Dr. BLARINGHEM in October 1913. The long fruits and the thick flower buds do not leave the least doubt concerning the identity of this specimen.

The most interesting discovery in this field of historical research, however, is that of a specimen of *O. Lamarckiana* Ser. in the collection of MICHAUX, described recently by BLARINGHEM.[27] I had the advantage of studying this sheet myself, when I visited Paris in October 1913. The printed label says "Herb. Mus. Paris, Herbier de l'Amérique septentrionale d'ANDRÉ MICHAUX." There is no further indication of the locality and no name. The specimen is a main spike, picked in the beginning of the flowering period, and without fruits (pl. XIX). It is excellently preserved and corresponds in all respects to my cultures of *O. Lamarckiana* Ser. The lobes of the stigma are seen to be widely spread above the anthers. The flowers and flower buds are exactly those of the present species.

ANDRÉ MICHAUX died in 1802, after having traveled during twelve years through the eastern United States from the Hudson River to Carolina. His celebrated collection constitutes one of the best sources of our knowledge of the flora of those parts of America at the end of the eighteenth century, that is, of the same period in which LAMARCK published his volumes of the *Encyclopédie*. His herbarium is at present at the Muséum d'Histoire Naturelle at Paris, and his plants were described after his death by his son FRANÇOIS ANDRÉ MICHAUX in a book entitled "ANDRAEAS MICHAUX, Flora boreali-americana, sistens characteres plantarum quas in America septentrionali collegit ANDRAEAS MICHAUX."[28] MICHAUX had the habit of collecting seeds of as many species as possible, besides his herbarium specimens, and of sending them to Europe to be sown.

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[27] BLARINGHEM, L., L'*Oenothera Lamarckiana* Seringe et les Oenothères de Fontainebleau. Rev. Gén. Botanique 25:1914.

[28] Editio nova, 1820, Paris. The genus *Oenothera* is dealt with in vol. I on p. 214; the plant is given under the name of *O. biennis*. For the ground covered by his travels, see the preface and the article of BLARINGHEM.

This beautiful specimen proves that *O. Lamarckiana* Ser. was a component of the flora of the eastern part of Northern America at the end of the eighteenth century, and that it has come down to us as completely unaltered as may be shown by old herbarium specimens. Moreover, it tends to make it at least very probable that the European strains, or at least some of them, are derived from the importation of seeds by MICHAUX. The specimen *A* in the herbarium of LAMARCK, designated as "d'Amérique sept.," probably belonged to this same strain.

The exact situation of the locality where MICHAUX collected this specimen is, of course, unknown. Much stress is laid by many authors upon the fact that no wild station for *O. Lamarckiana* has been discovered lately in any part of the United States. This argument evidently loses the main part of its weight when we know that it was observed by such a well known botanist as MICHAUX. Moreover, this situation is not peculiar to *O. Lamarckiana;* on the contrary, the same condition prevails for the other European species, *O. biennis* L., *O. muricata* L., and *O. suaveolens* Desf., whose original stations in the United States and Canada have not been rediscovered. Even *O. grandiflora,* which is known to occur in Alabama in different localities, is observed there to grow on cultivated soil only, especially on old fields of corn and cotton, and no one knows whence it came. Therefore, if our present ignorance of the origin of *O. Lamarckiana* is adduced in order to throw a doubt on its reality as a good species, the same doubt is attached to its nearest allies, and, in fact, to all the dozens of elementary species of the group *Onagra* which are now being found wild on waste fields and along roadsides all through the United States. Autochthonous stations are not known for any of them.

A most valuable contribution to the clearance of the historical data concerning the origin of *O. Lamarckiana* Ser. has been brought forward by DAVIS in his criticism of the alleged Texan origin of the present cultivated strain. This was introduced into the trade by Messrs. Carter and Co. of High Holborn in the neighborhood of London, about the middle of the last century. These horticulturists offered the seeds as coming from Texas. But, since then, no botanist is known to have seen the plant in that state, and DAVIS suggests (p. 523) that the statement might, perhaps, have been caused by a mistake.[29] Now, it is well known that such details are, as a rule, given more in the interest of advertising than in that of pure science. Moreover, no horticulturist likes to offer for sale seeds with the announcement that the same form may be found as a wild flower in his own country.

O. Lamarckiana has been, for many years at least, a component of the flora of England, growing in many localities, especially on the sand dunes along the coast. The most universally known station is that of St. Anne's on the Sea, near Liverpool, which has been studied by BAILEY, GATES, and other botanists, and where the species occurs in thousands of specimens. DAVIS received seeds from different English stations and recognized the plant in the cultures derived from them (*op. cit.* p. 237). In Lancashire the species locally grows together with *O. biennis* L., exactly as it does in the sand dunes of Holland. In such cases it produces hybrids such as I have described under the names of *laeta* and *velutina*, and as DAVIS has isolated as small-flowered races from those English localities (p. 237).

Now, if we agree with DAVIS that the seeds of Carter and Co. were derived from some English station, the probability at once arises that these English stations themselves owe their origin to the introduction of seeds from America, either by MICHAUX himself or by some other botanist of the same period. The history of the species would then become a very simple and clear one. In this respect it becomes of interest to look at the figure published in 1807 in SMITH'S *English Botany* (vol. VI. *pl. 1534*).[30] According to the description accompanying this plate, the "specimen was gathered on the extensive and dreary sand banks on the coast a few miles north of Liverpool, where millions of the same species have been observed by Dr. BOSTOCK and Mr. JOHN SHEPHERD growing perfectly wild and covering large tracts between the first and second range of sand hills." In this same locality *O. biennis* L. and *O. Lamarckiana* are now growing in the same abundance of individuals, partly separated and pure in different valleys and

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[29] See DAVIS in New Phytol. 12:234. 1913.

[30] Cf. DAVIS, *op. cit.* p. 532.

partly in mixtures which are known to contain also their hybrids. The specimen of 1807 is designated *O. biennis*, but both the flowers have the lobes of their stigma above the anthers, which is a differentiating mark of *O. Lamarckiana*. Moreover, it is the only decisive detail, all other characters of the figures applying equally to both species. If it is allowable to trust to this detail, we should be entitled to conclude that the station of Liverpool contained both forms as early as 1807, even as it is known to do at the present time. In this case, *O. Lamarckiana* must be assumed to have been introduced into England about the time of MICHAUX and LAMARCK, and a common origin for the specimens of their herbaria and the wild stations in England becomes highly probable.

The strain of Carter and Co. has been identified by LINDLEY as *O. Lamarckiana* Ser., and the high authority of this eminent botanist confirms my own determination of the same strain, made by comparing it with the authentic specimen of LAMARCK.[31]

At all events, the adduced facts indicate a very simple history of our species, which has come down to us unchanged, so far as we know, from the original American habitat.[32] There is no reason to suppose that it originated as a garden plant, and none at all to subject it to all the doubts ordinarily brought forward against the purity of descent of horticultural forms in general, simply on the ground that some garden plants are of known hybrid origin. *O. Lamarckiana* has remained unchanged through more than a century, and has kept as true to its type as any good wild species. "It is exceedingly fortunate," says DAVIS (*op. cit.* p. 527), "that the plant which serves as the type of *Oenothera Lamarckiana* Ser. should have come down to us so well preserved that there is scarcely a doubt of its identity." But the identity is with the species as it is still known under that name. Whether the species

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[31] DAVIS says (*op. cit.* p. 531) "the identification by LINDLEY of these plants with *O. Lamarckiana* Ser. was undoubtedly incorrect," but he does not give any reason for this assertion.

[32] DAVIS says (*op. cit.* p. 530) "that *Lamarckiana* has come down to us greatly modified, that its parentage is far from pure, that it is in fact of hybrid origin." This assertion, which is not based upon any facts, is clearly contradicted by the preservation in excellent condition of the three specimens of LAMARCK, POURRET, and MICHAUX, not known to DAVIS.

was in the same condition of mutability at the time of its first appearance as it is now, is of course a different question.[33]

Summing up the results of this historical investigation, we may say:

1. *Oenothera Lamarckiana* Ser. is represented by specimens in the herbaria of LAMARCK, POURRET, and MICHAUX (pls. XVII–XIX), and is, so far as this material enables us to judge, at the present time exactly the same plant as it was at that period. It has come down to us, through more than a century, as unaltered and as constant as true species usually do.

2. It has been a component of the flora of the eastern United States, where MICHAUX collected it and whence LAMARCK derived his specimen.

3. At the present time it is a component of the flora of England, and is as well established in that country as is *O. biennis* in different parts of Europe.

4. The strain which is now in cultivation, and which was introduced into the trade about the middle of the last century, was probably derived from some wild English locality, which itself may have come from an introduction into Europe of the seeds collected either by MICHAUX himself or by some other botanist of his period.

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EXPLANATION OF PLATES XVII–XIX

Plate XVII

Oenothera grandiflora Lam. (*O. Lamarckiana* Ser.): the authentic specimen in the herbarium of LAMARCK, two-thirds natural size, referred to as *A* in the text; in the left upper corner a bunch of flower buds of my culture of 1913, dried and pressed, is given for comparison, and photographed together with the main specimen.

Plate XVIII

Oenothera grandiflora Lam. (*O. Lamarckiana* Ser.): the specimen in the herbarium of Father POURRET, one-third natural size; on the label is written *Onagra vulgaris grandiflora* Spach.

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[33] Über die Dauer der Mutationsperiode bei *Oenothera Lamarckiana*. Ber. Deutsch. Bot. Gesells. 23:382. 1905.

OENOTHERA LAMARCKIANA SER.

HERBARIUM OF LAMARCK

OENOTHERA LAMARCKIANA SER.

Herbarium of Father Pourret

OENOTHERA LAMARCKIANA SER.
Herbarium of André Michaux

Plate XIX

Oenothera Lamarckiana Ser. in the "Herbier de l'Amérique septentrionale" of ANDRÉ MICHAUX, collected about 1800 in the eastern parts of the United States: *A*, top of spike photographed and reproduced about natural size; *B* and *C*, the whole specimen of MICHAUX, consisting of two parts, reduced about one-half; all three figures photographed for me by Dr. L. BLARINGHEM; in the reproduction the narrow bands of paper used to fix the specimen to its sheet and seen on the photographs have been omitted.

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OENOTHERA GIGAS NANELLA, A MENDELIAN MUTANT

HUGO DE VRIES

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OENOTHERA GIGAS NANELLA, A MENDELIAN MUTANT

HUGO DEVRIES

In a recent book GATES has studied the significance of the experiments made with species of *Oenothera* as proofs for the general theory of mutation, and has given an exhaustive and critical review of the facts in this rapidly increasing field of research.[1] He has laid special stress upon the results of crosses, which show the great diversity of these phenomena when studied in some wild plants, as contrasted with the now prevailing doctrine of Mendelism; for among the mutants of *Oenothera* instances of Mendelism are rare. The first known example is that afforded by *O. brevistylis*, which follows the law of MENDEL as a recessive in all its crosses with the parent species, with other mutants, and with other species of the same group.[2] But, unfortunately, the production of this form by means of mutation from *O. Lamarckiana* is so rare that it has not, as yet, been repeated under experimental control. Another instance is *O. rubricalyx*, discovered and studied by GATES (*op. cit.*, p. 103), which behaves as a dominant in its crosses with *O. Lamarckiana*.

In this article I hope to show that the dwarf character, which in so many instances complies with the formulae of MENDEL, but which behaves in a different way in crosses of the derivatives of *O. Lamarckiana*, may, at least in one instance in this group, follow that law as exactly as in any other pure Mendelian case. This

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[1] GATES, R. R., The mutation factor in evolution. London. 1915.

[2] DEVRIES, HUGO, Die Mutations-Theorie. 1:223; 2:151–179, 429.

instance, therefore, affords a means for the experimental study of the origin of such a form by mutation. The main result of this study is the proof of the occurrence of mutant Mendelian hybrids besides the pure dwarfs.

In my book on the mutation theory I have pointed out that the origin of *O. brevistylis* from *O. Lamarckiana* may have been induced by the mutation of a single sexual cell. If this combined in fertilization with a normal gamete, a hybrid would be produced which would not be distinct from the parent species in its external features. This hybrid would then, in its self-fertilized seeds, follow the law of MENDEL and produce, besides constant *Lamarckiana* plants, partly hybrids of the same type and partly specimens of the type of *O. brevistylis*. From this origin and the subsequent free intercrossing in the field, the yearly appearance of *O. brevistylis* would receive a sufficient explanation (DEVRIES, *op. cit.*, p. 506).

If the process of mutation into this type were more often repeated, it should be possible to discover the original hybrids. They would, it is true, not be discernible from their normal sisters by external marks, but would yield, after artificial self-fertilization, about 25 per cent of *brevistylis*. And since mutants are produced ordinarily in a proportion of 1–2 per cent or less, the difference would be large enough to be noticed. Until now, however, such cases have not been observed.

I have, therefore, been looking for another example in which a Mendelian behavior of the mutants might be associated with a normal coefficient of mutation from the parent species. Such cases would betray themselves by exceptionally high coefficients in single parent plants. Instances of such individual deviations are very rare, partly on account of the necessarily limited number of mother plants from which the seeds of our cultures are taken. But SCHOUTEN[3] has observed that *Oenothera gigas*, which ordinarily produces 1–2 per cent dwarfs, may be seen to throw them off in as large a number as 15 per cent. The same phenomenon has been described by GATES (*op. cit.*, p. 137), who counted 9 per cent and 11 per cent of dwarfs among the offspring of two self-fertilized plants of *O. gigas*.

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[3] SCHOUTEN, A. R., Mutabiliteit en Variabiliteit. 1908.

From time to time I have noticed the same deviating percentages in my own cultures. Thus, for instance, I fertilized in 1910 a specimen of *O. gigas* by its own pollen, and among 50 seedlings of its offspring 10 were dwarfs, pointing to a percentage of about 20 per cent.[4] Similar facts have since occurred more than once in my cultures.

SCHOUTEN and GATES have interpreted these figures as indicating a Mendelian proportion of dwarfs, and on this assumption the parent plant would have been a mutant hybrid in the same sense as explained above for *O. brevistylis*. Mutant hybrids would then occur in a race which produces dwarf mutants also, and the latter would then, of course, have to be considered as the products of the combination in fertilization of two sexual cells, both of which had mutated into *nanella*. The production of dwarfs from *O. gigas* would then follow the same process which is to be assumed for the origin of *O. gigas* itself from *O. Lamarckiana;* and the copulation of two similarly mutated cells would then more easily be accessible to experimental investigation.

In order to verify the exactness of this conception I have followed up the progeny of such a presumed mutant hybrid, and on the other hand have made crosses between *O. gigas* and *O. gigas nanella*. In both cases the truth of the assumption was easily ascertained.

Mutations of single gametes may be discovered by different means in other instances also, the production of potential *nanella* gametes by *O. Lamarckiana* being the most likely to be betrayed in this way.[5] I have observed such cases in crosses between *O. Lamarckiana* and *O. rubrinervis*. From these ordinarily two types arise in the first generation, one of which resembles the mother and the other the father. In my book on *Gruppenweise Artbildung* I have called them "*Lamarckiana*" and "*subrobusta*." Both types are usually constant after self-fertilization. But, from time to time, individuals appear which in their progeny produce an unexpected number of dwarfs. The following cases may be adduced.

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[4] DEVRIES, HUGO, Gruppenweise Artbildung. p. 340. 1913.

[5] Besides the production of gametes for *gigas* by *O. Lamarckiana*, as shown by the occurrence of specimens of *semigigas* in self-fertilized strains of the parent species, or by the production of the Hero-type in crosses of *O. Lamarckiana* with allied species.

The *rubrinervis* strain for these experiments had arisen as a mutant from *O. Lamarckiana* in 1895, and its second generation was cultivated in 1905. No dwarfs were produced in the first generation after the crosses, and in the second only from single individuals, the remainder giving either no dwarfs at all or only about 1 per cent, by ordinary mutation.

TABLE I

EXCEPTIONAL PRODUCTION OF DWARFS BY SINGLE PLANTS OF *Oenothera subrobusta*

Cross	Cross	1 Gen.	2 Gen.	Number of individuals	Percentage of nanella
Lamarckiana×rubrinervis....	1905	1913	1914	140	9
rubrinervis×Lamarckiana.....	1905	1907	1913	70	11
rubrinervis×Lamarckiana.....	1907	1913	1914	70	16

If we compare these figures with the results of the crosses between *O. rubrinervis* and *O. nanella* itself, as described in my *Gruppenweise Artbildung* (p. 215), we find a complete analogy, since these crosses give no dwarfs in the first generation, and in the second about 10–14 per cent from the self-fertilized specimens of *O. subrobusta.* It is evident, therefore, that the exceptionally high yield of dwarfs in these crosses of *O. Lamarckiana* and *O. rubrinervis* must be the product of latent mutations which occurred in some of the sexual cells of one of the parents. And since *O. Lamarckiana* is known to produce ordinarily 1–2 per cent dwarfs, while *O. rubrinervis* does not show signs of such a mutability, we may confidently assume that our figures indicate latent mutations of sexual cells of *O. Lamarckiana.*

BARTLETT[6] recently described a similar instance of an unexpectedly high mutability, and proposed for it the same explanation, on the assumption of a latent mutation of a sexual cell in a previous generation. This case is of the greatest interest since it relates to a pure species and not to the discovery of mutated gametes by means of crosses as in the experiments just described. The mutating species was *O. Reynoldsii* Bartlett, one of the forms of the old *O. biennis.* It produced in 1913 three marked types, one repeating the parental form, and the two others being dwarfs and called

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[6] BARTLETT, H. H., Mutation en masse. Amer. Nat. 1915.

mut. *semialta* and mut. *debilis*. The latter is, on the average, about half as high as the former. This curious segregation repeated itself in the next generation in 1914, not from all the individuals, but from only one of the two whose offspring have been tried in this respect.

Similar proofs of latent mutations of sexual cells may evidently be expected to occur in other strains also and will have to be looked for in all cases of an unexpectedly high degree of mutability.

I will now return to my experiments on the production of dwarfs by *O. gigas*. In order to obtain specimens of *O. gigas* yielding a high percentage of dwarfs from their seeds, I sowed in 1911 seeds of my pure strain, cultivated the plants as biennials, and fertilized them in 1912 by their own pollen, in bags. They were vigorous plants of the fourth generation (*Gruppenweise Artbildung*, p.175), and yielded a large harvest of seed, which was sown in 1913, and served as a criterion, since no essential differences were to be seen on the plants themselves. Moreover, I used the seeds of some good biennial specimens of the previous or third generation. The ancestors of all these plants had been fertilized by myself in bags down from the mutant in 1896 which started the race. The harvest of 1912 and 1910, sown in 1913, gave the result as shown in table II.

TABLE II

A. PERCENTAGES OF DWARFS AMONG OFFSPRING OF *O. gigas*

Generation	Number of seed-bearer	Total of seedlings	Dwarfs	Percentage of dwarfs
4th generation........	1	174	0	0.0
"	2	176	1	0.6
"	3	191	34	17.8
"	4	154	1	0.6
"	5	166	1	0.6
3rd generation........	6	164	0	0.0
"	7	43	1	2.3
"	8	52	0	0.0
"	9	132	2	1.5
"	10	130	0	0.0

From a second strain, derived from the same mutant and described in my *Gruppenweise Artbildung* (p. 175), I had in 1911–1912 nine biennial specimens which yielded a sufficient harvest.

Tried in the same way, they gave the percentages of dwarfs shown in table III.

TABLE III

B. DWARFS OF *O. gigas*

Generation	Number of seed-bearer	Total of seedlings	Dwarfs	Percentage of dwarfs
6th generation........	1	132	0	0.0
"	2	165	0	0.0
"	3	155	1	0.6
"	4	161	0	0.0
"	5	159	25	15.7
"	6	76	0	0.0
"	7	151	0	0.0
"	8	130	0	0.0
"	9	124	19	15.0

All in all, 19 specimens were studied. Among them three gave a percentage of 15–15.7–17.8, but the others gave only 1–2 per cent or no dwarfs at all. The dwarfs produced by this latter group were evidently due to ordinary mutability, but the figures for the former group differed too widely from these to be looked at in the same way. I consider them to be due to Mendelian segregation, and assume that the fact that they fall short of the expected 25 per cent is due to the difficulties of cultivation and to a less viability of the dwarfs as compared with the normal specimens.[7] I chose no. 3 of the first group (17.8 per cent dwarfs) for continuing the experiment.

If the segregation in this second generation followed the law of MENDEL, then among the plants of normal stature one-third must be constant in their progeny and the remainder must split up according to the same law. I succeeded in having a dozen of plants flower and ripen their seeds as annuals, fertilized them purely, and sowed the harvest in the spring of 1914. The result is given in table IV.

Three of the individuals yielded no more dwarfs than in ordinary mutation, and the seven others showed figures which approach the Mendelian law as nearly as might be expected. If we combine these figures with the 17.8 per cent of dwarfs of the former generation, we find for this about 18 per cent dwarfs, 57 per cent hybrids

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[7] See GATES, *op. cit.*, p. 89.

of high stature, and 25 per cent normal high specimens. This may be considered as sufficient proof that the splitting took place after the law of MENDEL.

TABLE IV

C. DWARFS AMONG THE OFFSPRING OF *O. gigas* (A, no. 3)

Number of seed-bearer	Total of seedlings	Dwarfs	Percentage of dwarfs
1	242	1	0.5
2	276	0	0.0
3	177	1	0.5
4	237	39	16.0
5	238	52	22.0
6	236	50	21.0
7	196	42	21.0
8	81	25	31.0
9	269	59	22.0
10	265	57	21.0

The dwarfs were counted in June and July, and the degree of development at this time corresponded with the photographs given in my *Gruppenweise Artbildung*, p. 316, *figs. 115* and *116*. At this period they are clearly distinct from the normal specimens and so there was no difficulty in counting them. In some specimens of *O. gigas* mut. *nanella* the number of chromosomes has been determined and was found to be the same as in *O. gigas* itself (28), as was to be expected. Partly on account of this fact, partly in consequence of the nearer relationship, the fecundations did not experience the difficulties which are connected with crosses between *O. gigas* and *O. Lamarckiana* mut. *nanella.* They succeeded fairly well and yielded, as we have seen, relatively large numbers of seeds.

The Mendelian behavior of the production of dwarfs by means of mutation from *O. gigas*, moreover, may be proved in another way. If the mutant hybrids of this form are fertilized by the pollen of *O. gigas nanella*, the expectation will, of course, be the production of 50 per cent of tall specimens and 50 per cent of dwarfs. But, on account of the smaller viability of the latter, we should have to be content with somewhat smaller numbers. In 1913, therefore, I crossed some specimens of apparently normal *O. gigas* with the pollen of a constant race of *O. gigas nanella*, my culture being the third generation derived from a mutant of 1910 (*Gruppenweise Artbildung*, pp. 315–316). I was fortunate in choosing, among some normal plants, two mutant hybrids, and will give the constitution of their progeny, together with that of two normal individuals of *O. gigas*, in table V. The numbers of seedlings have been very small in this case, owing to the small degree of fertility of the pollen of *O. gigas nanella.*

TABLE V

DWARFS IN THE FIRST GENERATION OF *O. gigas*×*O. gigas nanella*

Number of seed-bearer	Number of seedlings	Dwarfs	Percentage of dwarfs
1	38	11	30
2	65	28	43
3	28	1	3
4	59	2	

The first two seed-bearers had evidently about one-half of their egg cells mutated into *nanella*, which by the fertilization with the pollen of dwarfs must, all of them, become *nanella* specimens. The two last-named plants, although externally not differing from the others, had only very few mutated sexual cells, and therefore produced only about 3 per cent of dwarfs.

TABLE VI

DWARFS IN THE SECOND GENERATION OF *O. gigas*×*O. gigas* MUT. *nanella*

Seed-bearer	Total of seedlings	Dwarfs	Percentage of dwarfs
A. O. gigas nanella×O. gigas			
No. 1	291	45	15
No. 2	69	12	17
B. O. gigas×O. gigas nanella			
No. 1	60	16	27
No. 2	310	73	24
No. 3	304	62	20
No. 4	74	14	19
No. 5	283	46	16
No. 6	210	30	14
C. O. gigas mut. hybrid×O. gigas nanella	326	52	16

The experiment showed at the same time that hybrids between *O. gigas* and *O. gigas nanella* have the features and the stature of the former type, and thereby justified the assumption made above in the explanation of the behavior of mutant hybrids.

I made the reciprocal cross in the same year, fertilizing some dwarfs of my race by the pollen of normal plants of *O. gigas*. The fecundation was a difficult one and I got only 38 seedlings, all of which developed into tall plants of the stature and character of *O. gigas* (1914).

In order to study the segregation of dwarfs in the next generation I fecundated a number of specimens of the three described groups of artificial hybrids and sowed their seed in 1915. On the basis of Mendel's law the expectation is, for all of them, 25 per cent dwarfs, or somewhat smaller numbers on account of the lesser viability of these dwarfs. The sowings of 1915, counted in May and June, gave the results shown in table VI.

These figures give sufficient proof that the crosses between *O. gigas* and its dwarfs follow the law of MENDEL.

Summary

1. *Oenothera gigas* produces dwarfs (about 1–2 per cent) and mutant hybrids of normal stature, which after self-fertilization give 15–18 per cent, theoretically 25 per cent, of dwarfs.

2. These mutant hybrids split up, after self-fertilization, according to the law of MENDEL, yielding about 18 per cent dwarfs, 25 per cent normal specimens of tall stature, and 57 per cent hybrids of the same type. The latter gave about 21 per cent of dwarfs among their progeny.

3. The mutant hybrids, fertilized by *O. gigas nanella*, yield 30–43 per cent, theoretically 50 per cent, of dwarfs.

4. In artificial crosses with *O. gigas* the dwarfs follow the law of MENDEL.

5. The production of dwarfs from *O. gigas* by means of mutation, therefore, is to be considered as requiring the copulation of two gametes, both of which are potentially mutated into dwarfs. The mutant hybrids must then be the result of the fertilization of a mutated gamete by a normal one. They are correspondingly less rare than the dwarfs themselves.

6. In combination with the fact that the dwarfs of *O. Lamarckiana* do not follow the law of MENDEL, either in their origin by mutation or in artificial crosses with the parent species, these conclusions reveal a new differential character between *O. gigas* and its parent species.

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THE COEFFICIENT OF MUTATION IN OENOTHERA BIENNIS L.

HUGO DeVRIES

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THE COEFFICIENT OF MUTATION IN OENOTHERA BIENNIS L.

HUGO DEVRIES

The significance of the discovery of the mutability of *Oenothera Lamarckiana*, *O. biennis*, and allied forms is a double one. In the first place, it provides us with material for experimental investigations into the laws which govern the origin of living forms by means of the production of new characters and of the loss of existing ones. The knowledge of such laws must become of the highest practical value as soon as the evidently limited possibilities of producing new forms through the recombination of characters by means of crossing becomes exhausted. This conclusion seems especially well founded, since the old conception of improving agricultural races after the principle of slow and continued selections has now generally been abandoned and replaced by the direct selection of elementary types out of the mixtures which constitute the so-called agricultural races and varieties.

The appearance of really new characters seems to be a very rare phenomenon in nature, and a case in which such changes regularly occur in one or more per cent of all the individuals affords material for experiments, the results of which may be expected to apply to a large series of other species also, including, probably, an important number of agricultural crops.

In the second place, the mutability of the evening primroses has a distinct bearing upon the theory of mutation, or of the origin of all living species from one another by sudden leaps instead of by slow and almost invisible changes as was assumed by DARWIN. The theory itself does not, of course, depend on this or other single instances; it is founded upon general considerations taken from almost all branches of biological and paleontological research, as I have often pointed out.[1]

One of the main arguments is the statement that adaptations cannot, as a rule, have been produced by slow improvements, and that quite a large number of differentiations in organization, if not almost all the really important ones among them, are not adaptations at all.

Apart from our poetical admiration of nature, we have no other way of judging the reality and efficiency of supposed adaptations than by their effects in the struggle for life. Species which are distributed over large countries and occur in thousands of individuals are evidently well fitted for their life conditions. Newly introduced forms, which are spreading with astonishing rapidity and gaining a large territory often in the lapse of a few years, thereby show the highest degree of adaptation to their new environment. But a showy differentiation may be followed by a wide distribution, as in the case of *Drosera*, or limit the species to a relatively very small area, as in *Dionaea*.

Of late J. C. WILLIS has brought forward the most conclusive evidence against the theory of natural selection and in favor of an origin of species by mutation.[2] He bases some of his arguments upon his observations of the endemic species of Ceylon, such as are found in *Coleus*, *Acrotrema*, and other genera. If these endemics had evolved according to the law of natural selection, in consequence of a gradually increasing adaptation to their local environment, it would follow that they must now be better adapted than their parent types, conquer these in the struggle for life, and become quite common, while the old forms would tend to disappear. As a matter of fact, however, their behavior is quite the contrary.

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[1] DEVRIES, HUGO, The mutation theory. 2 vols. 1909–1910; Species and varieties, their origin by mutation, 2d ed., 1906; Die Mutationen in der Erblichkeitslehre. pp. 42. Berlin. 1912; The principles of the theory of mutation. Science **40**:77–84. 1914.

[2] WILLIS, J. C., Some evidence against the theory of the origin of species by natural selection of infinitesimal variations, and in favor of origin by mutation. Ann. Roy. Bot. Gard. Peradeniya **4**:1–15. 1907.

The endemics are rare, often strictly local, and grow in the midst of a luxuriant vegetation of their widely spread and thriving ancestors. It is hardly necessary to point out that this conclusion holds good not only for Ceylon, but for the origin of endemic and local species in general.

Willis has also called attention to the Podostemaceae and the allied group Tristichaceae. They show one of the most interesting illustrations of a very rich differentiation without the least indication of a relation to their environment. A very great uniformity in the conditions of life is combined with a most remarkable variety in their morphological structure. In the Podostemaceae the flowers are anemophilous, terminal, and erect, but combine with these characters of low organization the highest degrees of dorsiventrality and of differentiation, and this without any reference to advantages or disadvantages to be derived from them in their functions. Numerous points of similar significance in the structure of the vegetative and reproductive organs are pointed out by the author. Moreover, the genera *Tristicha* and *Podostemon*, which are widely distributed, are comparatively little modified from the earlier types of the orders, while the highly specialized forms are at the same time the rarest, exactly as in the case of the endemics of Ceylon.[3]

In the group of the evening primroses the same principles prevail. Their struggle for existence is limited by the difficulties which they have in producing roots. Cuttings almost never succeed in rooting, with the exception of the lateral rosettes at the base of the stem. Artificial transplanting becomes difficult as soon as the main root increases in size. In the field only a small percentage of the seeds germinate and thrive, and this only under special conditions. They want a stirred up soil and do not like to grow between other plants. These characters are common to all the forms which I have had an opportunity of studying in their native habitats. On the other hand, the numerous small specific differentiations, such as the form of the leaves, the branching of the stem, or the structure of the flowers and fruits, do not show

[3] Willis, J. C., On the lack of adaptation in the Tristichaceae and Podostemaceae. Proc. Roy. Soc. 8:532–550. 1914.

contradiction with the other hypotheses. If we accept these views, all reasons for supposing a correlation between the splitting phenomenon and the mutability would lose their value, and this latter process would come much nearer to the corresponding changes in *O. biennis* and allied species. The hypothesis, although resting on too large a number of suppositions, would in some sense be a support for the theory of mutation, since it is evidently impossible that these presumed qualities, which are incompatible with life, could have evolved slowly on the ground of their utility in the struggle for existence. Moreover, the hypothesis has no direct bearing on the observed phenomena of mutation, and the fact that in *O. biennis* such empty seeds are wholly or almost wholly absent proves beyond doubt that mutability may be independent of them. Thus the hypothesis of RENNER emphasizes the importance of a study of the mutation phenomena in *O. biennis*, in contradistinction to those in *O. Lamarckiana*, at least for the present, until facts are available to appreciate the correctness of his views.

Obviously the hypothesis that *O. Lamarckiana* might be a hybrid, whilst *O. biennis* is not, can in no way account for the phenomena of mutation which are common to both of these species. For this reason it seems important to describe the degree of mutability as it has been observed, up to this time, in *O. biennis*, which is, next to *O. Lamarckiana*, the most suitable species for this kind of research. The mutations in the other forms seem to be far more rare, and therefore require many more thousands of individuals for a statistical study or for experiments upon their causes.

Besides the assumption that *O. Lamarckiana* might be a hybrid, some authors have recently pointed out that hybridism may be one of the chief ways in which species are produced in nature, especially in the larger or so called polymorphous genera. LINNAEUS was the first to propose this hypothesis, at the time when the number of discovered forms was growing so fast as to make it almost impossible to assume a separate creation for every one of them. I have not the least doubt that LINNAEUS and his followers were right in this point, and that many wild species have been produced by the sexual combination of the characters of their allies. How great a rôle this kind of hybridization or of the recombination of characters has played in the production of species in nature is a question which it is impossible to answer at the present time. There is no doubt that numerous hybrids are continually produced in nature, but almost all of them disappear after a relatively short period of existence. Even in such genera as *Cirsium* and *Salix*, which are known to be rich in hybrids, our knowledge concerning the propagation of hybrid strains is very small.[7] It is quite possible that some as yet undiscovered principle of purification (Selbstreinigung der Arten) prevails on a large scale, and if this should be so, we must expect hybrid races to be rather rare in the field.

Focke has published a list of forms which have been duplicated by means of artificial crosses,[8] and quite a number of later instances have been added to this list, the latest of them being the reconstruction of *O. biennis leptomeres* out of *O. biennis* L. and *O. atrovirens* Bartlett (O. *cruciata* of my *Gruppenweise Artbildung*), by means of the expulsion of the undesirable characters in double reciprocal crosses.[9] But all such facts point rather to a relative rarity of hybrid races in nature, outside of the small number of well known polymorphic genera.

Gates assumes that crosses between species or between elementary species often occur in nature among allogamous or open-flowered forms.[10] But, according to my own experience, even in such cases hybrids are rare in the wild state, and hybrid races must be much rarer still. The slightest degree of weakening of the individual vigor will doom such hybrids to extermination, even as most of the occasional white flower mutations in nature disappear sooner or later, without starting a permanent variety.

In order to save the hypothesis of hybridism as a cause of the mutable condition of the evening primroses, different authors have

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[7] For the hybrids of *Cirsium* see C. Nägeli, Dispositio specierum generis *Cirsii* tam genuinarum quam hybridarum, in G. D. J. Koch, Synopsis Florae Germanicae et Helveticae, pp. 743–760. 1857; and for the willows see Max Wichura, Die Bastardbefruchtung im Pflanzenreich, erläutert an den Bastarden der Weiden. Breslau. pp. 95, mit zwei Tafeln. 1865.

[8] Focke, W., Die Pflanzenmischlinge. 465–468. 1881.

[9] Gruppenweise Artbildung. Berlin. 311–312. 1913.

[10] Gates, R. R., Mutation in *Oenothera*. Amer. Nat. 45:577–606. 1911; see pp. 578–579.

proposed different auxiliary suppositions. And since the possibility is acknowledged that mutability may be far more widely spread within this group than we now know, such suppositions must not be of a limited nature, but applicable to large divisions of the vegetable kingdom. KEARNEY, in studying the mutations of the Egyptian cotton, comes to the conclusion that these and other mutations might be the result of crosses between remote ancestors, but that these crosses have left no other traces in their descendants than "the disturbance of germinal equilibrium, which manifests itself in the production of mutants."[11] It is not very clear how this supposition is to bring the problem nearer to its solution.

In a recent article in this journal,[12] JEFFREY takes an opposite position. He assumes that the ancestral crosses have left another visible trace in their descendants, which is the partial sterility of their sexual cells. It is a well known fact that many hybrids have partially sterile pollen, while acknowledged species have, as a rule, only fertile pollen grains. JEFFREY assumes this rule to be without exceptions, but does not adduce any arguments in favor of this hypothesis. It is difficult to judge the value of an argument so long as the facts upon which it rests have not been submitted to criticism. But I might suggest that it seems rather hard to reconcile this view with the fact that in angiosperms three of the four megaspores are usually sterile, while only one produces an embryo sac. Are we to deduce from this fact, in connection with JEFFREY'S hypothesis, that all angiosperms are hybrids, at least on the maternal side?

Numerous special arguments could be adduced. It may suffice, however, to point out the genus *Carex*, in some of the best species of which the pollen is in the same condition, three of the grains of each tetrad being sterile and only one fertile.[13] Every single grain of the ripe pollen is a tetrad, showing the very reduced rudimentary remnants of three of its cells as a flattened investment of the fertile one.

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[11] KEARNEY, T. H., Mutation in Egyptian cotton. Jour. Agric. Research **2**:287–302. 1914.

[12] JEFFREY, E. C., Spore conditions in hybrids and the mutation hypothesis of DEVRIES. BOT. GAZ. **58**:322–336. 1914.

[13] JUEL, H. O., Die Entwickelung der Pollenkörner bei *Carex*. Jahrb. Wiss. Bot. **35**:649–656. 1900.

In the article just quoted, no parallelism has been attempted between the presence of sterile pollen grains and the already numerous published instances of mutations outside of the group of the evening primroses. Let us take for instance *Capsella Bursa-pastoris*, which has produced *C. Heegeri* and *C. Viguieri*.[14] Its pollen is devoid of sterile grains. Here we have a clear case of partial sterility not being the cause of mutability. On JEFFREY'S principle we must acknowledge *C. Bursa-pastoris* as a good species of undoubted gametic purity, and therefore it is evident that even the purest species may be in a mutable condition. From this we infer that mutability in itself does not justify the supposition of a hybrid origin, and that attacks on the gametic purity of the evening primroses have no real support on this side of the question. I have cultivated both *C. Heegeri* and *C. Viguieri* in my experiment garden; the first of them has globular and the other four-winged capsules. Both are historically known to have arisen suddenly from the parent stock, and come true to seed.

JEFFREY lays stress mainly on the fact that partially sterile pollen is a widespread phenomenon among the allies of the evening primroses. Whether it runs parallel to their mutability has not been investigated, and as a matter of fact it does not seem to be much more highly developed in *O. Lamarckiana* and *O. biennis* than in the other members of the group.

The question of the partial sterility of the Onagraceae has been most thoroughly dealt with by GEERTS.[15] He sums up his results as follows: The genera *Jussieua*, *Zauschneria*, *Epilobium*, *Boisduvallia*, and *Lopezia* are wholly fertile; they show neither rudimentary ovules nor sterile pollen grains. Only in *Epilobium* and *Boisduvallia* some rare pollen tetrads may sometimes miscarry. In the genera *Clarkia*, *Eucharidium*, *Godetia*, and *Gaura* all the ovules are fertile, but among the pollen grains about 30 per cent

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[14] SOLMS-LAUBACH, H., *Capsella Heegeri* Solms, eine neu entstandene Form der deutschen Flora. Bot. Zeit. **10**:167–190. *pl.* 7. 1900.

BLARINGHEM, L., Fleurs prolifères du *Cardamine* des prés. Bull. Soc. Bot. France **60**:304–311. 1913; and Les transformations brusques des êtres vivants. Bibl. Phil. Sci. Paris. 1911 (see pp. 119–147).

[15] GEERTS, J. M., Beiträge zur Kenntnis der Cytologie und der partiellen Sterilität von *Oenothera Lamarckiana*, Amsterdam. pp. 114, mit 24 Tafeln. 1901; see p. 93.

are sterile. *Kneiffia*, *Xylopleurum*, and *Lavauxia* have some rudimentary ovules as well as sterile pollen grains (10–50 per cent). In the genus *Oenothera*, with the subgenera *Onagra*, *Euoenothera*, and *Anogra*, the percentage of sterility is about 50 per cent in the ovary as well as in the anthers. In the first group about 40 species were studied, in the second 30, in the third 10, and in the last 40, making together about 120 species. If in the last three groups some species were pure, and devoid of sterile sexual cells, they would no doubt have been discovered, and the supposition that the remainder might be considered as their hybrids would have found support. But this was not the case, and if we wish to ascribe the presence of all these sterile sexual cells to ancestral crosses, the crosses must be supposed to have taken place, or at least to have begun, among the ancestors of the whole family, with the exception of the *Lopezieae*, the *Jussieueae*, and the *Epilobieae*. It seems hard to have to suppose that the whole pedigree of the *Xylopleurinae*, the *Clarkiinae*, and the *Oenotherinae* should have had to go through the development of partial sterility in order to produce the present mutability of *Oenothera Lamarckiana* and half a dozen or perhaps even a dozen of its nearest allies.

The second main supposition, namely that hybridism might be a cause of mutability, is dealt with by JEFFREY in a particular way. He assumes "that there is every reason to suppose that it has been an agency of great importance in *multiplying* species, although it is logically inconceivable in the present state of our biological knowledge that it could have presided at their origin." The first of these two alternatives represents, so far as I can see, a conviction which is at least very widely spread among biologists ever since the time of LINNAEUS. It by no means contradicts the theory of natural selection, nor that of mutation, nor any other evolutionary principle. It has no obvious reference to the phenomena observed in the evening primroses, since with them the production of new forms takes place in pure lines of a species which has come down to us unchanged during at least a century, since the time MICHAUX discovered it in the United States and sent it to Europe.[16] At least there is no direct recombination of characters

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[16] The probable origin of *Oenothera Lamarckiana*. BOT. GAZ. 57:345–360. 1914; see *pl. 19*.

by actual crosses between different elementary types, such as we ordinarily suppose to occur in polymorphic groups in nature.

The other alternative, that it is logically inconceivable that hybridism could have presided at the *origin* of new species, coincides exactly with the current conception of the mutability in the evening primroses. New forms originate through the evolution of new characters, as in *O. gigas* and *O. rubricalyx;*[17] or through the loss of existing ones, as in *O. nanella* and *O. rubrinervis;* or by means of the appearance of qualities, which were probably latent in the parent race, as in *O. lata* and *O. scintillans.*[18] These cases are evidently not recombinations of existing characters. If it is conceded that the hypothesis of a hybrid origin does not apply to them, it is obviously unimportant for the theory whether or not, besides them, there are other instances which may be considered as hybrid recombinations. *O. semigigas*, which is a hybrid between a normal and a mutated sexual cell, has never been considered as an argument against the mutation theory.

In cultures of chrysomelid beetles, W. L. TOWER has observed hereditary changes which run almost parallel to the mutations of *O. Lamarckiana.* He started from crosses between *Leptinotarsa decemlineata*, *L. multitaeniata*, and *L. oblongata*, and obtained constant races. When given proper treatment by changing their environic factors, these races could be made to break up, and they did so in a manner at least partially analogous to that of the evening primroses.[19]

It is obvious that the fact that mutations may be artificially induced in hybrid strains does not contradict the contention that they may arise in pure strains also. But from the experiments of TOWER it seems that some hybrid strains at least are more liable to show the phenomenon.

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[17] *O. gigas* is considered to be a progressive mutant on account of its double number of chromosomes and its special behavior in crosses. *O. rubricalyx*, which arose in the cultures of GATES from *rubrinervis*, and which I cultivated this summer from seeds kindly supplied by him, is perhaps the most beautiful among all the mutants of *O. Lamarckiana.* Its red color is something quite new in the group. It behaves as a Mendelian dominant in crosses with its parent species and is therefore obviously of a progressive nature; see GATES, R. R., Amer. Nat. **45**:600. 1911.

[18] See Gruppenweise Artbildung. Berlin. pp. 244–260. 1913.

[19] TOWER, W. L., Evolution of the chrysomelid beetles. Carnegie Institution of Washington Yearbook no. **12**:68–71. *pl. 3.* 1913.

Let us now consider the production of new forms analogous to the mutations of *O. Lamarckiana* observed in allied species. The theoretical significance of these facts lies in the proof that any hypothesis to explain such phenomena on the ground of qualities which are special to LAMARCK'S evening primrose is to be considered as wholly inadequate.

The first instance of mutability shown by another species than *O. Lamarckiana* was the production of a dwarf by *O. biennis cruciata*, a form which is now to be described as *O. biennis* var. *leptomeres* Bartl. This form was first discovered in 1900 by my son ERNST DE VRIES in the sand dunes near Santpoort in Holland, where a single specimen of *O. biennis* bore linear petals, while all the surrounding individuals were normal *O. biennis* L. It had evidently arisen there by mutation.[20] From it a constant strain has been derived, which is still in cultivation.[21] Among about 600 plants of this variety a single dwarf arose in 1903.[22] It had all the marks of *O. biennis* L. combined with the stature of a dwarf and the linear petals of the parent form.

Shortly afterward STOMPS discovered, in his cultures of hybrids between this *cruciata* variety and the original species, another dwarf and, moreover, a new mutant type, *O. biennis semigigas*.[23] Both arose from guarded seeds without any intermediate steps, in the same way that the mutants of *O. Lamarckiana* are known to arise. They had cordate petals, the dwarf having in other respects the same characters as the dwarf of *O. biennis leptomeres*, and the *semigigas* having 21 chromosomes in its nuclei. STOMPS was the first to lay stress on these facts as a proof that mutability is not limited to *O. Lamarckiana*, and that, even if this latter species should have to be considered as a hybrid, mutability cannot be explained as a result of such a condition, since there is not the least doubt concerning the gametic purity of *O. biennis* L.[24]

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[20] Die Mutationstheorie. Leipzig. 1900; see **2**:599.

[21] Pure seeds of this pure strain I shall be glad to send to any botanist interested in these questions.

[22] Über die Dauer der Mutationsperiode bei *Oenothera Lamarckiana*. Ber. Deutsch. Bot. Gesells. **33**:387. 1905.

[23] STOMPS, TH. J., Mutation bei *Oenothera biennis* L. Biol. Centralbl. **32**:532. 1912.

[24] DAVIS, B. M., Mutations in *Oenothera biennis* L. Amer. Nat. **47**:116. 1913; also Parallel mutations in *Oenothera biennis* L. Amer. Nat. **48**:498–501. 1914.

From these discoveries it was pretty safe to deduce that the pure *O. biennis* must also be in a state of mutability, and the first thing to do was obviously to make extensive cultures in order to find the pure line mutants. STOMPS cultivated over 900 individuals of the third and fourth generations of a pure line, derived from a rosette collected by him in the sand dunes near Beverwyk, Holland, in 1905.[25] Among these he found one *O. biennis* mut. *nanella*, one *O. biennis* mut. *semigigas*, and also four instances of the pale-yellow variety *O. biennis sulfurea*. The first two he calls *parallel mutations*, since they are analogous to the dwarfs and *semigigas* mutations of *O. Lamarckiana* and arise in the same way and with the same differentiating characters. The experimental origin of *O. biennis sulfurea* by mutation clearly shows that this variety, which is anything but rare in some parts of our sand dunes, may arise in the same way in the wild condition and afterward propagate itself by seeds.

The production of dwarfs from *O. biennis* by mutation has since been repeated more than once in my cultures of hybrids between this species and some of its allies,[26] and a *lata* mutant from *O. biennis* has been reported by GATES and described under the name of *O. biennis* mut. *lata*. Besides *O. biennis*, some allied species also are now known to show the phenomenon of mutation. Among these, an American form of *O. biennis*, which I cultivate under the preliminary name of *O. biennis Chicago*, has been studied more extensively than any other form. I had already found in the neighborhood of Courtney, Miss., in 1904, in a locality called "the bottom," along the shores of the Missouri River, a single specimen with narrow, almost linear leaves. Evidently it constituted a wild mutation from the surrounding type.[27]

Seeds taken from the normal specimens of this locality have since produced in my garden two mutations, which proved, in their progeny, to give constant and uniform strains and which I have cultivated during a series of years under the names of

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[25] STOMPS, TH. J., Parallele Mutationen bei *Oenothera biennis* L. Ber. Deutsch. Bot. Gesells. **32**:179–188. 1914; also Parallel mutations in *Oenothera biennis* L. Amer. Nat. **48**:494–497. 1914.

[26] Gruppenweise Artbildung. pp. 300–301. Berlin. 1913.

[27] *Op. cit.* p. 304.

O. salicastrum and *O. salicifolia.*[28] The first plants are as high as *O. biennis Chicago*, attaining 2 and sometimes (1914) almost 3 meters in height. They differ mainly in having narrower leaves. The *salicifolia*, on the contrary, is different from its parent species in almost all respects, being richly branched and rarely attaining one meter in height. It has almost linear leaves of a special blotted green, small erect flowers and long thin fruits. Analogous mutations have from time to time been observed in hybrid cultures of *O. biennis Chicago.*

Under the name of metaclinous hybrids I have described the curious phenomenon that heterogamous species from time to time produce among their hybrids from one cross, in one or a very few specimens, the type which is ordinarily that of the reciprocal hybrid.[29] For instance, the cross *O. biennis Chicago*×*O. Lamarckiana* gives the twin hybrids *densa* and *laxa*, while *O. Lamarckiana* ×*O. biennis Chicago* produces the twins *O. laeta* and *O. velutina.* Now among the first hybrid cultures sometimes a *velutina*, and more rarely a *laeta*, arises, and among the latter sometimes a *laxa.* Evidently some latent mutation, on the part of *O. biennis Chicago*, must be responsible for the production of these aberrant types. Analogous metaclinous hybrids have been described for *O. atrovirens* Bartl.[30]

Narrow-leaved mutations have also been seen in cultures of *O. muricata*, and of late (1914) in those of *O. suaveolens* Desf.[31] Moreover, *O. grandiflora*, collected by Mr. BARTLETT and myself at Castleberry in Alabama, throws off aberrant forms, one of which has broader and the other almost linear leaves.[32]

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[28] For descriptions and figures see Gruppenweise Artbildung. pp. 304–307.

[29] *Op. cit.* p. 308.

[30] This is the species described in my book Gruppenweise Artbildung under the name of *O. cruciata.* For its metaclinous hybrids see pp. 309–310.

[31] For the different varieties and mutations of *O. muricata* see also GATES, R. R., A contribution to the knowledge of the mutating Oenotheras. Trans. Linn. Soc. II. Bot. **8**:1–66. *pls. 1–6.* 1912.

[32] For *O. grandiflora* see GATES, *op. cit.* p. 38. If the three types of *O. grandiflora*, observed in my garden, occur also at Dixie Landing, Alabama, and have crossed, each of them, with *O. Tracyi*, and have perhaps produced twin hybrids and unlike reciprocals, this might explain the large number of forms observed on that spot; see Science **38**:600. 1912.

Lastly, mutations have been observed by H. H. BARTLETT[33] to arise in *O. stenomeres*, a new species of Montgomery, Maryland. In the fourth generation of a pure strain, embracing 106 individuals, he found three aberrant types. One was a self-sterile plant, the second had thick buds and short thick fruits, and the third was a stout and very hairy individual with densely hairy petals, which justify its new name *O. stenomeres* mut. *lasiopetala*. Hairy petals constitute quite a new discontinuous variation among the evening primroses, since all individuals of *O. stenomeres*, as well as the allied species now being studied in this respect, have petals which are glabrous, except under microscopic examination.

From this list we see that at least seven species, besides *O. Lamarckiana*, are now known to be in a condition of mutability, namely *O. biennis* L., *O. biennis Chicago*, *O. muricata* L., *O. atrovirens* Bartl., *O. suaveolens* Desf., *O. grandiflora* Ait.,[34] and *O. stenomeres* Bartl. Probably more or less numerous allied forms will prove to be in the same condition as soon as they are tried on a sufficiently large scale. Therefore, this mutability can no longer be explained on the ground of observed or supposed characters of *O. Lamarckiana* which would distinguish this species from the other types of the group *Onagra*.

O. biennis L., the European type of the species, which is growing wild and in large quantities in the sand dunes of Holland, where it had already been observed and collected by LINNAEUS, is, next to *O. Lamarckiana*, the most suitable for researches concerning mutability. DAVIS says, "No wild species of evening primrose has been so long under experimental and field observation or is better known to the workers with Oenotheras than this plant. The species has proven uniform to a remarkable degree, and it would be difficult to find a type of *Oenothera* so free from suspicion of gametic purity. The species appears to have been in Holland since pre-Linnean days, and is therefore very old. As material

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[33] BARTLETT, H. H., An account of the cruciate-flowered Oenotheras of the subgenus *Onagra*. Amer. Jour. Bot. **1**:226–243. *pls. 19–21.* 1914; see p. 236.

[34] Concerning the specific difference of the two last named forms, which have often been considered as synonyms, see L'*Oenothera grandiflora* de l'herbier de Lamarck, Travaux de biologie végétale dédiés à GASTON BONNIER, Rev. Gén. Bot. **25**^{2}:151–166. *fig. 1.* 1914.

for experimental studies on mutation, the Dutch *biennis* seems to the writer the best of all Oenotheras so far brought into the experimental garden.[35]

In order to determine the coefficient of mutation for *O. biennis* L., I have made a culture of about 8500 individuals, all of which have been studied from their germination to the period of flowering and of fruiting. In the interest of subsequent cultures they have been pulled out before ripening their seeds, with the exception of a sufficient number of their mutants, which were cultivated with some of the true individuals in another garden.

The seeds for this culture were taken from the pure line pedigree plants of STOMPS, which were derived from a single rosette of radical leaves collected by him in 1905 in our sand dunes near Wyk aan Zee.[36] In this part of our country, no other species of *Oenothera* are growing and no intermingling of forms has to be feared. From seed of this plant, self-pollinated, a second generation was grown in 1910 and a third generation in 1912. Self-pollinated individuals of these two generations gave the seed for the cultures of STOMPS in 1913 and for mine in 1914. These latter came from three and four parent plants, the descendants of which numbered respectively 5500 and 3000. Of course I sowed almost all the available seed, and their culture just covered the field at my disposal outside of my experimental garden (about 600 square meters). Thus all my plants belonged to the same pure line as those of STOMPS, and the individuals which supplied the seeds had been cultivated under the most favorable conditions obtainable.

The seeds were sown in January, the seedlings transplanted into wooden boxes in March, and brought on the field in the middle of April. This early sowing and transplanting is with us the most effective means of making the plants annual, and in my whole culture less than a dozen individuals failed to flower.

It was possible, this time, to pick out the dwarfs from the wooden boxes before the transplanting into the field. By this means a second change of place was avoided, and the dwarfs could

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[35] DAVIS, B. M., Parallel mutations in *Oenothera biennis* L. Amer. Nat. **48**:499. 1914.

[36] STOMPS, TH. J., Parallele Mutationen bei *Oenothera biennis* L. Ber. Deutsch. Bot. Gesells. **32**:179–188. 1914.

be cultivated together on a bed of my experiment garden, which enabled me to inspect them almost every day during their development and through the whole summer. The characters which distinguish the dwarfs in the stage of young rosettes, with leaves a few centimeters in length, were discovered in the following way.

The self-pollinated flowers of the dwarf specimen of STOMPS in 1913 had set no good seeds, but flowers pollinated from pure *biennis* had produced some fruits. Now my *O. Lamarckiana* mut. *nanella*, when crossed with *O. biennis*, yields only, or almost only, dwarfs. Therefore, the expectation was justified that such might also be the result of the cross *O. biennis* mut. *nanella*×*O. biennis*. Seeds from this cross had been sown about the same time; they yielded 108 seedlings, all of which have been planted out and have flowered. They were dwarfs without exception, reached in September a height of 40–45 cm. only, were richly branched, and had all the marks of *O. biennis* combined with the dwarfish stature and the liability to the same bacterial disease as is shown by the dwarfs of *O. Lamarckiana*. The young rosettes of these crossed *biennis* dwarfs clearly differed from the rosettes of the pure *biennis*. After the three or four first leaves with long petioles, there followed a group of leaves with smaller stalks and some sessile ones, thereby rendering the whole rosette far more compact than the corresponding ones of the pure *biennis*. With this character as a criterion, I isolated from my pure line boxes 8 individuals. One of them proved afterward to be a mistake; it was a pure *biennis*. Seven were dwarfs and have flowered; they were, in all external respects, like the crossed dwarfs of the control culture. Among the 8500 remaining plants I discovered later, in the field, only one dwarf. This shows that the characters were sufficiently reliable. All in all, I had 8 dwarfs in 8500 plants, making about 0.1 per cent. They occurred among the progeny of one of the self-pollinated mothers in the second generation (3 dwarfs), and of three of the parents in the third generation (5 dwarfs). Some of them have set good fruits after self-fertilization.

One of the most interesting and useful features of *O. biennis* L. is its propensity to make lateral rosettes from the base of the flowering stem. It is possible to isolate these rosettes and to have them grow separately. The experiment succeeds easily if the rosettes have produced one or two roots of their own, however young and slender these may be. *O. biennis nanella* shows the same character, and in August I succeeded in isolating from my 8 pure line dwarfs 8 rosettes, all of which have since developed into healthy young plants with some long and narrow leaves, followed by almost sessile ones, quite different from the rosettes of normal *O. biennis*.

Moreover, two *nanella* mutants occurred in the cultures of *O. biennis sulfurea* which I shall have to describe later. These cultures were grown from self-pollinated seeds of the four *sulfurea* mutants of STOMPS (1913), and embraced over 1000 flowering individuals, the flowers of which were pale yellow without exception. Two of these plants proved to be dwarfs and were transplanted into my experimental garden. Both of them have flowered with pale flowers, have been self-pollinated, and yielded a sufficient harvest of seeds. The coefficient of mutation in this race was therefore 0.2 per cent, which does not differ essentially from the first instance (0.1 per cent). These dwarfs are the founders of a new race, *O. biennis sulfurea nanella*, which I propose to cultivate next year. Its pedigree name would be *O. biennis* mut. (1913) *sulfurea* mut. (1914) *nanella*. It is a double mutant, such as are quite common in horticulture, and shows the way in which wild species would have to be analyzed.

I used the pollen of the *O. biennis nanella* of STOMPS, in 1913, for two crosses, which may be briefly mentioned here. In the first place, I fertilized castrated flowers of the pure line of *O. biennis*. The pollen was not abundant, and I got only 15 good seeds, all of which have germinated and become stout flowering plants. They differed from normal *O. biennis* in no respect and at no moment during their development. Their self-pollinated seeds will have to be sown next year. In the second place, I pollinated *O. Lamarckiana* with the pollen of *O. biennis nanella*. From this cross I had a culture of 55 individuals, all of which have flowered. One of them proved to be a *lata* mutant, having besides the *lata* marks the same characters as its sisters. These were all alike and in no way different from the ordinary and well known type of *O. Lamarck-*

iana×*biennis*, which, moreover, flowered at the same time on other plots of my garden. A number of these plants have been self-pollinated. Thus we see that the pollen of *O. biennis nanella* gives in these cases exactly the same forms as that of pure *O. biennis*, at least so far as the first generation is concerned.

The specimen of *O. biennis semigigas* of the cultures of STOMPS had only matured seed in the capsules which had been pollinated by pure *O. biennis*, without being castrated. From these seeds two types arose, neither of which was a *semigigas*. All in all, there were 19 plants, belonging to two forms, besides a mutant. This last was a dwarf, which, however, has not flowered. Of the remainder, ten individuals were pure *biennis* during their whole life and in all their marks. They had the normal number of chromosomes, namely 14, and gave a normal harvest of seeds. The others, 8 in number, were different from these in almost all respects, though but slightly. The color of their foliage was a whitish green, the leaves more flat, and with white veins. The spikes were more elongated, the flower buds more slender, the flowers small and erect, the fruits thin and cylindrical and relatively poor in seeds. These plants had 15 chromosomes, like the *O. Lamarckiana lata* studied recently by GATES and Miss THOMAS.[37] But they had none of the characters of a *lata*, showing thereby that the number of chromosomes, even if differing from the type, does not necessarily run parallel with the external features.

Further studies will have to show why one-half of the progeny of this cross came true to the characters of the pollen parent, while the other half constituted a new and uniform type, differing from all the mutations and hybrids hitherto studied in my experiment garden; and especially why the characters of the mother of the cross should be wholly absent in its progeny.

The first result of this state of affairs has been that the characters which the *semigigas* mutants might show in early youth remained unknown, and that it has not been possible to point them out before the time of flowering. In July, all the spikes

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[37] GATES, R. R., and THOMAS, N., A cytological study of *Oenothera* mut. *lata* and *O.* mut. *semilata* in relation to mutation. Quar. Jour. Micr. Sci. **59**:523. 1914.

were carefully mustered and four specimens of the *semigigas* type were discovered. This makes a proportion of 4 to 8500, or about 0.05 per cent, showing the *semigigas* mutants to be only half as frequent as the *nanella*. On later inspections no additional cases were observed, and likewise intermediate or doubtful instances were absent. The four plants were exactly alike, save that three were very vigorous, and one, grown in a shady part of the garden, was very weak. The chromosomes were counted in the first three instances and found to be 21, as in the corresponding mutant of STOMPS.

My four mutants were easily discovered by their broad conical flower buds and their elongated spikes, which strongly contrasted with the dense spikes of the surrounding *biennis*. They reached the same height as these, the lowest flower being 90 cm. above the soil, and the total height about 1.5 meters. The leaves had the same form as those of *biennis*, but were a darker green and slightly more pubescent. The pollen consisted of 3- and 4-cornered grains, both of which types seemed fertile only for about a quarter. Artificial self-fertilization, however, had no result, and on the stigmas of *O. biennis*, *O. gigas*, and *O. Lamarckiana* the effect of the pollen was very slight, inducing some swelling of the ovaries but no good seeds or almost none. Inversely, I have tried to fertilize the flowers with the pollen of the three species named, but got a good result only in the case of *O. biennis.* Numerous good capsules with a sufficient supply of apparently good but in reality empty seeds have been obtained by leaving the flowers free to the agency of insects in the midst of the thousands of their flowering sisters, while in the same garden no other Oenotheras were grown.

The three vigorous specimens of the mutant produced some lateral rosettes at the base of their stem, even as we have seen in the case of the parent species and the dwarf variety. These rosettes were isolated and planted in pots in the beginning of August; four of them were very vigorous, but the other one rather weak. They have thrown off lateral rosettes themselves, and the stems repeated the production in two instances. It is proposed to try to bring these plants through the winter and repeat with them the culture and the experiments of this year. After a month, their leaves reached 15 cm. and more in length and were clearly distinct from the normal type of *O. biennis*, being much broader and a darker green.

Of the four *semigigas* mutants, two arose from the seeds of the same parent which yielded the *semigigas* of STOMPS in 1913. All three belonged to the third generation of the pedigree. The two others were derived from two different parents of this same generation and therefore belonged to the fourth. The reason why three of the five came from the same lot of seed was probably no other than that the harvest of this plant had been the largest. More than one-third of my whole culture (3200 plants) were children of this mother.

No *gigas* with 28 chromosomes and fertile pollen occurred in my culture. With a chance of one sexual cell mutated into *O. gigas* in every 2000, the expectation for the copulation of two such cells is evidently only one in every 4,000,000. This would require a garden of more than five or six acres (two hectares) and the corresponding cost of labor. Perhaps some American institution is able to carry out the experiment. It may be reduced very essentially by a previous study of the marks of the young rosettes of *O. biennis semigigas*, so as to be able to plant out almost only these, hoping to find the *gigas* among them; or by studying the external influences which may increase the degree of mutability of the parents in the desired direction.

Sulfurea mutants have been far less rare. This was to be expected from the fact that STOMPS had 4 of them among 920 plants. From the parent type they differ only in the color of their petals, which is a very pale yellow. It is so pale that collectors, who see the variety in our sand dunes, often call the petals white. In the cultures they are easily seen as soon as the flowers open, especially in the evening. I found 27 of them among my 8500 plants, making a percentage of 0.3 per cent. They occurred in the progeny of all the 7 parents of my stock, 13 in the third, and 14 in the fourth generation. There were 6 parents, whose progeny contained 0.1–0.3 per cent, and one with 0.7 per cent (of the fourth generation). It is possible that this last parent had been more favored by external conditions than the three others of the same group, although it grew among them and did not show any higher degree of vigor.

The fact that *sulfurea* mutants were observed in the progeny of every one of the 7 parents of my culture directly proves this line of mutability to be hereditary in the whole family derived from the 1905 rosette from Wyk aan Zee. In combination with the sporadic occurrence of the pale-colored variety in our sand dunes, we may further infer that this mutability is hereditary in the whole stock of our country, and probably also in the whole species, since *sulfurea* plants have been found from the time of TOURNEFORT in France and other European countries.

From the mutants constant races may be derived. I sowed the self-pollinated seeds of the four mutants of STOMPS, and cultivated 205, 225, 271, and 358 seedlings, altogether 1059 plants, all of which have flowered and produced only pale-yellow petals, making a very striking impression of constancy.[38] When crossed with the pure species, the *sulfurea* strains give uniform hybrids which are patroclinous. Those of *O. biennis*×*sulfurea* have the pale flowers, those of *O. biennis sulfurea*×*biennis* show the same bright yellow as the parent species.[39]

On experimental germination of seeds

Of the seeds of *Oenothera Lamarckiana* ordinarily only about one-third produce seedlings, and this proportion is highly variable, depending mainly on the conditions of cultivation of the parent plant. Among the remaining seeds some contain a normal embryo, others a more or less completely decayed one, while still others are empty. The last have been thoroughly studied by RENNER, who found that they have been fertilized as well as the normal seeds and those with decayed embryos. Between these normal and externally normal seeds are seen the numerous rudimentary ovules which have not been fertilized, and have not essentially increased their size after the fertilization of the others. These rudimentary seeds have been described by GEERTS, as referred to above.

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[38] Self-pollinated seeds of this second generation of *O. biennis sulfurea* are available for exchange in return for other races of mutating primroses.

[39] Gruppenweise Artbildung. p. 298.

In the empty seeds the embryo develops only a little, just enough to stimulate the seed coats to an almost normal development, in size as well as in structure. For the most part these empty seeds are a little smaller and especially a little less broad than the others, and can therefore easily be picked out of a sample. But quite a good many are externally exactly like good seeds and cannot be distinguished from them without being opened. RENNER states that about one-half of the seeds are in this empty condition.

By means of a hard steel needle with a curved tip it is easy to make the seeds burst, especially after a thorough wetting. The seeds which contain a healthy embryo will discharge it; the unhealthy seeds will protrude a slightly brownish pulp; and the empty seeds show the lack of contents, except a thin layer of endosperm in the embryo sack. The various groups may be counted out in this way, but the limits between the originally empty seeds and those which have become more or less empty by an early decaying of their germs are not sharp and often dependent upon the health conditions of the seed-bearing individual.

Among the seeds with a normal and healthy embryo some will germinate during the first days after sowing, especially if the temperature is a favorable one. Others will follow sooner or later, some after weeks or months, while still others may remain dormant for years. It is not an uncommon case that the proportion of the rapidly germinating seeds is a very small one, and in this case a large quantity of seed is necessary to secure a small number of seedlings. Moreover, in those cases where the seeds do not produce a uniform progeny, but a mixture, as, for example, with twin hybrids or in hybrid splitting, the possibility cannot be denied that the numerical proportion of the components of the mixture may be different for the rapidly germinating seeds as compared with the others. In other words, percentage figures may be influenced to some degree by the occurrence of a more or less considerable proportion of dormant seeds.

In order to ascertain the value of this objection, I have made from time to time cultures in which the rapidly germinated seedlings were planted out separately from the slower ones. As a matter of fact, I have not found as yet any essential differences between the two groups; but the doubt remained that such might still be discovered if it were possible to bring to germination all, or almost all, the slow seeds of a given sample. For a number of years I have tried various means to reach this end, but only of late have I succeeded.

It is a well known fact that many kinds of hard seeds may be induced to germinate by means of filing. Filing machines, especially for the smaller leguminous seeds, are now often used in agricultural practice, the best known one being the Swedish type, constructed by HJALMAR NILSSON, the Director of the Swedish Agricultural Experiment Station at Svalöf. It files the seeds in a continuous current by throwing them against a rapidly revolving filing disk. Unfortunately, in the seeds of the evening primroses, the hard layer is not the external tissue, but that of the inner integument. The outer coat thus prevents the filing, and experiments which Professor NILSSON has had the kindness to make for me with his apparatus did not give the desired result.

In the soil the water is imbibed into the seeds through microscopic and very narrow slits in the hard layer. It is assumed that these slits are filled with air which, in the narrower ones, is a powerful obstacle against the penetration of the water. So long as this only reaches the cuticularized parts of the walls of the slits, no moisture can reach the embryo and this remains dormant. The question, therefore, is to compel the water to penetrate into the deeper parts of the slits so as to reach the spots which can be moistened.

In order to solve this difficulty, I have tried pushing the water into the slits under a high pressure. A compression of the surrounding air to 6–8 atmospheres has proved to be sufficient to induce all or almost all the healthy seeds to germinate in a few days. The apparatus used is a combination of an autoclave with an air-pump such as is used for automobiles, and the model known as the Michelin pump seems to be the easiest and cheapest available one, while any autoclave, as, for example, an ordinary steam sterilizer, will answer the purpose. Mine has 20 cm. inside diameter, and can be filled to 8 atmospheres in about five minutes.

Before compressing the air in the seeds, these are thoroughly soaked with water. Ordinarily they are exposed in small tubes, half filled with water, to a temperature of about 30° C. during one night. In the autoclave they remain from one to three days, at the temperature of the room. My apparatus can accommodate over 100 tubes at a time, each containing a different sample. After leaving the reservoir, the seeds may be sown in seed pans for cultivation or may be left to germinate in the same tubes, if it is only intended to determine the proportion of seedlings produced. In order to do this the water is poured off through a small sieve, the tube is closed by means of a cork, and the seeds are distributed along the upper inner side of the tube, this lying horizontally. In this way they get exactly the required amount of water and of air for a vigorous germination.

I will now give some figures to show the effect of this pumping in of air into the previously soaked seeds. After pumping, the degree of germination was determined by leaving the tubes in a stove at 30° C. and counting the seedlings in samples of about 200 seeds each. Out of 18 capsules from self-fertilized flowers of a spike of *O. Lamarckiana*, 3400 seeds were counted, a separate germinating tube being used for the contents of each fruit. Of these seeds, 15 per cent germinated during the first two days and only 3 per cent during the two following days, showing the normal germination power to be almost exhausted. Then the seeds remained three days in water under a pressure of 8 atmospheres, after which they were brought back to the stove. The next two days produced 22 per cent seedlings, and the four following ones added only 1 per cent to this number. Then the remaining seeds were tried with a needle. Only about 5 per cent contained embryos, half of which at least were evidently in a decaying condition.

The total of germs was 46 per cent, leaving 54 per cent for those with an undeveloped germ. From these figures we see that the production of seedlings from a sample of seeds may be more than doubled by the pumping method, while all or almost all the healthy germs may be made to germinate. Numerous similar instances could be added.

A sample of seeds of *O. biennis*, taken from a late flowering individual, produced only 2 per cent of seedlings in the first two days, while a control sample, after having been exposed in water to a pressure of 6 atmospheres, produced at once 80 per cent of seedlings. In the same way for *O. suaveolens*, the percentage was increased from 3 to 14 per cent, for *O. muricata* from 12 to 80 per cent, and for *O. Cockerelli*, a species which is often very slow in germinating, from 2 to 72 per cent.

It is not improbable that in *O. Lamarckiana* the hard seeds may contain more mutants than the easily germinating ones, which have thus far been studied. It seems even possible that they may conceal some new, as yet unobserved, types of mutations. The new method enables us to bring almost all the germs to germination, as well as to separate the seedlings of the different groups.

Before concluding, I may be allowed to recommend this method for the study of various other kinds of seeds also.

Summary

1. In a culture of 8500 specimens of pure line *Oenothera biennis* L., 8 mut. *nanella*, 4 mut. *semigigas*, and 27 mut. *sulfurea* arose, giving the percentages of about 0.1 per cent, 0.05 per cent, and 0.3 per cent. In cultures of *O. Lamarckiana* the corresponding numbers are for *O. nanella* 1–2 per cent, for *O. semigigas* 0.3 per cent (Gruppenweise Artbildung. p. 329), while no color mutations have been observed as yet. With the origin of *O. Lamarckiana* the mutability for dwarfs, therefore, must have increased at least tenfold, and for *gigas* types about sixfold. The material cause for this improvement is in all probability the same as or closely connected with the cause of the largely increased number of mutative forms which are known to start from *O. Lamarckiana.*

2. From the cross *O. biennis* mut. *nanella*×*O. biennis* only dwarfs of a uniform type arose (108 Ex). *O. biennis*×*O. biennis* mut. *nanella* was in the first generation exactly like pure *biennis; O. Lamarckiana*×*O. biennis* mut. *nanella* exactly like *O. Lamarckiana* ×*biennis*.

O. biennis semigigas is self-sterile, but when pollinated by *O. biennis* gives for one-half pure *biennis* with 14 chromosomes, and for the other half a new, slender type with 15 chromosomes.

O. biennis mut. *sulfurea* easily yields constant races of a uniform sulphur color.

3. The question whether there is any causal relation between partial sterility of the sexual cells, hybridism, and mutability has to be studied in all those instances in which mutations are known to occur or to have occurred. In some of these cases, at least, the conditions are far more simple than for the evening primroses, as for example in *Capsella Bursa-pastoris*.

4. The mutative condition of *O. biennis* may be ascribed to some "germinal disturbance" of its hereditary qualities. Or, if we replace this vague and meaningless expression by a sharp hypothesis, we may assume as its cause the presence of one or more pangens in a labile position. The transition from *biennis* to *Lamarckiana* would then require the addition of one or more pangens in the same state, in order to explain the higher percentage of mutants and the larger number of their different forms. The presence of such labile pangens seems well proven by the results of numerous crosses.

The contention, however, that the transition of "undisturbed germinal material into a state of disturbance," or of one or more pangens from the stabile into the labile condition, may be induced by external influences in pure species, has not as yet found general acceptance. Some authors believe that crosses between different types are required to secure this effect. At this moment, it seems difficult to give experimental evidence for or against this view. Until this is reached, we must rely upon comparative studies in order to answer the main question whether or not the observed mutations in the evening primroses are analogous to those by which the mutation theory explains the evolution of the animal and vegetable kingdoms.

5. The mutants of *O. Lamarckiana* all agree with that species in certain characters, and not one of them shows any indication of a reversion toward any of the allied wild types. If the mutability was an effect of crossing, some marks, at least, of the other parent would be expected to reappear.

Besides this consideration, the available evidence lies in the fact that the derivatives of *O. Lamarckiana*, originated in my garden, differ from one another in marks, which are, although not identical, strictly analogous to those which differentiate the wild species of the whole group. In some cases the differences are even larger. Those between the wild species are often very small and limited to certain life periods, leaving the species quite alike during the remainder of their development. No arguments have as yet been adduced to doubt the fundamental identity of the two groups of characters.

6. The phenomenon of mutability, observed in *O. Lamarckiana*, *O. biennis*, and allied forms, is therefore to be considered as a simple continuance of the supposed mutability which presided at the origin of the wild species of the evening primroses.

7. The seeds of the evening primroses are often very slow in germinating, leaving sometimes one half or more of the healthy germs in a dormant condition. This difficulty in the study of mutation percentages, etc., may be overcome by pressing the water into them. A pressure of 6–8 atmospheres during 1–3 days is ordinarily sufficient to stimulate all or almost all the good germs to a rapid germination.

The microscopic preparations and the counts of chromosomes, referred to in this article, have been made for me by my assistant Mr. C. VAN OVEREEM, to whom I wish to give my sincere thanks for his coöperation.

AMSTERDAM, HOLLAND

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NEW DIMORPHIC MUTANTS OF THE OENOTHERAS

(WITH FIVE FIGURES)

HUGO DE VRIES

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NEW DIMORPHIC MUTANTS OF THE OENOTHERAS

HUGO DEVRIES

(WITH FIVE FIGURES)

Among the previously described mutants of *Oenothera Lamarckiana* Ser. there is a form which, although fertile with its own pollen, yields a dimorphic progeny. Some of the individuals exactly repeat the stature and characters of their parent, but others return to the type of *O. Lamarckiana.* Besides these, new mutants, especially *O. oblonga*, are relatively numerous. The two main types are produced in varying proportions, according to the individual cultures. The typical specimens may be as few as 10 per cent, or as numerous as 80 per cent. In most instances, however, they show a proportion of about 35–40 per cent. Considering the much smaller individual strength of the typical ones, as compared with the atavistic specimens, these figures may be regarded as indicating a splitting, ordinarily, into nearly equal parts.

This inconstant mutant is *O. scintillans.*[1] Exactly the same phenomenon of splitting has been observed recently in a number of new types. In the first place, in *O. stenomeres* mut. *lasiopetala*, described by BARTLETT.[2] In the second place, it has occurred in my own cultures, among the new mutants of *O. Lamarckiana*, as well as among those of another American species, described under

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[1] The mutation theory. Chicago. 1909. Vol. I, p. 377; and Gruppenweise Artbildung, p. 257. 1913.

[2] BARTLETT, H. H., Mutations of *O. stenomeres.* Amer. Jour. Bot. 2:100–109; see also 2:146. 1915.

the preliminary name of *O. biennis Chicago*.[3] I shall deal with this one under the name *O. saligna*, and designate the new inconstant mutants of *O. Lamarckiana* as *O. cana*, *O. pallescens*, *O. Lactuca*, and *O. liquida*. As far as investigated, they all follow the rule that in every generation they split up into two ordinarily almost equal groups of typical specimens and of atavistic individuals which, in all cases, exactly duplicate the characters of *O. Lamarckiana*.[4] Moreover, they show a relatively high degree of mutability.

With one of them, *O. cana*, I have made a number of crosses with allied forms, in order to ascertain that it behaves in the same manner as *O. scintillans*, and that the same conception of heterogamy must be applied here also. In this mutant the pollen carries only the hereditary qualities of *O. Lamarckiana*, and the specific marks of the mutant are handed down to their progeny through the ovules only.[5] This conception of heterogamy may be considered to hold good for the other inconstant types also.

The same behavior is found in *O. lata*, but since this form never produces any fertile pollen in my cultures and has to be fertilized by *O. Lamarckiana* in order to produce seeds, the evidence which it affords is less stringent than that given by the self-fertile dimorphic races.

Oenothera Lamarckiana mut. *cana*.—Among a number of dubious mutants from *O. lata* which were cultivated as biennials in 1906–1907, a plant was noticed in the third generation of that family with narrower leaves of a gray color, evidently constituting a new type. It was very vigorous, reached a height of about 2 m., and was self-fertilized. It will be designated as *O. cana* from *lata* no. 1, since the first family of *O. cana* was derived from it.

Next year the same mutant type was recognized among the young rosettes, issuing from different samples of seeds of *O. lata* (fig. 1). All in all there were 5 specimens of *O. cana*. In order to determine the frequency of this mutant I have made two cultures

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[3] Gruppenweise Artbildung, p. 52. *fig. 18* and *pl. 6*. 1913.

[4] In the wild condition such a splitting would evidently cause a race to die out after a few generations, especially since the atavists are very fertile and much stronger than the mutant form. As a matter of fact, inconstant wild species of this type are not known. See The mutation theory, Vol. I, p. 380.

[5] Gruppenweise Artbildung, p. 273. 1913.

on a sufficiently large scale, using the seeds produced by my pure strain of *O. lata* fertilized by *O. Lamarckiana*. The seeds of 1909 gave 564 seedlings, with 18 per cent *lata* and 2 per cent *cana*. Those of 1908 gave 1550 seedlings, 8 per cent of which were *lata* and 9 per cent were *cana*. Other mutants appeared in these cultures in different proportions, as usual.

FIG. 1.—*Oenothera Lamarckiana* mut. *cana:* a young plant showing the narrow leaves by which it is easily distinguished from rosettes of the *Lamarckiana* type in the same sowings; June 11, 1915.

Among the seeds of pure *O. Lamarckiana*, *O. cana* is much the rarer. In 1913 I fertilized, on 5 strong biennial specimens, almost all the flowers during two months and got sufficient seed to have 20,000 seedlings in 1914. Of these only 6 were *cana*, giving a percentage of 0.03 per cent. In the same boxes 7 *rubrinervis* and 5 *scintillans* appeared as mutants, showing that the mutation coefficients for these three forms do not essentially differ from one another.

Stray mutations into *cana* have appeared in later years in different cultures, as, for instance, in 1913 in those of *O. laevifolia* and *O. scintillans*. Three mutations from *O. pallescens* will have to be recorded in the pedigrees relating to this form. It seems probable that *cana* mutants also have appeared in previous years, but have not been distinguished from other narrow-leaved types, of which there have always been quite a number in the larger cultures. Many other mutations also have escaped observation during a series of years until a single specimen developed into a strikingly new type.

I have cultivated *O. cana* mostly as annuals, but in some instances as biennials. In both cases the stature is the same as that of *O. Lamarckiana*, but in the annuals the stems are slender and the foliage rather loose, whereas the biennials have thick and strong stems with dense foliage. The leaves are narrow, with a shorter blade and a longer petiole, and of a very striking gray color. The flower buds are long and thin, contrasting sharply with those of *O. Lamarckiana* and even more so with those of *O. pallescens* and *O. Lactuca*. The spike is less dense than in the parent species and the fruits are more cylindrical and narrower, containing fewer seeds (fig. 2). In the flowering condition, as well as in the stage of young rosettes, the plants are now easily recognized, but at other periods of their development it is often difficult to identify and count them, some specimens showing their marks very clearly, but others resembling more or less their *Lamarckiana*-like sisters.

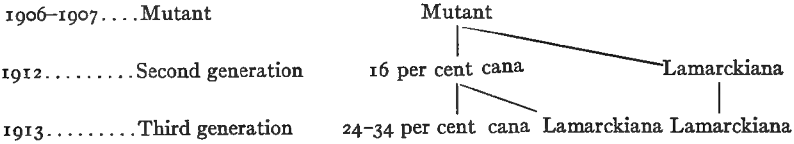
The easiest marks are afforded by the flower buds. Measured the day before opening and with the tube and ovary, their size varies, as a rule, from 75–80 mm., against 80–95 mm. in *O. Lamarckiana* cultivated under the same conditions; means 77.5 against 90 mm. The breadth, measured at the base of the conical part above the tube, is only 7 mm. The 4 tips at the top of the bud are more or less bent on one side, and this curious mark is so striking that it is often the first which draws the attention to a stray mutant of the *cana* type (fig. 2). The 4 lobes of the stigma are

FIG. 2.—*Oenothera Lamarckiana* mut. *cana:* flowering spikes of the two types into which each generation splits; on the left the *Lamarckiana* type, on the right the parental type, showing the thin buds and the bent tips of the calyx; the difference in height of the 2 spikes is the same as the mean difference in height of the 2 groups on the bed; third generation of mut. *cana* no. 3, photographed July 22, 1914.

more slender than in *O. Lamarckiana;* the anthers are thin, provided with a good supply of pollen on stout specimens, but often deficient in this production on the weaker ones, especially in annual cultures.

O. Lamarckiana mut. *cana.*—Among the *cana* mutants from *O. Lamarckiana* only one specimen has been self-fertilized. It arose in 1913 in the fourth guarded generation from a plant introduced into my garden in 1905 from the original field near Hilversum. It was only recognized at the end of July, when it opened its first flowers. It yielded few seeds, which gave rise to 19 seedlings only, all of which flowered in 1914. Of these, 13 exactly duplicated the type of *O. Lamarckiana,* 5 were *cana,* and one was a mutant *nanella.* These figures point to a percentage of 26 per cent *cana.*

O. cana from *lata* no. 1.—From the first mutant of 1906–1907, previously described, I have derived a pedigree family in order to try its constancy and got the following result:



The size of these cultures is given in table I.

TABLE I

YEAR	GENERATION	PARENT	OFFSPRING		PERCENTAGE OF CANA	MUTANTS
			Total	Flowering		
1912.........	Second	mutant	31	30	16	....
1913.........	Third	cana	49	48	24	1 nanella
1913.........	Third	cana	115	65	34	4 nanella
1913.........	Third	Lamarckiana	60	25	0	....

The offspring of two *cana* individuals of the second generation have been studied separately, as well as those of one specimen of the *Lamarckiana* type. The plants have been under observation through their whole lifetime, so far as space allowed, the numbers of the flowering individuals being given in the column next to that of the totals. The *cana* were all of the same type; the *Lamarckiana* exactly repeated the marks of the original species. Three of the dwarfs have flowered. They all had the marks of ordinary *O. La-*

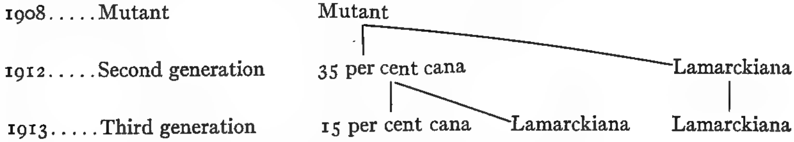
marckiana mut. *nanella* and none of those of *O. cana*. This has been the case in some of the other pedigree cultures of this type, but it should be remarked that in other cases the characters of *O. cana* may combine with the dwarf stature. Such dwarfs have the narrow gray foliage and are easily distinguished from typical *O. nanella* specimens.

The self-fertilized seeds of the *cana* individuals split in both generations into *cana* and *Lamarckiana*, just as *O. scintillans* splits into *scintillans* and *Lamarckiana*. The proportions 16–24–34 per cent with a mean of 25 per cent seem to indicate a splitting into nearly equal parts, with a loss on the side of the weaker form. The same deviation from equality will be seen in almost all the figures of this article, and the same explanation must be considered as applying to all of them. It is almost always the new type which is in the minority.[6]

The seeds of the *Lamarckiana*-like individuals do not give rise to a splitting of this kind, keeping true to their parent form. The same fact recurs in all the pedigrees to be mentioned later on, and for all the new dimorphic types. It may be taken to be the rule, therefore, although the trials have been only one or two in each instance. It agrees fully with the behavior of the analogous splitting products of *O. scintillans*.

O. cana from *lata* nos. 2 and 3.—In a culture of about 600 seedlings of *O. lata*, 4 mutants of the *cana* type arose in 1908. The *lata* strains had been derived from some annual mutants which had been produced by my *O. Lamarckiana* in 1905, and described in my *Gruppenweise Artbildung* (p. 247). From these mutants a second generation was cultivated in 1907, and fertilized by the pollen of *Lamarckiana*-like individuals of the same culture. Their seeds yielded the two *cana* mutants to be described here, and two others, from the seed of which only one generation has been studied.

The pedigree of mutant no. 2 is given below:



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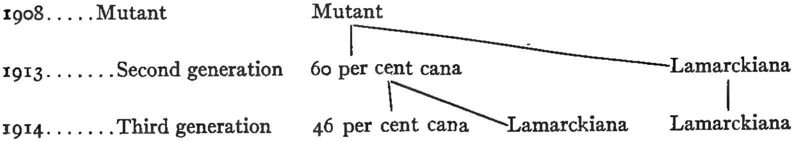
[6] Excepting the case of biennials; see later statement.

That of mutant no. 3 was as follows:



It is easily seen that they agree almost exactly with the pedigree of mutant no. 1, and simply give further proofs of the conclusions drawn from this. The size of the two cultures is given in table II.

TABLE II

YEAR	GENERATION	PARENT	OFFSPRING		PERCENTAGE OF CANA	MUTANTS
			Total	Flowering		
	A					
1908.....	mutant no. 2	....	....	....	....	....
1912.....	Second	mutant	17	16	35	2 nanella
1913.....	Third	cana	55	45	15	2 nanella 2 new
1913.....	Third	Lamarckiana	60	25	0	....
	B					
1908.....	mutant no. 3	....	....	....	....	....
1913.....	Second	mutant	30	30	60	1 lata, 3 nanella
1914.....	Third	cana	57	56	46	3 nanella
1914.....	Third	Lamarckiana	60	25	0	....

In each case the self-fertilized seeds of only one *cana* were studied, besides those of the mutants, and also those of only one atavist of the *Lamarckiana* type. The progeny of the latter proved to be uniform and like the parent, about one-half of the plants being studied in the flowering condition and the remainder in the stage of large rosettes of radical leaves in July. The *lata* mutant has flowered, as have the majority of the dwarfs. Two mutants of a new type arose, which will have to be described in another paper. They resembled *O. rubrinervis*, but lacked the characteristic brittleness of the stems of this form.

The second generation of mutant no. 3 has been the most vigorous one of all my annual cultures of *O. cana*. It was grown, moreover, under exceptionally favorable conditions. For this reason it has been chosen for making a series of crosses, which will be dealt with at the end of this article. The fact that, in this case, the percentage figures come so much nearer to equality of the two types than in the other cases is probably owing to this striking vigor of the race. The means are 25 per cent *cana* for no. 1 and no. 2, but 53 per cent *cana* for no. 3. The proportion of mutants among the seedlings of the *cana* individuals is 18 in 350, or about 5 per cent.

O. cana from *lata* nos. 4 and 5.—As previously mentioned, the progeny of two further mutants of the same origin have been studied. The offspring of one of them embraced only 15 individuals, of which 13 have flowered. There were 3 *cana*, 2 mutants (one *oblonga* and one of the same new type as in no. 2), the 10 remaining plants being externally like *O. Lamarckiana*. The second original mutant yielded only 11 offspring, among which 7 were *cana*, one *Lamarckiana*, and 3 *oblonga*. Although these cultures do not justify the calculation of percentage figures, they evidently support the conclusions drawn from the three former ones, and argue for the conception that this form of splitting is typical for *O. cana*.

INFLUENCE OF CULTURE ON PERCENTAGE FIGURES.—I have shown[7] that the percentage figures for the splitting of *O. scintillans* in the succeeding generations may differ for different families. Sometimes it is only 15 per cent, more often it varies between 34 and 39 per cent, and in rare cases it reaches 69–93 per cent. Subsequent experiences have suggested the idea that these differences are due mainly to outward conditions or to the method of cultivation, and that favorable influences must increase the percentage of individuals with the type of *scintillans* and diminish the percentage of *Lamarckiana*-like specimens.

The self-fertilized seeds of the *cana* individuals previously mentioned have given the following percentages of specimens with the *cana* type: 15 and 16 per cent, 24–34 and 35 per cent, and 46 and 60 per cent, the two latter being found in a culture which excelled the others in vigor. Evidently these figures run parallel to those of *scintillans* and the variability must have the same cause in both cases.

In order to ascertain the nature of this cause I have tried to answer two questions, namely: (1) are the percentage figures

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[7] The mutation theory. Chicago. 1909. pp. 388–391.

different on different parts of the main spike of a plant and on different branches; and (2) are they different for annuals and biennials, provided that the individual strength is in both cases as great as possible? The following experiments will show that the first question is to be answered in the negative, but the second in the affirmative; or in other words, the percentage figures depend upon individual vigor of the plants, and this between the widest possible limits.

The second generation of mutant no. 3, cultivated in 1913, was the most vigorous of all my annual cultures, as already mentioned. I chose for my experiment, therefore, the strongest individual of this group, having the largest supply of pollen in its anthers, and fertilized its flowers on the main spike and on a lateral branch in small bags, each with its own pollen. At the time of harvest I separated the fruits in groups of 10 each; there were 4 of these groups on the main spike and 2 on the branch. In the spring of the following year (1914) I sowed the seeds of these 6 lots separately. I counted the seedlings in the stage shown in fig. 1 without transplanting them. The *cana* were easily distinguished from the *Lamarckiana* by their narrower leaves and gray color. There were a number of dwarfs, which combined with this character those of *cana* and will be called *cana-nanella*. I have planted them out after finishing the countings and found them true dwarfs of the *cana* type. About a dozen of them flowered as annuals, and some flowered the following year as biennials. The result of the countings is given in table III.

TABLE III

	Number of seedlings	Percentage of cana	Percentage of cana-nanella	Percentage together
A, main spike				
base	57	40	5	45
second group	114	30	4	34
third group	121	31	4	35
top	129	35	5	40
B, lateral branch				
base	95	39	4	43
top	94	31	11	42

The means for the whole plant are 34, 6, and 40 per cent. It is easily seen that the deviations from the means fall within the limits of ordinary chance, although all the seeds from the 10 capsules of each group have been sown. Thus it is clear that the first and the last fruits of a spike and those of a side branch may give the same percentage figures of specimens of the parental type. Moreover, the mean value is not essentially different from the means of the pedigrees, as just given, which was 33 per cent. We may conclude, therefore, that the mean percentage for all my annual cultures is about 30–40.

In order to compare the influence of biennial culture upon this figure, I chose three healthy and very vigorous rosettes of 1913 and kept them through the winter under glass. They had been reared from seeds of a biennial mutant belonging to the group of *cana* mutants from *lata*, from which pedigrees no. 2 and no. 3 were derived; but this special culture stayed in the rosette condition during 1913. In 1914 three plants of the *cana* type became very vigorous, reaching about double the height of the annual plants and growing up to more than 2.5 m. Their stems also had twice the thickness of the others, the foliage and flower spikes were very dense, and the flowers much stouter. Every evening 4 or 5 flowers opened on the same spike, against 1 or 2 in ordinary cases. The number of fruits on a spike was 60–80, whereas 40 fruits, as just given, is a high value for an annual plant. All of these fruits were self-pollinated in little bags, and yielded 1–1.3 cc. of seeds from 10 fruits, whereas the annuals give only 0.5–0.9 cc. of seeds in 10 fruits. We may summarize these details by saying that my biennial specimens of 1914 were about twice as vigorous as the very best of all my annual cultures.

TABLE IV

Plant	Fruits	Seeds in cc.	Seedlings	Percentage of cana
No. 1.......	63	6.6	590	96
No. 2.......	79	10.0	1099	93
No. 3.......	64	6.3	277	97

All the seeds were sown in boxes in 1915 and the seedlings counted out, without being transplanted, in the stage corresponding to fig. 1, when the differentiating marks were very sharp. The three plants gave the results shown in table IV.

The remaining 4–7 and 3 per cent were mostly of the *Lamarckiana* type, with some mutants belonging to *albida*, *oblonga*, and *nanella*. I had saved the fruits and their seeds in 7 or 8 groups. beginning at the base of the spike, and sown the seeds separately, But, just as in the previous case, there were no appreciable differences in the percentage figures between the higher and the lower groups.

The main result is that the percentage of specimens of the *cana* type, which runs 15–60 per cent on annual individuals, may increase to 93–97 per cent on very vigorous biennial plants. It is thus clearly seen to be dependent upon the method of cultivation. Obviously this rule may be applied to the percentages of *O. scintillans*, as previously discussed, and to those of *O. pallescens* and the other new dimorphic mutants to be described in this article.

Oenothera Lamarckiana mut. *pallescens* (fig. 3).—Among all the mutants which arose in my garden from *O. Lamarckiana*, this form most closely resembles the parent type. In early stages the rosettes are the same, and in springtime, when still in the boxes, I have not as yet succeeded in distinguishing them. It is not until about 6 weeks after planting out on the beds that the differentiating marks begin to show (fig. 4). In the middle of June the leaves are clearly shorter, and the blade is set off from the narrowly-winged petiole by a sharp indentation. This character causes the rosettes to be more open because the petioles hardly touch one another.

This spatulate form of the leaves remains, for a long time, the best mark of the race; but when the stem grows up, the whole plant is much more slender than the parent form (fig. 3). The stem is thin and low; in July, when the first flowers open, it often reaches only 75 cm., when the corresponding specimens of *Lamarckiana* are already 1 m. and more in height. After a time, however, this difference disappears, since the spike is more elongated. It is less dense than in *Lamarckiana;* the bracts are much shorter and strikingly broader; the flower buds are large and conical, the flowers somewhat smaller, although still larger than those of *O. biennis;* the pollen is abundant and the fruits are short and thick, containing a good supply of seed. The foliage is of the same green

FIG. 3.—*Oenothera Lamarckiana* mut. *pallescens:* the 2 types into which each generation splits; to the left the *Lamarckiana* type; to the right the parental type; August 1914.

color as in the parent form, but much more crinkled and uneven, not as gray as in *O. cana*, nor as hairy as in this form.

The impossibility of distinguishing the young plants before planting out evidently makes this mutant less fit for the determination of splitting percentages, because the sorting and counting has to be done on the beds. In my experiments I have always counted the individuals of the two types at the beginning of the flowering period, since at this time the limits between the two groups are the most sharp.

Moreover, this similarity between the mutant and the parent species must diminish the chances of discovering mutant specimens of the new type. This is probably the reason why it was not observed before 1911. Since that year new mutants of the *pallescens* type have more than once arisen from *O. Lamarckiana* and from some of its derivatives, especially in 1914. All of these mutants exactly resembled the first one in their whole structure and in all their marks.

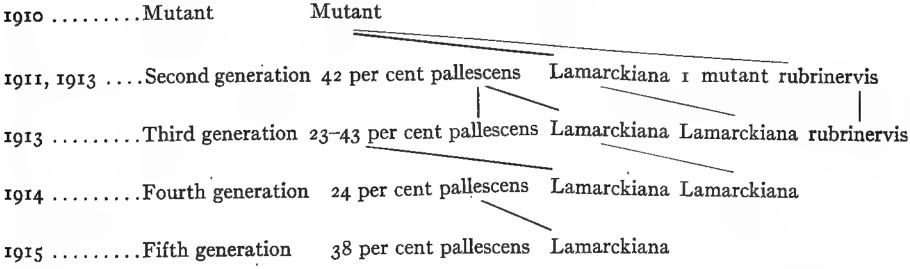
FIG. 4.—*Oenothera Lamarckiana* mut. *pallescens:* 3 typical leaves of the rosette of radical leaves; June 16, 1914.

I have made pedigree cultures of the offspring of my first three mutants. These arose from seed of the same parent plant of 1909, which belonged to the second generation of a guarded strain of *O. Lamarckiana*, derived from a rosette collected in 1905 in the original field near Hilversum. One part of this seed was sown in 1910 and yielded, among about 500 specimens, 1 *pallescens*, together with 1 *rubrinervis*, 3 *oblonga*, 2 *lata*, 1 *scintillans*, 1 *nanella*, the specimen of *O. Lamarckiana* mut. *semigigas* described by STOMPS,[8] and a narrow leaved specimen, exactly resembling the type described and figured by GAGER[9] for a derivative of *O. biennis*. The specimen of *pallescens* was discovered by chance, since almost none but mutants and a number of doubtful specimens had been planted out; it occurred among the latter and was distinguished as a new type only at the time of flowering. Thereupon, another part of the same sample of seeds was sown in 1911 and yielded two more specimens of *pallescens*, among about 250 flowering individuals.

The self-fertilized seeds of these three mutants gave rise to a mixed progeny, the smaller half of which resembled the parent, whereas the remainder presented the type of *O. Lamarckiana*, duplicating this in all of its special marks and during all the stages of their development. In the following description I will, therefore, indicate them simply as *Lamarckiana*, without discussing the question whether some internal characters might perhaps be different. But externally there is no difference; moreover, the progeny of this derivative *Lamarckiana* behaves exactly like that of normal ones. This splitting into these two types has repeated itself in the following generations and in all of the cases investigated.

Moreover, the *pallescens* seems to be mutable to a higher degree than *O. Lamarckiana* itself; for, although my cultures have been necessarily small, the number of mutants is very striking, reaching 20 among about 500 specimens, or 4 per cent. From the first three mutants I have derived three pedigree families, which I will now briefly describe.

PEDIGREE OF MUT. *pallescens* NO. 1



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[8] STOMPS, THEO. J., Die Entstehung von *Oenothera gigas* DeVries. Ber. Deutsch. Bot. Gesells. **30**:406. 1912.

[9] GAGER, STUART C., Cryptomeric inheritance in *Onagra*. Contrib. Brooklyn Bot. Garden no. 3, Bull. Torr. Bot. Club **38**: 461-471. *figs. 2.* 1911.

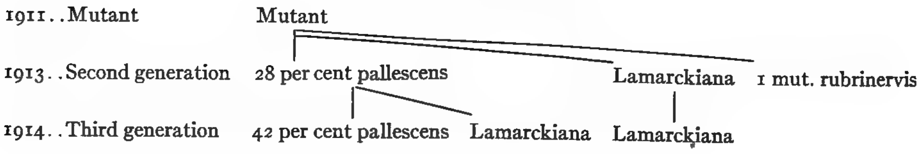
The size of these cultures is given in table V.

TABLE V

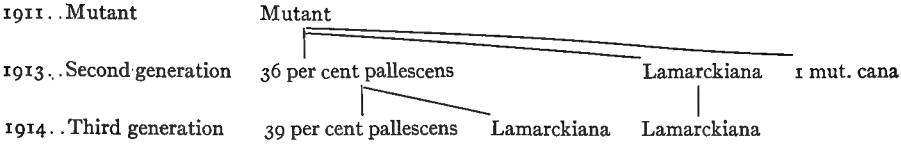
Year	Generation	Parent	Total offspring	Flowering individuals	Percentage of pallescens	Mutants
1911.....	Second	mutant	129	6	....	1 rubrinervis
1913.....	Second	mutant	40	40	42	1 liquida
1913.....	Third	pallescens	69	69	23	....
"	"	pallescens	65	65	43	1 nanella, 1 cana
"	"	Lamarckiana	90	50	0	1 scintillans, 1 lata, 1 albida
"	"	Lamarckiana	56	50	0	....
"	"	rubrinervis	70	25	0	....
1914.....	Fourth	pallescens	55	53	24	1 nanella
"	"	Lamarckiana	58	25	0	....
"	"	Lamarckiana	80	25	0	....
1915.....	Fifth	pallescens	60	25	38	....

The offspring of the 4 specimens of *Lamarckiana* had this uniform type, in the flowering specimens as well as in the other ones. These were examined in June and July when in large rosettes of radical leaves. The offspring of the mutant *rubrinervis* was also uniform and exactly resembled the race of this name in all its marks, and especially in the brittleness of its stems. The offspring of the original mutant, cultivated in 1911, embraced 129 plants, only 6 of which have flowered, the others having been destroyed before the significance of the culture had been realized. Among these 6, 2 were *Lamarckiana*, 3 *pallescens*, and 1 mut. *rubrinervis*. Their offspring were studied in 1913, as given in table V. Among the mutants the *rubrinervis*, *liquida*, *scintillans*, *lata*, and *cana*, as well as one *nanella*, flowered and proved their identity with the races of these names at that period.

PEDIGREE OF MUT. *pallescens* NO. 2



PEDIGREE OF MUT. *pallescens* NO. 3



The size of these cultures is given in table VI.

TABLE VI

Year	Generation	Parent	Total offspring	Flowering individuals	Percentage of pallescens	Mutants
A						
1911	mutant no. 1	. . . .	. . . .	. . . .	. . . .	. . . .
1913	Second	mutant	25	25	28	1 rubrinervis
1914	Third	pallescens	57	57	42	5 nanella
1914	Third	Lamarckiana	60	25	0	. . . .
B						
1911	mutant no. 2	. . . .	. . . .	. . . .	. . . .	. . . .
1913	Second	mutant	25	25	36	1 cana
1914	Third	pallescens	25	25	39	1 lata, 3 nanella, 1 cana
1914	Third	Lamarckiana	65	25	0	. . . .

Among the mutants the *rubrinervis*, both *cana*, one *lata*, and some *nanella* have flowered. The individuals of *pallescens* and *Lamarckiana*, which did not flower, were examined in June and July as large rosettes. Most of the flowering specimens were observed during the months of August and September.

The percentage figures of these tables vary from 23 to 43, the means for the 3 families being 33, 35, and 37 per cent, and the total mean being 35 per cent. On account of the evident weakness of the individuals of the *pallescens* type, as compared with their *Lamarckiana*-like sisters, these figures may be assumed to show that the splitting into two main types took place in about equal parts. The splitting is constantly repeated from the *pallescens* specimens, but the progeny of the *Lamarckiana* type retain this type uniformly.

I have made only one cross in these families, and that in order to ascertain the properties of the pollen of the *pallescens* individuals. I placed this pollen on the stigma of some flowers of

Lamarckiana in 1913, and got from the seeds a uniform generation of 60 flowering individuals, all of which proved to be *Lamarckiana.* I conclude from this fact that the pollen of the *pallescens* plants does not transmit the characters of the race, exactly as in *O. scintillans* and *O. cana.*

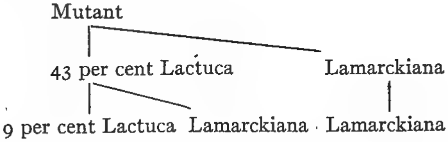
O. Lamarckiana lata mut. *Lactuca* (fig. 5, *C*).—In the summer of 1913 I found, in a race of *O. lata* which had been fertilized in the previous generations (1905 and 1907) by *O. Lamarckiana,* a weak plant which seemed to be new to me, but showed evident signs of affinity with the inconstant types of *O. cana* and *O. pallescens* as previously described. It was fertilized, therefore, purely by its own pollen. It yielded 0.8 cc. of seeds, which were sown in 1914 and gave rise to 65 plants, one of which was a mutant of the ordinary type of *O. nanella,* and subjected to the same bacterial disease which so often deforms the dwarfs of my race. Among the others, two types were represented in about equal numbers. One type was exactly like normal *Lamarckiana;* it counted 36 individuals, almost all of which have flowered, without showing any recognizable difference from the original wild species. The remaining 28 constituted a new and uniform type, repeating the characters of the parent plant of 1913, so far as these had been noticed and recorded. At the time of planting out, in the beginning of May, they very much resembled the compact rosettes of *O. nanella,* but without any signs of the disease. About the middle of June, when the rosettes of the type of *Lamarckiana* were growing very fast, those of the new

FIG. 5.—Typical radical leaves of *A*, *Oenothera Lamarckiana* mut. *liquida; B*, mut. *cana; C*, mut. *Lactuca;* June 1914.

type remained small, their leaves reaching only about half the length and half the breadth of those of their sisters (7×3 cm. against 14×5 cm.). Their blades were sharply set off from the winged petioles (fig. 5, *C*), and thereby they much resembled those of *O. pallescens* (fig. 4). This resemblance continued during the development of the stem and the flower spikes; but even as the rosettes were smaller and more densely leaved, the stems were lower and weaker and less branched. The leaves were narrower and folded along the middle vein, instead of being broad and flattened, as in *O. pallescens*. The flower buds were as thick and as large as those of this species, and the flowers also reached the same size, the petals having a length of 4 cm. During the flowering period the differences from *O. pallescens* grew gradually less, and at the end, in September, the new type seemed to be only a weak form of this latter, reaching a less height and being almost unbranched. Artificial self-fertilization has been difficult, since in many flowers the pollen was in an imperfect condition. Four specimens yielded a sufficient harvest (0.5–1 cc.). The sister plants of the *Lamarckiana* type showed an abundance of seed, exactly as the *Lamarckiana* of pure origin does.

The next year (1915) I sowed the seeds of one specimen of the parental type and of two of the type of *Lamarckiana*. The first gave only 44 seedlings, of which 4 were *Lactuca*, one *nanella*, and the others *Lamarckiana*. The two other sowings gave 248 and 283 offspring of their own type, without any *Lactuca* specimens, but with some dwarfs. The number of them was 11, or 4 per cent in the first group, but only one in the latter group. Combining these results we get the following pedigree:

1913..........Mutant
1914 ....First generation
1915..........Second generation



Although only two generations from the seeds of the original mutant have been cultivated, it is evident that this new form behaves exactly like the inconstant races of *O. scintillans*, *O. cana*, and *O. pallescens*. Under favorable conditions it splits into about equal numbers of the mutant type and of the type of *O. Lamarckiana*. Moreover, a mutant dwarf has been produced.

O. Lamarckiana mut. *liquida* (fig. 5, *A*).—In 1912 and 1913 a new type of mutant was discovered, which came next to *O. scintillans*, had flat and smooth leaves like that form; but the foliage was much broader and lighter green. The individual mutants resembled one another in all respects, save the size of the flowers; they were very slender and had leaves about two-thirds the size of those of *O. Lamarckiana*. The pollen was sometimes abundant, but in other flowers rather scanty.

All in all, I had 6 mutants of this type. One came from seed of *O. Lamarckiana*, but unfortunately it failed to produce good seeds, although the fruits were well developed. Four others arose from *O. lata*×*Lamarckiana*, two in 1912, which also did not yield fertile seeds, and two in 1913. The last one was found in the culture of *O. pallescens* mut. no. 1, and mentioned previously. The seeds of the 3 fertile mutants were sown in 1914 and yielded small cultures, which split up into two types, one repeating the mutant parents in all respects, and the other differing in no visible way from ordinary *O. Lamarckiana*. Besides these there were some mutants which happened to belong to allied types. Table VII gives the size and constitution of these cultures.

TABLE VII

SECOND GENERATION OF *O. liquida*

Mutant 1913 from	Lamarckiana	liquida	Mutant	Total	Percentage of liquida
pallescens	11	6	....	17	35
lata	61	26	1	88	30
lata	13	8	2	23	35
Total	85	40	3	128	31

In each of these cultures 15 individuals have been allowed to flower, about one-half of these being the *liquida* type and the other half the *Lamarckiana* type. The 3 mutants were *scintillans*, *pallescens*, and *cana*. All 3 have grown vigorously and flowered in August and September; they differed in no respect from the races of the same names.

The percentage of typical individuals in the second generation is about the same as for *O. cana* (25 and 53 per cent), for *O. pallescens* (35 per cent), and for *O. Lactuca* (43 per cent). From this it may be concluded that the 4 races have the same hereditary constitution which, moreover, is the same as in *O. scintillans*.

The next year (1915) I cultivated a third generation of the second mutant of the table (mutant no. 1 from *lata*). The harvest had been small, as in the previous generation, and only 33 seeds germinated. Of these 9 were *liquida*, 1 was *pallescens*, 1 *oblonga*, and the others *Lamarckiana*. All of them have flowered. The percentage for *liquida* was 27, or about the same as in the first generation. Moreover, I have sown for each of the 3 cultures of 1914 the seeds of one or two typical individuals, and also for each of them the seeds of two of the atavistic or *Lamarckiana* type. These 6 last sowings contained 150–300 seedlings each, together 1311, of which 8 were mutants (3 *oblonga*, 4 *lata*, 1 *cana*); the remainder were all of the *Lamarckiana* type, no *liquida* occurring among them. The seedlings of the 4 *liquida* specimens gave the results indicated in table VIII.

TABLE VIII

THIRD GENERATION OF *O.* MUT. *liquida*

Race issued from	Total of seedlings	Percentage of liquida
pallescens..........	84	25
pallescens..........	47	28
lata no. 1..........	80	41
lata no. 2..........	26	35
Total..........	237	32

The countings were made in June and July in the boxes in which the seeds had been sown; the plants were all young rosettes with leaves 15 cm. long in the *Lamarckiana* type, and 6–10 cm. long in the *liquida* specimens. The differences were clear and sharp. The table shows that the splitting was almost exactly the same in the third as in the second generation.

Dimorphic races do not seem to be rare among the mutants of *O. Lamarckiana*, and have been observed to spring also from its hybrids with other species; but the characters are not always as sharp as in the instances described, or the production of seeds is too insufficient for further cultures. Only one case may still be mentioned here. It was a mutant from *O. lata*, discovered in 1914, the self-fertilized seeds of which gave a dimorphic second generation, consisting of 19 plants of the parental type, 47 of the *Lamarckiana* type, besides 2 mut. *oblonga* and 2 mut. *lata*. Almost all of these flowered in 1915. Those of the parental type were strikingly like one another, constituting a wholly new form, with very long, narrow, dark green leaves, the stems low and scarcely branching, the spikes rich with bright flowers like those of *Lamarckiana*, and with a good supply of pollen. The fruits, however, were cylindrical and very thin, containing only a few good seeds. The plants excelled in beauty the species and most of its other mutants, but on account of its slight fertility I do not propose to continue the culture. It may be called *O. superflua*.

O. biennis Chicago mut. *saligna*.—In the second generation of my race of *O. biennis Chicago*[10] I found in 1913, among 870 normal individuals, two specimens of a weaker, narrow-leaved type, which differed sufficiently from the former mutants of this species, namely, from *O. biennis Chicago* mut. *salicifolia* and mut. *salicastrum*,[11] to be considered a new form. One of these new mutants died before flowering, the other yielded, after self-fertilization, a small but sufficient harvest of seeds. One-half of these seeds were sown, but only 17 specimens germinated and grew up into flowering plants. Of these 9 repeated the type of the parent, but 8 returned to the size, vigor, and characters of *O. biennis Chicago*, the grandparent. Although the numbers are very small, they point to a splitting into equal parts, as in the splitting mutants of *O. Lamarckiana* just described.

The difference was already evident in March, when the seedlings were only two months old. In June the rosettes were large, but smaller than those of the species, the leaves smooth and narrow. The stems grew up to about one-half the height of their atavistic sisters, and began to flower in September, having a length of 60–120

[10] Gruppenweise Artbildung, pp. 34, 52, etc. 1913.

[11] Gruppenweise Artbildung, p. 304. *figs. 110, 111.*

cm. The spikes were densely flowered, the flowers a little smaller, the fruits thin and long. The production of pollen was insufficient in many flowers, but this may have been the effect of the individuals being transplanted from their boxes to the bed in June, which is relatively late in the season. The seed developed badly and contained only a small percentage of normal grains.

I have sown the seeds of 8 of the 9 specimens with the parental type, and of two of the type of *O. biennis Chicago*. The first split into two types, the second only repeated the form of the parent. The splitting percentages were 11, 12, 13, 15, 15, 17, 18, and 25, with a mean of 16 per cent, but the germination had been very poor, giving only 444 seedlings for the 8 boxes. The progeny of the two specimens of the *Chicago* type was uniform with 252 and 60 seedlings. I counted them in May and June, and left one group of each type to flower. The group from the *saligna* type contained two flowering *saligna*, identical with those of the second generation; that of the atavists 60 flowering plants of the uniform type of *O. biennis Chicago*. From these facts we may conclude that in this race all of the specimens of the parental type give a dimorphic progeny, while the offspring of the plants with an atavistic type remains uniformly so. Resuming the cultures, we get the following pedigree:

1913..........	Mutant	Mutant		
1914.........	Second generation	50 per cent saligna		Chicago
1915.........	Third generation	16 per cent saligna	Chicago	Chicago

The behavior is exactly the same as in the dimorphic races issued from *O. Lamarckiana*.

Crosses of *Oenothera Lamarckiana* mut. *cana*.—As indicated on p. 258 I chose in 1913 the second generation of a *cana* mutant which arose from *O. lata* (no. 3) for a series of crosses. This culture was the most vigorous one of all my annual *cana* families, and its percentage figures seemed to be more normal than in the other cases. The crosses were made in both directions with the pure strains of my species and races described in *Gruppenweise Artbildung*, and the seeds were sown in 1914. This first generation was counted in July, during the beginning of the flowering period, but about one-half of some of the cultures were kept in the boxes so as to reach only the stage of rosettes at that time. No second generations have been cultivated. I will first describe the results, and afterwards give the necessary details concerning the several cultures.

The main purpose of these crosses was to decide the question whether the special characters of *O. cana* are handed down by the ovules only, as in *O. scintillans* and *O. lata*, or by the pollen also. Table IX gives the result of the crosses with wild species other than *O. Lamarckiana*. Here a splitting occurs into *laeta* and *velutina* or into *densa* and *laxa*, exactly analogous to that produced by *O. Lamarckiana* itself. The only exception is the pollen of *O. biennis*, which does not split; it gives with *O. cana* the same type as with the parent species. The result was very striking on the beds. No specimens of the *cana* type occurred in the cases where this mutant had been the father, whereas such individuals abounded in the results of the reciprocal crosses.

TABLE IX

CROSSES OF *O. cana* WITH OTHER SPECIES

Cross	Percentage of cana	Percentage of laeta	Percentage of velutina	Percentage of mutants
A				
O. cana×O. biennis Chicago	25	11	63	1
O. cana×O. Cockerelli	17	17	63	3
O. cana×O. Hookeri	28	14	58	
O. Hookeri×O. cana	0	4	96	
O. Cockerelli×O. cana	0	54	46	
O. syrticola×O. cana	0	51	49	
O. biennis×O. cana	0	58	42	
B		Percentage of densa	Percentage of laxa	
O. biennis Chicago×O. cana	0	24	75	1
O. atrovirens×O. cana	0	36	64	
C				
O. cana×O. biennis	49	51		

In this table, *O. syrticola* Bartlett is the *O. muricata* L. of my *Gruppenweise Artbildung*, and *O. atrovirens* Bartlett has been described in that book as *O. cruciata* Nutt. The other names are still the same as in my book.

With the same purpose crosses were made with *O. Lamarckiana* and some of its derivatives.

TABLE X

CROSSES OF *O. cana* WITH *O. Lamarckiana* AND ITS MUTANTS

Crosses	Percentage of cana	Percentage of Lamarckiana	Percentage of other forms
O. cana×O. Lamarckiana.....	42	58	....
O. cana×O. nanella..........	21	71	8 nanella
O. cana×O. rubrinervis......	40	25	35 subrobusta
O. Lamarckiana×O. cana	0	98	2 nanella
O. lata×O. cana	1	62	35 lata, 3 mutants
O. nanella×O. cana.........	1	5	94 nanella
O. oblonga×O. cana	0	82	15 oblonga, 3 mutants
O. rubrinervis×O. cana	0	52	48 subrobusta

The main result is the same. *In all the crosses of both tables the characters of O. cana are handed down through the ovules to a large part of the progeny, but not through the pollen.* The behavior is exactly the same as in *O. scintillans* and *O. lata*. The two specimens of *O. cana* from the crosses of *O. lata* and *O. nanella* must evidently be considered as mutants, that is, as having arisen from the fertilization of mutated sexual cells, since we have seen that such mutations occur from time to time, especially among the seeds of *O. lata*.

Apart from the appearance of plants of the *cana* type, the results of the crosses are, in every case, such as would be expected if *O. Lamarckiana* had been used instead of *O. cana*. In this respect they simply confirm the conclusions given in my book.

Let us now consider in its details the analogy of *O. cana* with the allied forms of *O. scintillans* and *O. lata*. Two cases offer themselves for this consideration. The first one is afforded by the crosses with *O. biennis*. Apart from stray mutants, these produce two types, one of which combines the visible marks of both parents, whereas the other wholly lacks the characters of the mother, but is simply like the hybrid of *O. Lamarckiana* and *O. biennis*, as described in my book. In the first group the combination is such as to make the characters of the mother the most striking in the hybrids, whereas those of the father, *O. biennis*, have only a less influence on the general type.

In table XI the figures of table IX are combined with the percentages derived from my *Gruppenweise Artbildung*, by taking the means of the two crosses for each case given on pp. 251 and 261.

TABLE XI

O. cana×*O. biennis* COMPARED WITH *O. lata* AND *O. scintillans*

Forms	Percentage of type of mother	Percentage of type of O. Lamarckiana ×O. biennis	Mutants
O. cana×O. biennis	49	51	....
O. scintillans×O. biennis	60	36	4
O. lata×O. biennis	57	43	....
Mean	55	43	....

In this table we see *that the characters of O. cana, even as those of O. scintillans and O. lata, are repeated in about one-half of the progeny, but not in the other half.* We may consider this as the simplest case. In the other crosses the proportions of *cana* are 17, 25, 28, with a mean of 23 per cent in table IX, and 21, 40, 42, mean 34 per cent in table X, and these figures may be assumed to point to a splitting into nearly equal parts with a loss on the side of the weaker form. Exactly the same behavior occurred among the progeny of the self-fertilized individuals of *O. cana*, as we have seen previously.

Let us now compare *O. cana* with the two allied forms in those crosses where the progeny splits into the twin hybrids *O. laeta* and *O. velutina*, as shown in table XII.

The types of *O. laeta* and *O. velutina* have been compared in each case with the twins derived from *O. Lamarckiana* by the same father.[12] The comparison embraced the whole lifetime from the germination in February until the production of the fruits in September. No differences have been observed.

From table XII we see that the splitting percentages are practically the same, whether the pollen is taken from *O. biennis Chicago*, *O. Cockerelli*, or *O. Hookeri*. For this reason I have given

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[12] DEVRIES, HUGO, On twin hybrids. BOT. GAZ. 44:401–407. 1907.

the mean for each group in the last columns of the table, and the reliability of this mean evidently depends strongly on this fact.

TABLE XII

Splitting into *laeta* and *velutina*

Forms	Percentage of type of mother	Percentage of laeta	Percentage of velutina	Means for the groups		
				Type of mother	laeta	velutina
O. cana×O. b. Chicago...	25	11	63	23	14	61
O. cana×O. Cockerelli....	17	17	63			
O. cana×O. Hookeri......	28	14	58			
O. scintill.×O. b. Chicago.	33	32	32	30	36	30
O. scintill.×O. Cockerelli..	21	49	29			
O. scintill.×O. Hookeri...	35	28	29			
O. lata×O. b. Chicago....	21	24	55	27	25	46
O. lata×O. Cockerelli....	21	31	48			
O. lata×O. Hookeri......:	39	18	43			
O. Lamarckiana×O. b. Chicago..............	....	19	81	......	18	82
O. Lamarckiana×O. Cockerelli	....	11	89			
O. Lamarckiana×O. Hookeri.................	....	23	77			
O. nanella×O. b. Chicago.	....	41	59	......	41	59
O. nanella×O. Cockerelli..	....	38	62			
O. nanella×O. Hookeri....	....	45	55			

Theoretically a splitting into 4 groups of equal size should be expected, namely into *cana-laeta*, *cana-velutina*, *laeta*, and *velutina*.[13] Evidently one of the first two groups is suppressed. This conclusion holds good for *O. cana* just as for *O. scintillans*, but in the case of *O. lata* the fourth group is sometimes visible, a few specimens of the *lata*-like hybrids assuming at the same time the marks of *O. laeta* (about 1 per cent, *Gruppenweise Artbildung*, p. 255), whereas the remainder are clearly *lata-velutina*. It is probable that the same group is suppressed in both the other cases, and for the same reasons, which are as yet unknown. The fact that there are so often more *velutina* than should be expected probably has the same cause as the exuberant occurrence of this form in the crosses of *O. Lamarckiana* (82 per cent). The analogous crosses of *O. nanella*, given in the lower part of the table, show that these

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[13] De Vries, Hugo; On triple hybrids. Bot. Gaz. 47:1–8. 1909.

diminutions of the *laeta* type may, at least in part, be considered as influenced by neighboring characters. The combination *O. cana nanella* has occurred in many instances during these experiments, either from the crosses of *O. cana* with the dwarfs of my race, or as occasional mutations in other cases. A repetition of my experiments, in which *O. cana nanella* would be chosen for fertilization by the other species or mutants used, would probably give the material to decide these questions.

Putting aside all of these more special considerations, we may conclude that *O. cana behaves in its crosses, as well as after self-fertilization, exactly after the manner of O. scintillans and O. lata.* From this fact and from the cross *Lamarckiana*×*pallescens*, previously mentioned, it seems probable that the other new dimorphic mutants, namely *O. pallescens, O. liquida*, and *O. Lactuca*, will follow the same rule if tried in the same way. This rule is evidently independent of the external types of their characters, but must depend upon internal properties of their hereditary qualities.[14]

I will now give briefly the necessary details concerning the crosses mentioned in tables IX and X. As already mentioned, all these crosses were made in 1913 with plants of the same origin. For every cross a single specimen was chosen and some flowers on the lower part of its main spike were castrated. The seeds were sown in February 1914, the seedlings transplanted into boxes, and from these, as a rule, about 25 specimens of each culture were placed in a bed in April and May, giving them a good soil and light exposure and plenty of space to insure a vigorous development until the time of flowering and of fruiting.

O. cana×*O. biennis Chicago.*—A group of 71 specimens, all of which produced high stems and 25 of which have flowered. One was a mutant, combining the gray narrow leaves of *O. cana* with the marks of the stature, foliage, and flowers of *O. lata*. The plants of the type of *O. cana* were exactly like pure *O. cana* at the beginning of the flowering period, in July, when they had reached a height of 70 cm. The remaining plants were like (*O. Lamarckiana*×*O. biennis Chicago*) *laeta* and *velutina*. The reciprocal cross yielded 59 specimens, of which 5 remained in the condition

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[14] On these questions see Gruppenweise Artbildung, pp. 268–295. 1913.

of rosettes. Of the remaining 54, about one-half or 25 have flowered, the others reaching this stage approximately at the time when they were pulled up and counted. One plant was a mutant, being a metaclinous *velutina*, just as described in my book on pp. 308–311. The others were *densa* and *laxa*, as should be expected, and agreeing with these types throughout their whole life.

O. cana×*O. Cockerelli*.—A culture of 63 specimens embracing 4 *cana*, 5 *laeta*, and 15 *velutina*, which have flowered, and a large number of rosettes of radical leaves. Two plants were mutants of the type of *O. lata* and one of them has flowered. Neither in the rosette stage nor at the time of flowering have the plants of the *cana* type showed any difference from ordinary *O. cana*, the characters of the father, also of its twin hybrid type, being invisible in them. Such was the case in almost all the beds containing the hybrids whose mother was *cana*, and this made the distinguishing and counting of this type quite easy and sharply defined, and therefore fully reliable. Short narrow leaves of a gray color, a slender spike with long, thin flower buds with nodding tips were everywhere the same distinguishing marks. The *laeta* and *velutina* had the ordinary type of these twins, as produced by *O. Cockerelli*.

The reciprocal cross yielded 19 annual and 13 biennial *laeta*, besides 4 annual and 23 biennial *velutina* of the same type. The annual plants have flowered; the biennials became stout rosettes in July and August.

O. cana×*O. Hookeri*.—Represented by 25 flowering plants, 3 younger ones, and 40 rosettes, and among the flowering individuals 5 *cana*, 5 *laeta*, and 4 *velutina*. The *cana* were like those of the pure type; the *laeta* and *velutina* did not differ from those of the cross *O. Lamarckiana*×*O. Hookeri*, some of the *velutina* being of a yellowish green in such a degree as not to be able to produce a stem. The reciprocal cross yielded only two *laeta*, one of which has flowered, among a culture of 60 specimens. The remainder were *velutina*, 24 flowering plants and 34 rosettes of radical leaves. The types were the same as those in the reciprocal cross.

O. syrticola×*O. cana*.—Represented by 60 specimens of the type of (*O. syrticola*×*Lamarckiana*) *laeta* and *velutina*. Of these 19 *laeta* and 6 *velutina* have flowered, reaching a height of 2 m. in

August. The remaining plants were pulled out as large rosettes in July.

O. atrovirens×*O. cana.*—Represented by 55 plants, among which 8 *densa* and 17 *laxa* have flowered. They were in all respects like the twins of the corresponding cross of *O. Lamarckiana.* Just as in this cross, some specimens had cordate petals and others had linear ones, repeating the *cruciata* type. But on the first plants stray flowers with narrower petals were found, from time to time, indicating a high degree of fluctuability rather than a splitting into two constant and uniform types.

The reciprocal cross yielded only 23 seedlings, 20 of which were yellow and died very early, and the 3 remaining ones were very weak, reaching only a height of 40–60 cm. when they flowered. They had the type of the *gracilis* of the corresponding cross of *O. Lamarckiana.* They were not mentioned in table IX.

O. cana×*O. biennis* L.—Among 70 plants of this culture, one-half had the type of *O. Lamarckiana*×*biennis*, and of these 15 have flowered. The other half were evidently *cana.* Of these, 28 had the stature of typical *O. cana*, but with some marks which indicated an influence of the father. The foliage was less gray, a darker green, with broader bracts, and more dense spikes with smaller flowers than in the other crosses. The stigmas were surrounded by the anthers, insuring natural self-fertilization, as in *O. biennis.* Besides these intermediate types there were 7 dwarfs, which had the gray, narrow, and pointed foliage of *O. cana*, and which in the table have been calculated together with the high specimens of the *cana* type.

The reciprocal cross yielded only *laeta* and *velutina*, together 57 plants, of which about one-half of each type have flowered.

O. cana×*O. Lamarckiana.*—The two types of this culture were exactly the same as in the self-fertilized offspring of the mutant. There were only 19 specimens, of which 6 were *cana*, 11 *Lamarckiana*, and 2 *nanella.* The dwarfs combined the marks of *cana* with those of *nanella* and have been calculated in the table with the *cana* specimens of tall stature.

The same cross had been made in 1907, the seeds being sown in 1913. In this case there were 50 offspring, among which 26 were *cana* and 23 were *Lamarckiana*, while one dwarf occurred. The percentage figures, 52 *cana* and 46 *Lamarckiana*, confirm those of table X.

The reciprocal cross yielded only normal *Lamarckiana*, 60 specimens with one dwarf. Of these 23 have flowered.

O. lata×*O. cana*.—In this case the differences were already very clear at the beginning of June. There were 34 *lata*, 61 *Lamarckiana*, and 3 mutants (one each of *cana*, *nanella*, and *oblonga*). In August 7 *lata* and 9 *Lamarckiana* flowered. They repeated the type of the hybrids of *O. lata* with the parent species.

O. cana×*O. nanella*.—Only 24 seeds germinated. These produced 5 *cana*, 17 *Lamarckiana*, and 2 dwarfs which had the characteristics of *O. cana*. All these plants have flowered.

The reciprocal cross gave 111 plants, of which one was a *cana* of normal stature, 105 were *cana* with the dwarfish stature of *O. nanella*, and 5 had the type of *O. Lamarckiana*. Two of this last type, the normal specimen of *cana*, and 22 dwarfs flowered in August.

O. oblonga×*O. cana*.—Already in June the differences were clear and unmistakable. Among 72 plants 59 were of the *Lamarckiana* type, 11 *oblonga*, 1 *albida*, and 1 *rubrinervis*. Of these, 2 *oblonga* and 12 *Lamarckiana* flowered; most of the others lived through the summer in the condition of large rosettes of radical leaves.

O. cana×*O. rubrinervis*.—Only 20 seeds germinated, and yielded 8 *cana* of the normal type, 5 *Lamarckiana*, and 7 *subrobusta*, all of which have flowered.

The reciprocal cross yielded 59 plants, but in only two types, which were the same as those in the first instance. Of these, 17 *Lamarckiana* and 8 *subrobusta* have flowered.

Summary

1. Besides *O. scintillans*, which splits under ordinary circumstances in every generation into nearly equal groups of plants of the same type and others of the type of *O. Lamarckiana*, I have cultivated pedigree families of 4 other mutants of *O. Lamarckiana* which behave in the same manner. They have been designated

as *O. cana*. *O. pallescens*, *O. Lactuca*, and *O. liquida*. Their *Lamarckiana*-like offspring are constant in their progeny. Besides the two main types, they produce, as a rule, a relatively high percentage of other mutants.

2. The specimens of the parental type are on the average produced in about 40 per cent, the other 60 per cent being *Lamarckiana* with some mutants; but these figures vary with the cultures and with the plants according to their individual strength. They may even increase, on very strong biennials, to 93–97 per cent for the parental type.

3. Dimorphic mutants of this type occur also in allied species of the *biennis* group, as has been discovered by BARTLETT in the case of *O. stenomeres* mut. *lasiopetala* and described in this article for *O. biennis Chicago* mut. *saligna*.

4. In the crosses with older species or with *O. Lamarckiana* and its derivatives, *O. cana* follows exactly the type of the analogous crosses of *O. scintillans* and *O. lata*.

5. In the dimorphic mutants, the special characters are handed down to the next generation through the ovules only. The pollen lacks these characters, and is, so far as investigated, not different from that of pure *O. Lamarckiana*.

6. The dimorphic mutants constitute a group in which the hereditary phenomena are evidently independent of the externally visible characters of the special members of the group, but must be assumed to have the same intrinsic causes in the different cases.

BOTANIC GARDEN
AMSTERDAM

7

Die endemischen Pflanzen von Ceylon und die mutierenden Oenotheren.

Von

Hugo de Vries.

Sonderabdruck aus dem „Biologischen Centralblatt“.
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Die endemischen Pflanzen von Ceylon und die mutierenden Oenotheren.

Von Hugo de Vries.

Für die Mutationslehre ist es augenblicklich eine Hauptfrage, wie Arten in der freien Natur entstehen. Die Forschung hat sich hier offenbar zunächst an diejenigen Arten zu wenden, welche in der jetzigen geologischen Periode entstanden sind, und am besten an die, welche noch an Ort und Stelle leben, wo sie zuerst auftraten und wo die Lebensbedingungen seit ihrer Entstehung noch als unverändert angenommen werden können. Es handelt sich also im wesentlichen um endemische Arten mit möglichst geringer Verbreitung.

Eine zweite sehr wichtige Frage ist die nach dem Parallelismus zwischen der Entstehungsweise solcher lokalen Arten und den Erscheinungen, welche das Auftreten neuer Arten im Versuchsgarten begleiten. Je mehr es gelingt, diese Analogie in Einzelheiten nachzuweisen, um so sicherer wird offenbar die experimentelle Grundlage für die neue Auffassung der Abstammungslehre werden.

Zwei Forschungsrichtungen bieten sich augenblicklich für einen solchen Vergleich dar. Einerseits die Mutationsvorgänge in der Gattung *Oenothera,* andererseits die Studien von Willis über die endemischen Pflanzen von Ceylon[1]).

Die Flora von Ceylon ist für diese Untersuchung ganz besonders geeignet, da sie seit über 70 Jahren von zahlreichen Forschern genau bearbeitet worden ist und die Resultate in der großen Flora von Trimen und Hooker zusammengestellt sind. In diesem Werke hat Trimen für jede der 2809 beschriebenen Arten den Grad der Seltenheit angegeben. Er teilte dazu die Pflanzen in sechs Klassen ein, u. zw. Sehr gemein, Gemein, Ziemlich gemein, Ziemlich selten, Selten und Sehr selten. Diese Angaben beruhen selbstverständlich auf Schätzungen, welche aber unabhängig von jeder möglichen theoretischen Verwertung gemacht worden sind. Die Ausführungen und Berechnungen Willis' zeigen, dass sie im allgemeinen sehr genau und zuverlässlich sind. Bezeichnet man die sechs Klassen von Trimen mit Zahlen (1 = sehr gemein, 6 = sehr selten u. s. w.), so lässt sich die mittlere Seltenheit einer willkürlichen Gruppe von Arten in folgender Weise berechnen.

In der Gruppe werden die Arten nach den sechs genannten Klassen zusammengestellt; für jede solche Unterabteilung wird die Zahl ihrer Arten mit dem Faktor der Seltenheit multipliziert, die Produkte werden addiert und ihre Summe durch die ganze Zahl der Arten dividiert.

Das Ergebnis ist die mittlere Seltenheit der Gruppe, in Zahlen zwischen 1 und 6 ausgedrückt. Die Methode lässt sich offenbar für den Vergleich beliebiger Gruppen von Arten anwenden, z. B. für Familien und größere Gattungen, für die endemischen Arten, für Pflanzen der trockenen und der feuchten Regionen der Insel, für Arten mit auffallenden sogen. Anpassungen u. s. w.

Das Mittel aus den Zahlen 1—6 ist 3,5, und dieselbe Ziffer erhält man, wenn man die mittlere Seltenheit aller Arten der Insel zusammen berechnet. Die weiteren Berechnungen sind in zahlreichen Tafeln mitgeteilt worden, deren auffallend regelmäßige Ergebnisse zeigen, dass der Grad der Seltenheit von einem allgemein gültigen Gesetze beherrscht wird. Und dieses gilt nicht nur von den Pflanzen von Ceylon, sondern das Gesetz muss überall für die geographische Verbreitung bestimmter Gruppen seine Gültigkeit haben.

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1) J. C. Willis, The endemic flora of Ceylon, with reference to geographical distribution and evolution in general. Phil. Trans. Roy. Soc. London, Series B, Vol. 206, S. 307—342.

J. C. Willis, Some evidence against the theory of the origin of species by natural selection. Ann. Roy. Bot. Garden Peradeniya, Vol. IV, Prt. 1, S. 1.

Indem ich für die Einzelheiten der Tafeln und deren Zusammenfassungen den Leser auf die Schrift von Willis verweise, will ich hier nur die von ihm gezogenen Folgerungen als Grundlage für meinen Vergleich benutzen.

Dazu ist es aber erforderlich, zunächst eine gedrängte Übersicht über die bis jetzt bekannten Mutationsvorgänge bei den Oenotheren zu geben. Ich entnehme diese teilweise der vorhandenen Literatur, teilweise meinen eigenen noch nicht veröffentlichten Beobachtungen.

Die Untergattung *Onagra* umfasst augenblicklich etwa 50 Arten²). Von diesen sind die meisten erst in den letzten Jahren unterschieden und beschrieben worden, namentlich von H. H. Bartlett. Dieser Forscher hatte die Freundlichkeit, mir Samen seiner neuen Arten und von mehreren ihrer Mutanten zu senden, und da sie alle reichlich in meinem Garten geblüht haben, hatte ich die Gelegenheit, mich von ihrem Werte und ihren auffallenden Unterschieden zu überzeugen. Von jenen 50 Arten haben 8, also 16% bis jetzt mehr oder weniger zahlreiche Mutationen hervorgebracht, während für einige weitere Arten Andeutungen eines ähnlichen Verhaltens vorliegen. Da die meisten Arten in dieser Beziehung aber nur nebenbei untersucht worden sind, darf wohl angenommen werden, dass das Mutieren in dieser Gruppe eine ziemlich weitverbreitete Erscheinung ist.

Die acht mutierenden Arten sind: *O. Lamarckiana* Ser., *O. biennis* L., *O. biennis Chicago*, *O. stenomeres* Bartlett, *O. pratincola* Bartl., *O. Reynoldsii* Bartl., *O. grandiflora* Ait. und *O. suaveolens* Desf. Ich werde jetzt ihre Mutanten für jede Art einzeln anführen.

O. Lamarckiana. Diese Art ist noch stets weitaus die reichste an neuen Formen, sowohl nach der Zahl der verschiedenen aus ihr hervorgehenden Typen, als nach dem Prozentsatze der in jedem Jahre auftretenden Mutanten.

Unter diesen wird von den meisten Schriftstellern *O. gigas*, welche durch die doppelte Anzahl der Chromosomen gekennzeichnet ist, als progressiv betrachtet. *O. brevistylis*, *O. rubrinervis* und *O. nanella* sind retrogressive Mutanten, während in *O. lata* und *O. scintillans* ein in der Mutterart latentes Merkmal als tätig angenommen wird. Diese beiden Formen sind somit degressiver Natur. In Bastardierungen folgt *O. brevistylis* den Mendel'schen Gesetzen, ein für die Oenotheren seltener Fall. An diese schließt sich *O. rubricalyx* an, welche in den Kulturen von Gates aus *O. rubrinervis* hervorgegangen ist und sich der Mutterform gegenüber als

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2) R. R. Gates, The Mutationfactor in evolution (Liste von 39 Arten, S. 10). H. H. Bartlett, Twelve elementary species of Onagra (12 weitere Arten). Cybele Columbiana Vol. I, S. 37—56

Mendel'sche Dominante verhält[3]). Ich habe diese prachtvolle Neuheit aus Samen, welche Herr Gates mir zu senden die Liebenswürdigkeit hatte, durch zwei Generationen kultiviert und mich von der Richtigkeit dieser Angabe überzeugt. *O. scintillans* bildet eine dimorphe Rasse, indem sie sich alljährlich in *scintillans* und *Lamarckiana* spaltet.

Solche dimorphe Mutanten habe ich in der letzten Zeit mehrfach isoliert; an anderer Stelle werde ich von ihnen vier neue Typen als *O. cana*, *O. pallescens*, *O. Lactuca* und *O. liquida* beschreiben. *O. semigigas* hat 21 Chromosomen und ist somit als halbe Mutante vom *Gigas*-Typus zu betrachten. Ich habe neulich gefunden, dass sie mit ausreichender Sicherheit als junge Rosette an den breiteren Wurzelblättern erkannt werden kann und ziemlich regelmäßig in einem Exemplare unter 1000 vorkommt. Eine erhebliche Anzahl von anderen Mutanten sind bereits beschrieben worden[4]) und wenn man unter 10—20000 jungen Rosetten die abweichenden Typen auswählt, findet man wohl stets eine Reihe neuer Formen. Einzelne von diesen haben bereits gute Rassen gegeben, die meisten sind aber wegen mangelhafter Samenbildung unter unserem Klima oder aus anderen Gründen nicht weiter kultiviert worden. Solche umfangreiche Versuche machen den Eindruck, als ob das Mutationsvermögen der *O. Lamarckiana* nahezu unerschöpflich sei. Demgegenüber steht aber der Umstand, dass gewisse, sehr erwünschte und anscheinend einfache Sprünge, wie konstant fünfzählige Blüten, weiße Blumenkronen u. s. w., bis jetzt nicht vorgekommen sind.

O. biennis L. mutiert in *semigigas*, *nanella*, *sulfurea*, *leptomeres*, *lata*, *rubrinervis* und *laevifolia*. Die beiden ersteren sind von Stomps entdeckt worden und seitdem wiederholt aus der reinen Rasse der *O. biennis* in meinem Garten entstanden[5]).

Die Mutation von *Oenothera biennis* in *O. biennis sulfurea* wurde von Klebahn an Pflanzen aus der Lüneburger Heide studiert[6]). Dieser Forscher beobachtete auch die *O. biennis cruciata*, welche auch in unseren Dünen als Mutante entstanden ist und welche jetzt von Bartlett *O. biennis leptomeres* genannt wird. Die drei zuletzt genannten Formen, unter denen *O. biennis lata* wohl die wichtigste ist, sind von Gates beschrieben worden[7]). Überdies ist eine

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[3]) R. R. Gates, The new Phytologist Vol. 12, Nr. 8, p. 291, Oct. 1913.

[4]) F. W. T. Hunger, Recherches exp. s. l. mutation chez *Oe. Lam.* Ann. Buitenz. 2e Série, T. XII, p. 92—113.

[5]) Th. J. Stomps, Parallele Mutationen bei *Oenothera biennis*. Ber. d. deutsch. bot. Gesellsch. Bd. 32, 1914, S. 179 und a. a. O.

De Vries, The coefficient of mutation in *Oe. biennis* L. Bot. Gaz. Vol. LIX, Nr. 3, 1915, S. 169—196.

[6]) H. Klebahn, Formen, Mutationen und Kreuzungen bei einigen Oenotheren aus der Lüneburger Heide. Jahrb. Hamb. Wiss. Anst. Bd. XXXI, 1913.

[7]) R. R. Gates, The mutationfactor in evolution. London 1915, S. 153.

schmalblätterige Form von *O. biennis* von C. Stuart Gager in Radiumkulturen erhalten worden[8]).

O. biennis Chicago ist eine, den Bartlett'schen neuen Arten gleichberechtigte, mit *O. biennis* nicht näher verwandte und nur vorläufig unter diesem Namen aufgeführte Art, von der ich zuerst in einem Walde unweit Courtney am Ufer des Missouri-Flusses eine Mutation entdeckt habe und welche seitdem in meinem Garten neue Typen hervorgebracht hat. Unter diesen nenne ich hier nur *O. salicastrum*, *O. salicifolia* und *O. saligna*; sie sind alle durch schmale Blätter und andere Merkmale von der Mutterart durchaus verschieden.

Die beiden ersteren sind in meinem Buche Gruppenweise Artbildung S. 304—307 beschrieben und abgebildet worden, die letztere soll an anderer Stelle besprochen werden. Sie ist eine dimorphe Form, welche in jeder Generation in etwa der Hälfte der Individuen zum Typus der Mutterart zurückkehrt, welche sich also in dieser Beziehung verhält wie *O. scintillans* u. a.

O. stenomeres Bartlett hat zwei Mutanten geliefert, welche von Bartlett unter den Namen *gigas* und *lasiopetala* beschrieben worden sind. Beide sind progressive Mutationen mit für die Gruppe neuen Merkmalen. Die erstere hat, wie die *O. Lamarckiana mut: gigas*, die doppelte Anzahl von Chromosomen und die entsprechenden dicken Blütenknospen. Sie hat in meinem Garten in etwa 30 Exemplaren geblüht, neben einer gleich großen Kultur der Art selbst. Alle Teile, sowohl die vegetativen Organe als die Blüten zeigten deutlich die *Gigas*-Merkmale. *O. stenomeres mut: lasiopetala* hat stark behaarte Blumenblätter, während bekanntlich die Petalen der Oenotheren sonst glatt und unbehaart sind[9]).

O. pratincola Bartlett. In den Kulturen dieses Forschers sind entstanden *mut: gigas*, mit 28 Chromosomen, und *mut: formosa*, mit schmalen, runzeligen Blättern, ähnlich wie meine *O. biennis Chicago mut: salicifolia*, aber weit höher und kräftiger als diese (in meiner Kultur 1,5 m gegen etwa 0,6 m). Ferner die Mutationen *nummularia*, *tortuosa*, *rubricentra* und *nitida*[10]).

O. Reynoldsii Bartlett bringt drei Arten von Zwergen hervor, welche die Namen *debilis*, *semialta* und *bilonga* führen. Die ersteren sind die kleinsten und schwächsten; die *semialta* sind intermediär zwischen dieser und der Mutterart, und die *bilonga* sind der *semialta* in jeder Hinsicht gleich, mit Ausnahme der Früchte, welche doppelt

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[8]) C. Stuart Gager, Cryptomeric inheritance in *Onagra*. Bull. Torr. Bot. Club T. 38, S. 461 und Brooklyn Inst. of Sc., Contrib. Nr. 3, 1911.

[9]) H. H. Bartlett, The experimental study of genetic relationships. American J. of Bot. II, S. 132—155, 1915 (S. 143 *mut: gigas*; S. 146 *mut: lasiopetala*).

[10]) A. a. O. und H. H. Bartlett, Additional evidence of mutation in *Oenothera*. Bot. Gaz. Vol. 59, S. 81—123, 1915.

so lang sind. Leider haben diese Mutanten in meinem Garten wegen des zu nördlichen Klimas zu spät geblüht und keine Früchte ausgebildet. Die Art des Mutierens ist hier von der gewöhnlichen verschieden, indem gewisse Individuen der *O. Reynoldsii* anscheinend keine Zwerge hervorbringen, während andere deren 60—80% abwerfen[11]).

O. grandiflora Ait. hat in den Kulturen von Davis und von Gates eine Reihe von Formen geliefert, deren einige vermutlich Bastarde sind, da der Fundort, von welchem ihre Samen stammten, eine Mischung von *O. grandiflora*, *O. Tracyi* und über ein Dutzend intermediären Formen enthält und somit als Ausgangspunkt für reine Kulturen unbrauchbar ist[12]). Als sichere und wichtige Mutation ist unter diesen Neuheiten jedenfalls ein von Gates erhaltener Zwerg anzuführen[13]). Außer bei Dixie-Landing in der Nähe von Tensaw wächst die *O. grandiflora* noch an anderen Stellen in Alabama und von diesen besuchte ich 1912 mit Herrn Bartlett die Umgegend des Dorfes Castleberry. Die Pflanze wuchs hier auf einem Maisfelde, und soviel wir feststellen konnten, als reine Rasse. Aus den dort eingesammelten Samen habe ich seither drei Generationen kultiviert. Sie brachten regelmäßig zwei Mutationen hervor, welche ich *mut : ochracea* und *mut : lorea* nenne. Die erstere ist von niedriger Statur und hat blasse grüne Blätter, die zweite ist kräftig und durch lange, dunkelgrüne, riemenförmige Blätter ausgezeichnet.

Die *ochracea* entstand in den beiden letzteren Generationen in vielen, die *lorea* dagegen nur in wenigen Exemplaren; beide sind samenfest. Eine ausführliche Beschreibung soll aber erst nach fortgesetzter Kultur gegeben werden.

Außerdem entstand aus den Samen meiner zweiten Generation eine Mutation, welche die dicken Blütenknospen und andere Merkmale des *Gigas*-Typus führte, deren Chromosomen aber bis jetzt noch nicht gezählt worden sind. Sie trat in zwei Individuen in einer Kultur von mehreren Hundert blühenden Pflanzen auf.

O. suaveolens Desf. Seitdem ich diese Form neben der *O. grandiflora* aus Alabama in meinem Garten kultiviere, hat sie sich als von dieser durchaus verschieden herausgestellt[14]). Die Samen zu meiner Kultur erhielt ich von Herrn Prof. L. Blaringhem,

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[11]) H. H. Bartlett, Mutation en masse. Americ. Naturalist, 1915. S. 135. In ähnlicher Weise erzeugt *O. Lamarckiana mut : gigas* Individuen, welche etwa 25% Zwerge unter ihren Nachkommen enthalten. Vgl. Bot. Gaz. T. 60, 1915.

[12]) De Vries und Bartlett, The evening primroses of Dixie-Landing, Alabama, Science N. S. 36, S. 599—601, 1912.

[13]) R. R. Gates, Mutationfactor, S. 150.

[14]) L'*Oenothera grandiflora* de l'herbier de Lamarck. Revue gén. d. bot. XXV bis, S. 151.

der mir auch den Fundort im Forste von Fontainebleau zeigte. Hier bringt die Art von Zeit zu Zeit Exemplare mit schwefelgelben Blüten, *O. suaveolens mut: sulfurea* hervor, und dieselbe Mutation ist im verflossenen Sommer auch in meinem Garten aufgetreten.

Außerdem erhielt ich in der zweiten Generation (1914) meiner Kultur eine Zwergform mit dunkelgrünen langen und schmalen und sehr lang zugespitzten Blättern, welche ich *mut: jaculatrix* nenne. Sie ist unter unserem Klima sehr schwach und die Pflanze gab aus zahlreichen anscheinend guten Früchten nur zwei keimfähige Samen, welche zu der Mutter gleichen Pflanzen aufgewachsen sind. Ebenso entstand die *mut: jaculatrix* in der dritten Generation meiner Rasse, und zwar aus einer Kultur von über 1600 Exemplaren in einer Reihe von Individuen, von denen etwa ein Dutzend geblüht haben. In derselben Kultur traten zwei neue Formen *O. suaveolens mut: lutescens* und *mut: fastigiata* auf, beide in mehreren Exemplaren. Die erstere ist schwach, gelblichgrün, niedrig und dünnstengelig; sie erinnert an die *mut: ochracea* aus *O. grandiflora*. Die *fastigiata* ist zwar niedriger als die Art, aber kräftig und dicht beblättert; ihr Hauptmerkmal ist aber der aufgerichtete Stand ihrer Seitenzweige, Blüten und Blütenknospen. Diese sind bei der Mutterart im weiten Bogen aufwärts gerichtet, bei der Mutation aber der sie tragenden Achse dicht angedrückt. Schließlich sind noch zwei Exemplare einer *mut: lata* und eine Pflanze mit dicken, an den *Gigas*-Typus erinnernden Blütenknospen zu erwähnen.

Alle diese Formen sollen ausführlich beschrieben werden, sobald sie in zweiter Generation kultiviert sein werden.

Überblicken wir die ganze Liste der bis jetzt bei den Oenotheren gefundenen Mutationen, so fällt es auf, dass gewisse Typen aus je zwei oder mehreren Arten entspringen.

So geben *O. biennis* und *O. suaveolens* die *mut: sulfurea*; *O. Lamarckiana*, *O. stenomeres* und *O. Reynoldsii* geben *mut: gigas*, und in derselben Richtung variiert *O. biennis*, und wahrscheinlich auch *O. grandiflora* und *O. suaveolens*. Zwerge und schmalblättrige Formen sind gleichfalls nicht selten, und auch die *mut: lata* ist für drei Arten beobachtet worden. Daneben gibt es aber auch Typen, welche bis jetzt nur von einer Mutterart abgeleitet worden sind, sei es von der formenreichen *O. Lamarckiana*, sei es von anderen Arten. Ohne Zweifel deuten diese Erscheinungen darauf hin, dass die Mutabilität auf bestimmte innere Ursachen zurückzuführen ist, welche, da sie so vielen Arten gemeinsam sind, wohl als durch Vererbung von der einen auf die andere übergegangen angenommen werden müssen. Gleichfalls darf man wohl annehmen, dass der hohe Grad der Mutabilität der *O. Lamarckiana* nicht etwa plötzlich entstanden ist, sondern sich bereits in den Vorfahren dieser Art ganz allmählich entwickelt hat.

Vergleichen wir jetzt die Mutabilität der Oenotheren mit den Ergebnissen, welche Willis für die Entstehung der endemischen Pflanzen von Ceylon aus seinen vergleichenden statistischen Untersuchungen abgeleitet hat.

Unter diesen Arten gibt es 108, welche je nur auf einem Berggipfel oder an einer kleinen Stelle im Gebirge vorkommen. Dort sind sie oft nur in sehr wenigen Exemplaren vertreten, z. B. *Coleus elongatus* auf dem Berge Ritigala nur in etwa einem Dutzend von Individuen. Mehrfach sind sie an Bedingungen gebunden, welche nur ganz lokal vorkommen und oft auf weniger als einen Hektar beschränkt sind. Außer diesem engen Gebiete findet man sie nicht, teils wegen der Eigenschaften des Bodens, teils wegen der mit der Höhe der Lage rasch wechselnden klimatischen Einflüssen.

Sie können somit wohl nie eine bedeutend größere Verbreitung gehabt haben als die jetzige. Trotzdem bilden sie gute, systematische Arten und sind sie nicht durch Übergänge mit den nächstverwandten Arten verbunden. Diese sind gewöhnlich viel weiter verbreitet, an Individuen reich und wachsen oft in der nächsten Nähe der endemischen Formen.

Diesen Mangel an Übergangsformen findet man bekanntlich auch in dem schönsten Beispiel der europäischen Mutationen, der *Linaria vulgaris peloria*[15]). Überall wo diese, sei es im Freien, sei es im Versuchsgarten, aufgetreten ist, geschah es ohne jede Vorbereitung oder Vermittlung. Genau so verhalten sich die Mutationen der Oenotheren, welche ja auch sprungweise Umbildungen darstellen.

Die sichtbaren Eigenschaften der lokalen endemischen Pflanzen Ceylons weisen nirgendwo bestimmte Beziehungen zu der Umgebung auf und stellen offenbar keine Vorzüge im Kampf ums Dasein dar. Die von Willis gegebenen vergleichenden Beschreibungen zeigen dieses klar. Wesentlich ist aber die Tatsache, dass es den endemischen Formen nicht gelungen ist, ihre Vorfahren zu verdrängen und sich an deren Stelle auszubreiten. Solches kommt selbstverständlich unter den 800 endemischen Arten Ceylons bei einigen vor, aber weitaus die meisten sind verhältnismäßig selten geblieben. Sie sind also offenbar nicht unter dem Einflusse einer natürlichen Auslese von kleinen nützlichen Abweichungen durch deren allmähliche Anhäufung zum Vorteil der sie tragenden Pflanzen ausgebildet worden, wie es die alte Lehre annahm. Die Tabellen von Willis lehren, dass diese Vorstellung in keinem einzigen Falle zutrifft. Es bleibt keine andere Möglichkeit übrig als die Annahme von Sprüngen, mittelst deren die neuen Arten mit einem Schlage und in voller Ausbildung aus ihren Vorfahren entstanden sein müssen.

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15) Die Mutationstheorie. Bd. I, S. 562.

Bei den Oenotheren aber lehrt die unmittelbare Beobachtung die Mutationen als solche kennen.

Die endemischen Arten sind samenfest und pflanzen sich, soweit bekannt, ohne Rückschläge auf ihre Vorfahren fort.

Ebenso verhalten sich die meisten Mutationen der Oenotheren, und zwar vom Anfang an. Ob es in Ceylon auch dimorphe Spezies gibt, welche sich in jeder Generation ähnlich spalten wie die *O. scintillans*, ist selbstverständlich unbekannt. Dieses ist aber sehr unwahrscheinlich, da solche Formen bereits im Laufe weniger Jahre von ihren atavistischen Spaltungsprodukten verdrängt werden müssten[16]).

Ob dieselben Mutationen im Freien nur je einmal oder wiederholt entstehen, ist eine Frage, welche der Beobachtung nicht zugänglich ist, wie Willis hervorhebt (a. a. O. S. 331). Er hält es für nicht unwahrscheinlich, dass sie oft in mehreren Exemplaren aus den Samen eines und desselben Individuums hervorgehen. Von solchen Samen könnten dann die meisten durch äußere Umstände verloren gehen, aber die Aussicht wäre größer, dass wenigstens einzelne zu blühenden Pflanzen aufwachsen würden. Unter den Oenotheren ist es Beobachtungssache, dass die Samen einer selbstbefruchteten Mutter gar oft mehrere Exemplare derselben Neuheit enthalten und die *Linaria vulgaris peloria* lehrt ohne weiteres, dass eine bestimmte Mutation im Freien zu wiederholten Malen aus einer Spezies hervorgehen kann. Und seitdem dieselbe Mutation, wie z. B. die *Gigas*, aus verschiedenen Arten entstanden ist, kann es wohl nicht fraglich sein, dass sie auch mehrfach aus derselben Spezies hervorgehen kann. Es ist in dieser Beziehung vielleicht wichtig, dass die *O. gigas*, welche ja eine progressive Mutation darstellt und somit am nächsten mit den Endemismen zu vergleichen ist, in meinen Kulturen bis jetzt nur einmal aus der *O. Lamarckiana* entstanden ist. Auch für *O. brevistylis* und *O. laevifolia*, welche bis jetzt nur auf dem Felde bei 's Graveland gefunden worden sind und welche somit eigentlich auch als lokale endemische Formen betrachtet werden können, genügt die Annahme einer einmaligen Entstehung vollkommen. Wir folgern also, dass Mutationen sowohl im Versuchsgarten als im Freien entweder nur je einmal bezw. ganz selten oder in verschiedenen Graden häufiger entstehen können.

Die Mutationen der Oenotheren sind bekanntlich richtungslos, d. h. keine bestimmte Richtung waltet unter ihnen vor.

Ebenso verhalten sich die Endemismen in Ceylon, welche sich über Veränderungen in fast allen Organen und Eigenschaften erstrecken.

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16) J. Delboeuf, Ein auf die Umwandlungstheorie anwendbares mathematisches Gesetz, Kosmos, 1. Jahrg., Bd. II, S. 112 und Die Mutationstheorie, Bd. I, S. 147.

Die 800 endemischen Arten von Ceylon sind über nahezu 100 natürliche Familien und über eine viel größere Anzahl von Gattungen ziemlich gleichmäßig verteilt.

Einzelne Gattungen gibt es mit 15—30 endemischen Arten, weitaus die meisten aber haben deren weniger als zehn. Diesem Verhalten kann man die Tatsache an die Seite stellen, dass in der viel kleineren und erst seit kurzem in dieser Richtung untersuchten Gruppe der Oenotheren etwa ein halbes Dutzend von Arten je 1—6 Neuheiten hervorgebracht haben, während deren Zahl bis jetzt nur bei der *O. Lamarckiana* eine viel höhere ist.

Eine sehr wichtige Frage ist von Willis aufgeworfen worden in bezug auf den möglichen Umfang der Mutationen (a. a. O. S. 329). Er betrachtet es als eine unrichtige Folgerung aus der Theorie, dass diese Sprünge klein sein müssen und stellt als seine Ansicht auf, dass man ruhig annehmen darf, dass kein Unterschied zwischen zwei nächstverwandten Arten einer Gattung zu groß sei, um in einem Sprunge zu entstehen. Sogar Untergattungs- und Gattungsmerkmale bedürfen nach ihm häufig nicht der Annahme von Reihen von aufeinander folgenden Mutationen. Er führt eine Reihe von Stützen für diese neue Ansicht an. Erstens sind auch die kleinsten endemischen Arten gute Spezies, welche in vielen Merkmalen von ihren nächsten, oft mit ihnen zusammenwachsenden Verwandten unterschieden sind. Sie werden denn auch von den besten Systematikern als Arten und nicht als Varietäten betrachtet. Dennoch sind sie so lokal, dass sie wohl kaum anders als durch einen einmaligen Sprung entstanden sein können. M. a. W. die ganze Gruppe von Merkmalen, welche einer Speziesdiagnose zugrunde liegt, muss durch eine einmalige Mutation ins Leben gerufen werden können. Ferner gibt es in Ceylon 17 endemische Gattungen mit je nur einer Art und in diesen Fällen ist die geographische Lage gleichfalls eine solche, dass es auf der Hand liegt, für die ganze monotype Gattung ein einmaliges Entstehen anzunehmen. Es gibt nur vier endemische Gattungen mit je 2—3 Arten und nur zwei mit einer größeren Anzahl, u. zw. *Doona* mit 11 und *Stemonoporus* mit 15 Arten. Hier müssen offenbar nach der Entstehung der Gattung noch weitere Mutationen stattgefunden haben.

Dieser Auffassung von Willis stimme ich gerne bei und meine, dass auch bei den Oenotheren die Mutationen weit zusammengesetztere Erscheinungen sind als wir bis jetzt angenommen haben. Ob man dabei den ganzen Sprung als eine Mutation bezeichnen oder die Umwandlung jedes einzelnen Faktors als eine solche beschreiben will, ist offenbar gleichgültig. In meinem Buche über die Gruppenweise Artbildung habe ich mich bemüht, für jede Mutation eine bestimmte Umänderung in den Vordergrund zu stellen und die übrigen als sekundäre, von dieser mehr oder weniger abhängige Vorgänge zu beschreiben. Doch gibt es offenbar Fälle, in denen zwei oder mehrere Umänderungen regelmäßig zusammengehen, ohne dass wir einen ursächlichen Zusammenhang zwischen ihnen auffinden könnten. Es mögen davon einige Beispiele angeführt werden. *O. rubrinervis* unterscheidet sich von der Mutterart durch die mangelnde oder mangelhafte Verdickung ihrer Holz- und Bastfasern, überdies verhält sie sich in Kreuzungen mit der *O. nanella* anders als die *O. Lamarckiana*. *O. nanella* selbst unterscheidet sich nicht nur durch die niedrige Statur, sondern auch durch größere Empfindlichkeit für durch gewisse Bakterien verursachte Krankheiten. *O. gigas* hat die doppelte Anzahl von Chromosomen und die dadurch bedingten äußerlich sichtbaren Eigentümlichkeiten. Neben diesen hat sie eine ganze Reihe von Eigenschaften, welche weder damit, noch miteinander notwendigerweise zusammenhängen. Sie wird z. B. nicht, wie die *O. Lamarckiana*, von älteren Arten in *Laeta* und *Velutina* gespalten; sie bildet für gewöhnlich intermediäre Bastarde von sehr geringer Fruchtbarkeit und sie folgt in ihren Kreuzungen mit dem von ihr erzeugten Zwerge: *O. gigas nanella*, dem Mendel'schen Gesetze, was bekanntlich die *O. Lamarckiana* mit ihren Zwergen nicht tut. Dennoch ist diese ganze Gruppe von merkwürdigen Eigenschaften in meinem Garten in einem Sprunge entstanden.

Auch in dieser Beziehung verhalten sich somit die Oenotheren in derselben Weise, wie die endemischen Arten von Ceylon und es scheint mir, dass der von Willis ausgesprochene Satz mit vollem Rechte eine sehr eingehende Berücksichtigung bei der ferneren Bearbeitung der experimentellen Mutationserscheinungen beansprucht. Voraussichtlich werden sich diese Mutationen als mehr oder weniger und bisweilen als in hohem Grade zusammengesetzte Vorgänge ergeben, deren Analyse dann einen wichtigen Gegenstand für weitere Forschung bilden wird[17]).

Fassen wir das Ergebnis der obigen Ausführungen kurz zusammen, so dürfen wir sagen, dass die von Willis ausgeführten floristischen und statistischen Studien der endemischen Flora von Ceylon eine sehr wichtige empirische Stütze für die Mutationslehre bilden, und dass der Prozess der Artbildung, wie er von ihm für diese Flora dargelegt worden ist, in nahezu allen Zügen mit den bei den Oenotheren beobachteten Mutationserscheinungen übereinstimmt. Dadurch erhält die jetzige experimentelle Methode den erwünschten Beweis für die Anwendbarkeit ihrer Ergebnisse auf die Vorgänge in der freien Natur.

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17) Solche Analysen habe ich seit einigen Jahren angefangen zu machen, teils auf dem Wege der Kreuzungen, teils durch das Sammeln seltener, in einer und derselben Richtung zu verschiedenen Stufen schreitender Mutationen der *O. Lamarckiana*. Ich werde darüber aber erst später berichten können.

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Das

Biologische Centralblatt

begründet von J. Rosenthal

in Vertretung geleitet durch

Prof. Dr. Werner Rosenthal

Priv.-Doz. für Bakteriologie und Immunitätslehre in Göttingen

herausgegeben von

Dr. K. Goebel und **Dr. R. Hertwig**

Professoren in München

hat den Zweck, die Fortschritte der biologischen Wissenschaften zusammenzufassen und den Vertretern der Einzelgebiete die Kenntnisnahme der Leistungen auf den Nachbargebieten zu ermöglichen. Ohne nach Vollständigkeit zu streben, welche ja doch nicht zu erreichen sein würde, sollen doch alle wichtigen und hervorragenden Forschungen, besonders aber diejenigen, welche ein allgemeineres Interesse haben, ausführlicher berücksichtigt werden. Zur Erreichung dieses Ziels enthält das Blatt:

1) Original-Mitteilungen, besonders Berichte über Forschungsresultate, welche ein allgemeineres Interesse über den Kreis der engeren Fachgenossenschaft hinaus beanspruchen können.

2) Referate, welche den Inhalt anderweitig veröffentlichter gelehrter Arbeiten in knapper, aber verständlicher Weise wiedergeben. Besonders auch Selbstanzeigen, in denen die Herren Gelehrten von ihren an anderen Stellen erschienenen Arbeiten, soweit sie in das Gebiet unsres Blattes gehören, sachlich gehaltene Auszüge liefern.

3) Zusammenfassende Übersichten. Während die Referate einzelne Arbeiten behandeln, wird über wichtigere Fortschritte der Wissenschaft in besondern, zusammenfassenden Übersichten Bericht erstattet, wo nötig unter Rücksichtnahme auf frühere Erscheinungen der Literatur, um so die dauernden Bereicherungen unsres Wissens, gesondert von der Spreu der nur vorübergehend geltenden Einzelbeobachtung, festzustellen und den Boden kennen zu lehren, auf welchen neue Bestrebungen mit Aussicht auf Erfolg sich stützen können.

4) Endlich füllen Besprechungen von Büchern, bibliographische Nachweise und kürzere Notizen die in den vorerwähnten Abschnitten gebliebenen Lücken so viel als möglich aus und ergänzen dieselben.

Ausser den Hauptfächern der biologischen Naturwissenschaften (Botanik, Zoologie, Anatomie und Physiologie) mit ihren Nebenfächern (Entwickelungsgeschichte, Paläontologie u. s. w.) finden auch die Ergebnisse andrer Wissenschaften Berücksichtigung, soweit sie ein biologisches Interesse haben, somit alles was imstande ist, die wissenschaftliche Erkenntnis der Lebenserscheinungen zu fördern und zu vertiefen.

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Goblot, E. (*Lyon*): Le concept et l'idée. - **1912**, n. **1**.

Golgi, C. (*Pavia*): La moderna evoluzione delle dottrine e delle conoscenze sulla vita. Parte I: I problemi fondamentali bio-fisiologici (L'évolution moderne des doctrines et des connaissances sur la vie. Ière Partie: Les problèmes fondamentaux bio-physiologiques). - **1914**, n. **5**.

— La moderna evoluzione delle dottrine e delle conoscenze sulla vita. Parte II: I problemi fondamentali psico-fisiologici (L'évolution moderne des doctrines et des connaissances sur la vie, IIème Partie: Les problèmes fondamentaux psycho-physiologiques). - **1914**, n. **6**.

Grammont, M. (*Montpellier*): Phonétique historique et phonétique expérimentale. - **1912**, n. **4**.

Gregory, J. W. (*Glasgow*): The structural and petrographic classifications of coast-types (Les classifications structurelle et pétrographique des types des côtes). - **1912**, n. **1**.

Guignebert, Ch. (*Paris*): Les origines chrétiennes. - **1910**, n. **3**.

— L'évolution du christianisme ancien. - **1910**, n. **4**.

— De Saint Augustin à Pie X. - **1911**, n. **1**.

— Le dogme de la Trinité. Ière Partie: Les triades primitives et la formule baptismale. - **1913**, **n. 6**.

— Le dogme de la Trinité. IIème Partie: L'évolution des deux triades et les premiers conflits. - **1914**, n. **1**.

— Le dogme de la Trinité. IIIème Partie: La crise arienne, S. Augustin et le symbole d'Athanase. IVème Partie: Immobilité, décadence et ruine. - **1914**, n. **5**.

Günther, S. (*München*): Pseudo- und kryptovulkanische Erdbeben (Tremblement de Terre pseudo- et crypto-volcaniques). - **1913**, n. **4**.

Haberlandt, G. (*Graz*): Ueber Bewegung und Empfindung im Pflanzenreich (Du mouvement et de la sensibilité dans le règne végétal). - **1908**, n. **2**.

Hahn, E. (*Berlin*): Die Entstehung der Bodenwirtschaft (Les origines de l'économie agricole). - **1911**, n. **1**.

Hartog, M. (*Cork*): The dynamics of mitotic celldivision (La dynamique de la division cellulaire mitotique). - **1907**, n. **3**.

— Samuel Butler and recent mnemic biological theories (Samuel Butler et les récentes théories biologiques de la mémoire). - **1914**, n. **1**.

Lugaro, E. (*Modena*): Preformismo ed epigenesi nello sviluppo del sistema nervoso (Préformisme et épigénèse dans le développement du système nerveux). – **1910**, n. **2**.

Mach, E. (*Wien*): Die Leitgedanken meiner naturwissenschaftlichen Erkenntnislehre und ihre Aufnahme durch die Zeitgenossen (Les idées directrices de ma théorie de la connaissance dans les sciences naturelles et l'accueil qu'elles ont reçu des contemporains). – **1910**, n. **2**.

Maunder, E. W. (*Greenwich*): The « canals » of Mars (Les « canaux » de Mars). – **1910**, n. **2**.

— The Sun-Spots (Les taches du Soleil). – **1913**, n. **1**.

Maunier, R. (*Paris*): La sociologie française contemporaine. – **1910**, n. **3**.

Mazzarella, G. (*Catania*): L'etnologia giuridica, i suoi metodi, i suoi risultati (L'ethnologie juridique, ses méthodes, ses résultats). – **1910**, n. **3**.

Mecklenburg, W. (*Klausthal i. H.*): Die Lehre von den Elektrolytlösungen (La théorie des solutions électrolytiques). – **1913**, n. **6**.

Meillet, A. (*Paris*): Linguistique historique et linguistique générale. – **1908**, n. **4**.

— Différenciation et unification dans les langues. – **1911**, n. **2**.

— L'évolution des formes grammaticales. – **1912**, n. **6**.

— Le problème de la parenté des langues. – **1914**, n. **3**.

Miceli, V. (*Palermo*): Gli elementi vivi del diritto (Les éléments vivants du droit). – **1910**, n. **4**.

Michels, R. (*Torino*): Economia e politica (Économie et politique). – **1914**, n. **3**.

Mieli, A. (*Roma*): Le teorie delle sostanze nei presocratici greci. Iª Parte: Dalle prime speculazioni fino ad Empedocle (Les théories des substances chez les présocratiques grecs. Ière Partie: Des premières spéculations à Empédocle). – **1913**, n. **5**.

— Le teorie delle sostanze nei presocratici greci. IIª Parte: Anassagora e gli atomisti (Les théories des substances chez les présocratiques grecs. IIème Partie: Anaxagore et les atomistes). – **1913**, n. **6**.

Milhaud, G. (*Montpellier*): Cournot et le pragmatisme scientifique contemporain. – **1911**, n. **4**.

Millosevich, E. (*Roma*): Dalla torre di Babele al laboratorio di Groninga (De la tour de Babel au laboratoire de Groningue). – **1912**, n. **5**.

Moreux, Th. (*Bourges*): Le Soleil et la prévision des pluies. – **1910**, n. **4**.

— Où nous entraîne notre Soleil? – **1913**, n. **5**.

Naville, E. (*Genève*): La méthode scolastique dans la science du langage. – **1913**, n. **2**.

Nernst, W. (*Berlin*): Sur quelques nouveaux problèmes de la théorie de la chaleur. – **1911**, n. **4**.

Oppenheimer, F. (*Berlin*): Wesen und Entstehung des Kapitalismus (L'essence et l'origine du capitalisme). – **1908**, n. **2** et **4**.

— Wert und Mehrwert. I. Teil: Die Monopol-Theorie des Mehrwertes (Valeur et plus-value. Ière Partie: La théorie de monopole de la plus-value). – **1913**, n. **2**.

— Wert und Mehrwert. II. Teil: Kritik der Marx'sche Theorie des Mehrwertes (Valeur et plus-value. IIème Partie: Critique de la théorie de la plus-value de Marx). – **1913**, n. **3**.

Ostwald, W. (*Leipzig*): Zur modernen Energetik (De l'énergétique moderne). – **1907**, n. **1**.

— Der Wille und seine physische Grundlegung (La volonté et sa base physique). – **1911**, n. **2**.

— Ueber Organisation und Organisatoren. I. Teil: Allgemeine Theorie (De l'organisation et des organisateurs. Ière Partie: Théorie générale). – **1912**, n. **5**.

— Ueber Organisation und Organisatoren. II. Teil: Moderne Probleme (De l'organisation et des organisateurs. IIème Partie: Problèmes modernes). – **1912**, n. **6**.

Pareto, V. (*Losanne*): L'économie et la sociologie au point de vue scientifique. – **1907**, n. **2**.

Pearl, R. (*Orono, Maine – U. S. A.*): Biometrical ideas and methods in biology: their significance and limitations (Les idées et méthodes biométriques en biologie: leur signification et leurs limitations). – **1911**, n. **3**.

Perozzi, S. (*Bologna*): Socialismo giuridico (Le socialisme juridique). – **1911**, n. **3**.

— Precetti e concetti nell'evoluzione giuridica (Préceptes et concepts dans l'évolution juridique). – **1912**, n. **3**.

Rosa, D. (*Firenze*): Delle leggi che regolano la variabilità filogenetica (Des lois qui gouvernent la variabilité phylogénétique). - **1908**, n. **4**.

— I dilemmi fondamentali circa il metodo dell'evoluzione (Dilemmes fondamentaux touchant la méthode de l'évolution). - **1912**, n. **2**.

Rouse, W. H. D. (*Cambridge*): Classical work and method in the twentieth century (Les études classiques pendant le XX^e^ siècle). - **1908**, n. **3**.

Rudzki, M. P. (*Cracovie*): L'âge de la Terre. - **1913**, n. **2**.

Russell, B. (*Cambridge*): On the notion of cause (Sur la notion de cause). - **1913**, n. **3**.

— The relation of sense-data to physics (Les rapports des données sensorielles avec la physique). - **1914**, n. **4**.

Russell, E. S. (*London*): The evidence of natural selection (Les preuves de l'existence d'une sélection naturelle). - **1909**, n. **1**.

— Vitalism (Le vitalisme). - **1911**, n. **2**.

Rutherford, E. (*Manchester*): The structure of the atom (La structure de l'atome). - **1914**, n. **6**.

Sagnac, Ph. (*Lille*): De l'importance relative des faits économiques dans l'évolution historique. - **1909**, n. **2**.

— L'esprit et les progrès de la Révolution Française: I^ère^ Partie: Les origines de la Révolution. - **1914**, n. **1**.

Sayce, A. H. (*Oxford*): The laws of Babylonia (Les lois de Babylone). - **1912**, n. **1**.

Schiaparelli, G. (*Milano*): I primordi dell'astronomia presso i Babilonesi (La naissance de l'astronomie chez les Babyloniens). - **1908**, n. **2**.

— I progressi dell'astronomia presso i Babilonesi (Les progrès de l'astronomie chez les Babyloniens). - **1908**, n. **3**.

Scialojà, V. (*Roma*): L'arbitrio del legislatore nella formazione del diritto positivo (L'arbitraire du législateur dans la formation du droit positif). - **1910**, n. **1**.

Scott, D. H. (*London*): The evolution of plants (L'évolution des plantes). - **1912**, n. **5**.

See, T. J. J. (*Mare Island, California - U. S. A.*): The new science of cosmogony (La nouvelle science de la cosmogonie). - **1912**, n. **1**.

— The law of nature in celestial evolution (La loi de nature dans l'évolution céleste). - **1914**, n. **2**.

Seeliger, H. (*München*): Ueber die Anwendung der Naturgesetze auf das Universum (Sur l'application des lois de la nature à l'Univers). - **1909**, n. **4**.

Semon, R. (*München*): Die physiologischen Grundlagen der organischen Reproduktionsphaenomene (Les fondements physiologiques des phénomènes organiques de reproduction). - **1910**, n. **2**.

Sergi, G. (*Roma*): Lacune nella scienza antropologica (Quelques lacunes dans la science anthropologique). - **1909**, n. **3**.

Severi, F. (*Padova*): Ipotesi e realtà nelle scienze geometriche (Hypothèses et réalité dans les sciences géométriques). - **1910**, n. **3**.

Sherrington, Ch. S. (*Liverpool*): The « rôle » of reflex inhibition (Le rôle de l'inhibition réflexe). - **1911**, n. **2**.

Simmel, G. (*Berlin*): Beiträge zur Philosophie der Geschichte (Quelques considérations sur la philosophie de l'histoire). - **1909**, n. **4**.

Smoluchowski, M. (*Lemberg*): Anzahl und Grösse der Moleküle und Atome (Nombre et dimensions des molécules et des atomes). - **1913**, n. **1**.

Soddy, F. (*Glasgow*): The parent of radium (Le père du radium). - **1909**, n. 2.

— Transmutation, the vital problem of the future (La transmutation, problème vital de l'avenir). - **1912**, n. **2**.

— The periodic law from the standpoint of radioactivity (La loi des périodes envisagée au point de vue de la radioactivité). - **1913**, n. **3**.

Solla, R. (*Pola*): Die Pflanzenphysiologie in ihren Beziehungen zu den anderen Wissenschaften (La physiologie végétale et ses rapports avec les autres sciences). - **1907**, n. **2**.

Sollas, W. J. (*Oxford*): The evolution of man (L'évolution de l'homme). - **1911**, n. **1**.

Sombart, W. (*Breslau*): Die Entstehung der Städte im Mittelalter (L'origine des villes au moyen âge). - **1907**, n. **3**.

— Judaïsmus und Kapitalismus (Judaïsme et capitalisme). - **1912**, n. **3**.

— Liebe, Luxus und Kapitalismus (Amour, luxe et capitalisme). - **1914**, n. **2**.

Sommerfeldt, E. (*Tübingen*): Grundlagen der theoretischen Kristallographie (Les bases de la cristallographie théorique). - **1907**, n. **3**.

Suali, L. (*Pavia*): Esiste una filologia indiana? (Existe-t-il une philologie indienne?) - **1911**, n. **4**.

Suess, F. E. (*Wien*): Moderne Theorien der Erdbeben und Vulkane (Les théories modernes sur les tremblements de terre et les volcans). - **1909**, n. **3** et **4**.

Supino, C. (*Pavia*): Il carattere delle leggi economiche (Le caractère des lois économiques). - **1907**, n. **1**.

Tannery, J. (*Paris*): Questions pédagogiques: L'enseignement secondaire. - **1907**, n. **1**.

Thomson, A. (*Aberdeen*): What determines sex? (Qu'est-ce qui détermine le sexe?). - **1912**, n. **3**.

— Sex-characters (Les caractères sexuels). - **1914**, n. **3**.

Turner, H. H. (*Oxford*): The periodicities of Sun-Spots (La périodicité des taches solaires). - **1914**, n. **1**.

Uexküll, J. v. (*Heidelberg*): Die neuen Fragen in der experimentellen Biologie (Nouvelles questions de la biologie expérimentale). - **1908**, n. **3**.

Vacca, G. (*Roma*): La scienza nell'Estremo Oriente (La science dans l'Extrême-Orient). - **1912**, n. **2**.

Volterra, V. (*Roma*): Il momento scientifico presente e la nuova Società italiana per il progresso delle scienze (Le moment scientifique présent et la nouvelle Société italienne pour l'avancement des sciences). - **1907**, n. **4**.

Walden, L. (*Riga*): Ueber das Wesen des Lösungsvorganges und die Rolle des Mediums (Sur la nature du processus de solution et le rôle du solvant). - **1907**, n. **4**.

Wallerant, F. (*Paris*): Les liquides cristallisés. - **1907**, n. **2**.

Westermarck, E. (*Helsingfors*): The origin of religious celibacy (Les origines du célibat religieux). - **1907**, n. **4**.

White, W. H. (*London*): The place of mathematics in engineering practice (La place des mathématiques dans la pratique du génie). - **1912**, n. **6**.

Wiesner, J. (*Wien*): Der Lichtbedarf der Pflanze (La quantité de lumière nécessaire à la plante). - **1907**, n. **4**.

Xénopol, A. D. (*Jassy*): L'idée de loi scientifique et l'histoire. - **1912**, n. **6**.

Zeeman, P. (*Amsterdam*): L'origine des couleurs du spectre. - **1909**, n. **1**.

Zeuthen, G. H. (*Kopenhagen*): Quelques traits de la propagation de la science de génération en génération. - **1909**, n. **1**.

Ziegler, H. E. (*Jena*): Die natürliche Zuchtwahl (La sélection naturelle). - **1907**, n. **1**.

Ziehen, H. (*Frankfurt a. M.*): Die Kultur der Gegenwart (La culture intellectuelle de notre temps). - **1910**, n. **1**.

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Première Livraison — Janvier.

A. C. D. Crommelin - *The capture theory of satellites.* — **E. Rignano** - *Le forme superiori del ragionamento. Parte Iª: Il ragionamento matematico nelle sue fasi del simbolismo diretto e indiretto.*

LA DIRECTION - *L'enquête de « Scientia » sur la guerre.* — **L. Lévy-Bruhl** - *Les causes économiques et politiques de la conflagration européenne.* — **W. J. Ashley** - *The economical side of the European conflagration.* — **W. Wundt** - *Deutschland im Lichte des neutralen und des feindlichen Auslandes.*

Deuxième Livraison — Février.

J. Costantin - *Les lois de l'hybridation et l'action du milieu.* — **E. Rignano** - *Le forme superiori del ragionamento. Parte IIª: Il ragionamento matematico nelle sue fasi di condensazione ed inversione simbolica.*

A. Landry - *Les origines, les causes, les lendemains de la guerre actuelle.* — **O. Lodge** - *The war from a british point of view.* — **G. von Below** - *Militarismus und Kultur in Deutschland.*

Troisième Livraison — Mars.

F. Frech - *Die Salzseen Anatoliens und ihre Bedeutung für das Problem der Entstehung der Salzstöcke der Erdrinde.* — **E. Rignano** - *Le forme superiori del ragionamento. Parte IIIª: Matematiche e logica matematica.*

V. Pareto - *La guerra e i suoi principali fattori sociologici.* — **W. J. Collins** - *The Aetiology of the European Conflagration.* — **E. Meyer** - *Englands Krieg gegen Deutschland und die Probleme der Zukunft.*

Quatrième Livraison — Avril.

A. Mieli - *La posizione di Lavoisier nella storia della chimica.* — **J. W. Gregory** - *The reported progressive desiccation of the Earth.*

N. Kostyleff - *Les facteurs psychologiques de la guerre actuelle.* — **L. M. Hartmann** - *Ueber die Ursachen des Weltkrieges.* — **Lujo Brentano** - *Die letzten Ursachen des gegenwärtigen Krieges.*

Cinquième Livraison — Mai.

M. P. Rudzki - *Les théories les plus récentes sur l'origine des continents.* — **E. Carnevale** *Democrazia e giustizia penale. Parte Iª: Democrazia e attitudine mentale al giudizio.*

P. Vinogradoff - *The causes of the War.* — **J. Andrassy** - *Weltkrieg und Weltfreiheit.* — **W. L. de Jaworski** - *La guerre actuelle au point de vue de la question polonaise.*

Sixième et Septième Livraison — Juin-Juillet.

G. Bohn - *Idées nouvelles sur l'adaptation et l'évolution. Ière Partie: Les désharmonies des êtres vivants.*

L. Havet - *D'une guerre à l'autre.* — **J. H. Rose** - *The war and nationality.* — **E. Rignano** *I fattori della guerra ed il problema della pace.*

Huitième Livraison — Août.

G. Bohn - *Idées nouvelles sur l'adaptation et l'évolution. IIème Partie: Conception physico-chimique de l'évolution.* — **E. Carnevale** - *Democrazia e giustizia penale. Parte IIª: Democrazia, garanzie processuali, e metodi della lotta giudiziaria.*

W. J. Ashley - *The economic conversion of England.* — **Ch. Guignebert** *L'Église romaine dans le conflit européen.*

Neuvième Livraison — Septembre.

G. Peano - *Importanza dei simboli in matematica.* — **The. Svedberg** - *Structure et formes des molécules.* — **E. H. Starling** - *The animal machine and its automatic regulation.*

A. Meillet - *Les langues et les nationalités.* — **R. Michels** - *Cittadinanza e nazionalità.*

Dixième Livraison — Octobre.

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R. Muir *The antipathy between Germany and England.*

Onzième Livraison — Novembre.

A. S. Eddington - *The stellar universe as a dynamical system.* — **Ch. Fabry** - *Les atomes lumineux et leurs mouvements. Ière Partie: Les mouvements des particules lumineuses.* — **M. Vallauri** - *La medicina indiana.*

P. Bonfante - *Verso la confederazione europea.*

Douzième Livraison — Décembre.

G. Loria - *L'infinito e l'infinitesimo secondo i matematici dell'antichità.* — **Ch. Fabry** - *Les atomes lumineux et leurs mouvements. IIème Partie: La constitution de l'atome lumineux.* — **W. H. Bragg** - *The new crystallography.*

R. Muir - *The problems of the future peace.* — **P. Fedozzi** *Gli insegnamenti della guerra circa il trattamento degli stranieri.*

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A. Graziani - *Le future conseguenze economiche della guerra.* — **A. Weiss** - *Le droit international d'hier et de demain.*

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Deuxième Livraison - (N. XLVI) - (Février 1916)

Th. Moreux - *Les « Novæ » et la constitution de l'univers.* — **F. Bottazzi** - *Le attività fisiologiche fondamentali. Secondo Articolo: L'attività muscolare.* — **A. S. D. Maunder** - *Iranian Migrations before History.*

Ch. Gide - *Les dépenses de la guerre et leurs conséquences économiques.* — **A. Loria** - *Riflessioni e previsioni a proposito della guerra.*

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C. G. Abbot - *The Nature of the Sun.* — **E. Bouty** - *La théorie cinétique des gaz. 1ère Partie: Ses fondements.* — **L. Matruchot** - *Le problème du cancer éclairé par la pathologie végétale.*

G. Jespersen - *Réflexions d'un Danois sur la guerre.* — **C. Supino** *Le fonti economiche della guerra.*

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J. H. Rose - *The Future of Europe.* — **C. A. Reuterskiöld** *Les lignes directrices du droit des gens après la guerre.*

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A. H. Sayce - *The Assyrian empire. A lesson in history.* — **R. Michels** *Il naufragio dell'« Internazionale operaia » e l'avvenire.*

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E. Ciccotti *Dopo la guerra.* — **J. G. K. Wicksell** - *La guerre, la paix et l'accroissement de la population.*

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Septième Livraison - (N. LI) - (Juillet 1916)

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W. R. Scott - *On Repairing the Waste of War.* — **F. Virgilii** - *I principali effetti economici mondiali dell'interruzione degli scambi internazionali.*

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WILHELM ENGELMANN

MILANO — TIPO-LIT. REBESCHINI DI TURATI E C.

On n'a, jusqu'à présent, découvert qu'un seul groupe d'organismes qui révèlent dans toute leur richesse les phénomènes de l'hérédité et de l'hybridation. Presque tous les autres groupes sont constants et uniformes, en ce qui concerne l'hérédité, et suivent dans leurs croisements la loi de Mendel. Seule, la primevère du soir se comporte différemment dans différents cas, aussi bien après l'auto-fécondation pure qu'après le croisement. Ici, le groupe des phénomènes est tellement vaste qu'on n'a pas encore réussi à découvrir le principe fondamental qui les rattache les uns aux autres. L'hypothèse de conditions diverses pour chacun des facteurs de l'hérédité et de leurs combinaisons en groupes plus ou moins grands indique la voie dans laquelle on pourra probablement trouver une solution, mais nous ne possédons pas encore, quant à présent, de principe susceptible d'expliquer tous les phénomènes dont il s'agit, sans l'aide d'hypothèses auxiliaires.

Ailleurs, la loi de Mendel présente le grand avantage de nous fournir un principe de ce genre et de pouvoir être appliquée aux nombreux cas empruntés à des groupes d'organismes le plus divergents. Des groupes de plantes ou d'animaux, reproduisant les phénomènes des primevères du soir, doivent encore être cherchés au moyen d'épreuves nombreuses et répétées. Le principal résultat obtenu jusqu'à présent dans cette nouvelle branche de recherches a été la découverte que les types d'hérédité qu'on croyait autrefois constituer une caractéristique exclusive de l'*Œnothera Lamarckiana,* ont été reconnus comme étant communs à plus d'une demi-douzaine d'espèces. Ce nouveau champ ne tardera sans doute pas à subir de nouvelles extensions.

En plus de la forme ordinaire de l'hérédité, nous devons distinguer les espèces hétérogamiques, les races dimorphiques et les mutations. Chez les premières, l'hérédité de certains caractères est limitée par le sexe, tels caractères étant transmis par les ovules seulement, tels autres uniquement par le pollen. Les races dimorphiques, dans la mesure où elles ont été étudiées sous ce rapport, se scindent dans chaque génération en deux types, dont l'un demeure constant, tandis que l'autre répète la division. Les mutations marquent le commencement de nouvelles espèces et de nouvelles variétés; elles peuvent être produites par des types hétérogamiques et dimorphiques aussi bien que par les espèces ordinaires.

Les hybridations, chez les primevères du soir, comprennent en premier lieu, ainsi qu'on pouvait s'y attendre, les cas explicables à l'aide de la loi de Mendel. Mais ces cas semblent être rares parmi elles. Les hybrides constants sont plus typiques pour ce groupe, soit purs, soit à l'état de combinaison avec l'un ou l'autre des types suivants. On a également rencontré des exemples de scission unilatérale, différant largement des formules symétriques de Mendel. Mais les cas les plus intéressants sont ceux où l'on voit la division se produire dans la première génération et où, par conséquent, les changements visibles sont dûs à une cause autre que la conjugaison pure et simple de leurs porteurs matériels, admise dans les croisements mendéliens. Ce groupe de phénomènes se compose de deux principaux types: ou bien les produits de la division répètent simplement les caractères des deux parents, comme dans les croisements amphiclines, ou les deux types hybrides sont, l'un et l'autre, plus ou moins nettement intermédiaires entre leurs parents. Ces derniers hybrides sont appelés jumeaux.

En outre, on rencontre d'autres types d'hérédité et d'hybridation, mais ils sont encore trop rares et trop imparfaitement étudiés pour que nous nous en occupions dans cet article.

Afin d'élucider plus complètement les principaux types, il est nécessaire d'entrer dans les détails et de nommer quelques exemples. Sous ce rapport, la voie la plus facile qui s'offre à nous consiste à commencer par l'hybridation et à choisir en premier lieu les cas de croisements mendéliens. Leur principe peut être exprimé dans des termes très simples. Les unités fournies par les deux parents n'exercent aucune influence l'une sur l'autre dans l'acte du croisement, mais sont séparées plus tard dans les cellules germinales de la descendance. Cette séparation a lieu dans la production aussi bien des éléments mâles que des éléments femelles, et la recombinaison des unités dans l'acte de fécondation consécutif suit la loi de probabilité. C'est en partant de ce principe que Mendel a calculé ses formules, et on a trouvé qu'elles s'appliquent à d'innombrables cas, en dehors de ceux qu'il avait étudiés lui-même.

Comme exemples d'hybrides mendéliens parmi les Oenothera, on peut citer les croisements d'*O. brevistylis* et ceux d'*O. gigas nanella.* L'un et l'autre suivent la règle des monohybrides, qui est la forme la plus simple du mendélisme, un seul caractère différentiel se trouvant alors impliqué. Chez l'*O. brevistylis* la marque doit être cherchée dans le style qui est tellement court qu'il dépasse à peine le tube du calice. L'ovaire est allongé et pénètre dans la base du style, ce qui rend la fécondation extrêmement difficile. En croisant cette forme avec son parent, l'*O. Lamarckiana,* nous obtenons une première génération hybride uniforme, dont les membres ne diffèrent pas sensiblement de l'*O. Lamarckiana* lui-même. Nous voyons ainsi que le caractère du style court est récessif par rapport à celui du style long. Après l'auto-fécondation de ces hybrides, la deuxième génération embrasse les trois types exigés par la formule de Mendel, à savoir des plantes à style long et d'autres à style court, dont la descendance sera constante, et des individus à style long qui reproduiront la division dans leur descendance. La même règle s'applique à l'*O. gigas nanella,* quand celui-ci est croisé avec l'*O. gigas,* les nains agissant comme type récessif.

Il convient de faire remarquer qu'en plus de leur basse stature, les nains diffèrent du grand *O. gigas* par un autre caractère. Nous voulons parler de leur sensibilité aux attaques de certains microorganismes du sol qui ordinairement les rendent malades, dans une certaine mesure du moins. Mais, dans le croisement, les deux caractères se comportent comme une unité, et on peut faire la même remarque au sujet des caractères secondaires de l'*O. brevistylis,* qui est souvent reconnu à ses feuilles arrondies, longtemps avant l'époque de la floraison.

La division unilatérale est rare, même parmi les primevères du soir. L'exemple le mieux connu de cette division est donné par le croisement entre l'espèce californienne *O. Hookeri* et la forme européenne *O. biennis*. La première génération est uniforme et intermédiaire entre les parents. La deuxième se divise en deux types dont l'un reproduit les marques de la première génération et répète la scission au cours des années suivantes. L'autre type ressemble par son port au *Hookeri,* et n'en diffère que par quelques marques tout à fait secondaires. Il est constant dans sa progéniture. L'arbre généalogique donnerait l'impression d'une généalogie mendélienne dont un type, qui aurait dû être le *biennis,* manquerait. Les deux espèces parentales diffèrent sous plusieurs rapports, quant à la grandeur de leurs fleurs, à la longueur de leur style, à la couleur et à la largeur de leurs feuilles, à la quantité de leurs poils, à la forme des fruits et des graines, etc. Mais, malgré cette grande diversité, elles ne produisent que deux types d'hybrides.

Les hybrides constants sont sujets à être masqués par des caractères mendéliens. Toutes les fois que certains signes se confondent, alors qu'un ou deux autres présentent la séparation selon la loi bien connue, l'hybride est considéré comme suivant cette loi et le fait, pourtant si intéressant, des signes confondus est négligé. Ici, la pauvreté des Œnothères en caractères mendéliens constitue un avantage appréciable, puisqu'elle laisse pur l'hybride constant. *O. Cockerelli,* du Colorado, *O. strigosa,* du Parc Yellowstone, et *O. Hookeri,* déjà mentionné, donnent des hybrides constants à la suite de chaque croisement opéré entre eux. Opérées inversement ou réciproquement, les combinaisons fournissent les mêmes formes. Toutes sont intermédiaires entre leurs parents et constantes après auto-fécondation.

La constance est souvent associée à d'autres types d'hybridisme, la descendance de croisements entre espèces hétérogamiques, d'hybrides amphiclines et d'hybrides jumeaux étant en général uniforme à travers toutes les générations successives. Mais nous nous occuperons de ces cas plus loin.

Des hybrides constants intermédiaires ont été produits également dans d'autres genres, comme, par exemple, parmi les Anémones par M. Janczewski. Il sont probablement très répandus dans la nature. On admet généralement que dans les groupes polymorphes un nombre plus ou moins considérable d'espèces et d'espèces élémentaires peut avoir été produit par l'entrecroisement de celles qui sont nées par mutation.

Nous arrivons maintenant aux groupes de croisements dont la première génération est double, c'est-à-dire se compose de deux types différents. Ici les facteurs différentiels doivent exercer une influence l'un sur l'autre pendant l'acte de la copulation, avec ce résultat qu'une partie de la descendance se trouve rejetée d'un côté, et l'autre partie de l'autre côté de la combinaison attendue. Dans les cas simples, une partie ressemble au père, l'autre à la mère. C'est pourquoi on appelle ces hybrides amphiclines. Dans des cas plus complexes les deux types seront intermédiaires, mais certains signes d'un des parents seront plus fortement prononcés dans un groupe, tandis que l'autre groupe penchera de l'autre côté. Les deux types d'une pareille génération hybride sont appelés jumeaux. Dans les deux cas, les proportions numériques des deux groupes antagonistes dépendent des conditions de culture des parents du croisement. Dans les conditions ordinaires de culture soignée, les deux groupes tendent à l'égalité numérique, mais dès que les conditions deviennent moins favorables ou mal appropriées, l'un des types l'emportera sur l'autre. D'autre part, cette dernière forme apparaîtra en excès, dès que les conditions ambiantes deviendront très favorables. Ces influences peuvent se manifester jusqu'à la disparition à peu près complète de l'un ou l'autre des jumeaux. Les rapports mendéliens dépendent, on le sait, de la loi de probabilité et diffèrent par conséquent clairement de la règle applicable aux amphiclines et aux hybrides jumeaux.

Comme exemple d'hybrides amphiclines, je choisis le croisement entre l'*O. Lamarckiana* et son nain *O. nanella.* Il n'en résulte pas de forme intermédiaire et la seconde génération ne montre pas de division. Mais dans la première quelques-uns des hybrides ressemblent au parent à grande taille, tandis que d'autres ressemblent aux nains. Après auto-fécondation les deux types fournissent des races constantes, ne déviant en rien de leurs grands-parents. Lorsque le parent *Lamarckiana* est cultivé comme une plante annuelle, sans précautions spéciales, et lorsque les nains sont sujets à la maladie bactérienne, que nous avons mentionnée en parlant de l'*O. gigas nanella*, la proportion de nains parmi les hybrides est petite, variant entre 1 °/₀ et 50 °/₀, avec une moyenne d'environ 22 °/₀. Mais lorsque nous choisissons des plantes bisannuelles du *Lamarckiana* et très vigoureuses, ou lorsque nous transplantons les annuelles avec toutes les précautions possibles en vue du plein et rapide développement de leurs racines et que nous prenions enfin le pollen de nains sains, cette proportion peut augmenter au point de faire pencher la balance en faveur de ce dernier type. On peut, en procédant ainsi, s'attendre à plus de 60 °/₀ de nains, et dans quelques cas même à 90 °/₀ et davantage.

Il est intéressant de comparer le croisement de l'*O. Lamarckiana* avec ses nains à celui de l'*O. gigas* avec le nain de cette forme. Dans la première combinaison, les deux parents ont dans leurs noyaux le nombre ordinaire de chromosomes, à savoir quatorze. Dans l'autre, les chromosomes des deux parents ont été doublés dans l'acte original de la mutation. Ils sont au nombre de 28 dans chaque noyau. On voit ainsi que le croisement entre parents à noyaux normaux donne une séparation dans la première génération, tandis qu'un croisement analogue entre parents à noyaux doublés suit la loi de Mendel. Il est difficile de dire s'il existe un rapport causal entre ces phénomènes.

Les hybrides jumeaux se rencontrent couramment, toutes les fois que l'*O. Lamarckiana* est croisé avec d'autres espèces. Ils ont été, en outre, étudiés d'une façon approfondie. Des jumeaux analogues sont produits, à la suite de croisements correspondants, par une autre espèce, l'*O. grandiflora,* de l'Alabama. Ils ont été observés dans les cultures de M. Davis et dans celles faites à Amsterdam, mais aucune description détaillée n'en a encore été publiée. Ils nous avertissent cependant que toute explication proposée pour ce phénomène doit pouvoir s'appliquer aux deux cas.

Les jumeaux diffèrent selon le choix de l'autre parent. Dans certaines combinaisons ils portent les noms de *Læta* et *Velutina,* dans d'autres ceux de *Densa* et de *Laxa.* La division se produit lorsque l'*O. Lamarckiana* ou l'*O. grandiflora* sont employés comme parents fournissant la graine, aussi bien que lorsqu'ils fournissent le pollen pour le croisement. Souvent les combinaisons donnent les mêmes jumeaux dans les deux croisements réciproques et aucune différence n'est observée entre les deux cas. Nous en concluons que les deux sexes sont également susceptibles de division; mais, malgré cela, les deux hybrides sont constants après l'auto-fécondation. Il est donc évident que la division est due à des causes autres que celles agissant dans les croisements mendéliens.

Les jumeaux les plus beaux et les plus typiques sont produits par le croisement de l'*O. muricata* par l'*O. Lamarckiana.* Les *Læta* sont très vigoureux et hauts, pourvus de feuilles tendres et de rares poils, d'épaisses racèmes et de petits fruits. Les *Velutina* sont relativement faibles et bas, avec de longs entre-nœuds dans les épis, des feuilles étroites de couleur grise, avec un limbe courbé longitudinalement. Leurs fruits sont en forme de massue et épais, mais leurs graines sont souvent insuffisamment développées. Cultivés en groupes de dix spécimens ou davantage, les jumeaux constituent des types aux contrastes très accentués.

Après la considération des hybrides, nous en venons à considérer le comportement des races auto-fécondées, d'origine pure. Cette origine peut avoir été perdue dans le passé, comme chez les espèces sauvages, ou observée dans le jardin, comme dans le cas des mutations. Dans un cas comme dans l'autre il existe un type spécial qui mérite d'être traité ici d'une façon détaillée.

Ce sont d'abord les espèces hétérogamiques. Considérées au point de vue morphologique, elles semblent ne différer sous aucun rapport de l'image ordinaire d'une bonne espèce sauvage, et au point de vue physiologique elles sont aussi fidèles à leur type et aussi uniformes que possible. Dans la nature, il est impossible de les distinguer des espèces ordinaires. Malgré cela, on trouve qu'elles constituent un groupe propre, dès qu'on aborde l'étude de leurs hybrides. Ceux-ci diffèrent du tout au tout, selon qu'une des espèces en question est employée comme parent fournisseur de la graine ou qu'elle entre dans la combinaison à titre de porteur du pollen. En d'autres termes, les espèces hétérogamiques donnent des hybrides réciproques différents, aussi bien quand elles subissent les croisements réciproques entre elles, que lorsqu'elles sont unies à des espèces normales. Prenons, à titre d'exemple, les deux types européens les plus communs. *O. muricata* croisé par *biennis* donne un hybride vigoureux, à feuillage épais, avec une tige ferme et un épis riche en fleurs. *O. biennis,* fécondé par l'*O. mu-*

ricata, donne, au contraire, un hybride frêle, avec une tige penchée à son extrémité, un feuillage lâche, de couleur pâle, et un épis allongé sur lequel on ne voit s'ouvrir tous les soirs que d'une à trois fleurs. Nous pouvons en conclure que les cellules sexuelles femelles transmettent à leur descendance d'autres caractères que ceux transmis par les éléments mâles.

Nous pouvons faire un pas de plus et dire que certains facteurs héréditaires présentent une limitation sexuelle, en ce sens qu'ils sont transmis par l'intermédiaire d'un seul sexe, et non par celui de l'autre. Ceci nous amène aux expériences sur les croisements réciproques doubles. Lorsqu'une espèce hétérogamique est employée dans deux croisements successifs, une fois comme père et l'autre fois à titre de mère, aucun de ses caractères hétérogamiques ne peut atteindre la descendance, chaque groupe se perdant au cours de l'une ou de l'autre des deux phases. Les deux phases réunies constituent le croisement réciproque double. Dans notre exemple, cette combinaison serait fournie par *O.* (*biennis* × *muricata*) × *O.* (*muricata* × *biennis*), qui donnerait un *O. biennis,* parce que le *muricata* ne saurait passer successivement par les conditions de père et de mère. Inversement, *O.* (*muricata* × *biennis*) × *O.* (*biennis* × *muricata*) fournit *O. muricata.*

Ce curieux résultat des croisements réciproques doubles peut être combiné expérimentalement à l'hérédité des caractères non-hétérogamiques des mêmes espèces. Tel est le cas, par exemple, dans la combinaison de l'*O. biennis* avec une espèce à pétales linéaires, connue sous le nom d'*O. cruciata.* La double combinaison *O.* (*biennis* × *cruciata*) × *O.* (*cruciata* × *biennis*) perdra les caractères hétérogamiques d'une de ces espèces, l'*O. cruciata,* pour retourner purement et simplement, sous ce rapport, à l'autre espèce, l'*O. biennis.* Mais les fleurs suivent d'autres lois et les pétales linéaires peuvent en conséquence réapparaître chez l'hybride qui se présente alors comme étant un *O. biennis* sous tous les rapports, sauf ses pétales qui seront linéaires. Il est à noter que la même forme est née par mutation de l'*O. biennis* pur, et nous avons là un exemple de la répétition expérimentale de l'origine d'un type pur au moyen du croisement.

Les races dimorphiques forment, au point de vue des effets de l'auto-fécondation, un type absolument différent. Elles se divisent, dans chaque génération, en deux formes, dont l'une répète la division, et l'autre non. Dans la nature la forme soumise à la division serait bientôt dépassée par la forme constante, le pourcentage de ses individus dans une population donnée devant décroître rapidement tous les ans. Aussi, de telles formes dimorphiques ne sont pas connues à l'état sauvage. Dans un jardin cependant elles peuvent être préservées indéfiniment, tout simplement en sélectionnant tous les ans le type soumis à la division. Nombre de races dimorphiques sont nées à titre de mutations de l'*O. Lamarckiana* et d'une espèce affine, le meilleur exemple connu de ce genre étant celui de l'*O. scintillans.* Cette race mutante a des feuilles luisantes et minces de couleur foncée, mais elle est faible et grêle en comparaison avec l'espèce parente. Après auto-fécondation, elle fournit à chaque génération un nombre variable de plantes ayant le port et les caractères de l'*O. Lamarckiana.* Ces plantes restent constantes dans leur progéniture, tandis que les individus à feuilles luisantes répètent la division. Comme dans d'autres cas, la proportion des deux groupes dépend dans une grande mesure des conditions de culture.

Les mutations ont lieu, lorsque des espèces ou des variétés produisent de nouveaux types dans certains de leurs descendants. Le changement est brusque, sans qu'on observe des transitions et sans que des formes intermédiaires accompagnent l'acte. D'un autre côté, la même mutation est généralement plus ou moins souvent répétée par la même forme parente, soit simultanément, lorsqu'elle apparaît dans deux individus ou davantage, soit successivement, au cours des générations. Ceci indique une tendance à des changements distincts, condition qu'on désigne ordinairement comme un état de mutabilité dans ces directions particulières. Plus d'une demi-douzaine d'espèces sauvages, parmi les Œnothera, se trouvent dans cette condition, les unes étant plus riches, d'autres plus pauvres quant à cette production de nouveautés. La plus riche de toutes est l'*O. Lamarckiana* qui a produit plusieurs douzaines de types nouveaux, dont quelques-uns sont assez fréquents, d'autres rares, d'autres encore insuffisamment connus, ou attendant leur description.

Certaines mutations produisent les mêmes changements chez des espèces différentes et sont pour cette raison nommées parallèles. Le doublement du nombre de chromosomes a été observé dans l'*O. Lamarckiana,* l'*O. stenomeres* et d'autres; des nains ont été produits par les deux espèces que nous venons de nommer et par l'*O. biennis,* et ainsi de suite. Ceci indique probablement une origine commune de l'état de mutabilité qui est la cause de ces phénomènes, et si cela est vrai, il doit s'agir évidemment d'une condition très ancienne.

Les mutations marquent le commencement de nouvelles variétés, races et espèces et il est admis que celles des Œnothèras suivent les mêmes lois que les changements à l'aide desquels s'est développée, aux époques géologiques, la généalogie des règnes végétal et animal. Quelques-unes d'entre elles sont progressives, produisant des caractères qui auparavant n'ont pas été observés dans le groupe, mais la plupart sont de nature régressive, se manifestant par la disparition de quelque signe spécial. Le doublement des chromosomes, qui accompagne la stature de l'*O. gigas,* est considéré comme appartenant au groupe progressif; tandis que le nanisme est dû évidemment à la perte d'un des facteurs de la stature ordinairement élevée.

L'étude de l'origine des mutations des Œnothera nous a procuré un ensemble rapidement croissant de faits pouvant servir à la discussion de l'origine des espèces en général.[1] Elle a, en outre, éveillé un vif intérêt pour le traitement expérimental de cette question importante entre toutes.

Amsterdam, Hortus Botanicus.

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[1] *L'évolution des êtres organisés, par sauts brusques,* « Scientia », N. XLV, janvier 1916, p. 28.

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9

Über die Abhängigkeit der Mutations-Koeffizienten von äusseren Einflüssen.

Von

Hugo de Vries.

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1. Hugo de Vries: Über die Abhängigkeit der Mutations-Koeffizienten von äußeren Einflüssen.

(Eingegangen am 14. Januar 1916.)

Das Studium der numerischen Verhältnisse, in denen die verschiedenen Arten von *Oenothera* neue Formen hervorbringen, wird teilweise durch die geringen Prozentsätze und teilweise durch die Mannigfaltigkeit der begleitenden Erscheinungen erschwert. Bekanntlich weisen die Oenotheren einen viel ausgedehnteren Kreis von Bastardierungsvorgängen auf, als die meisten Kulturpflanzen, Haustiere und Insekten. Die MENDELschen Gesetze, welche in so vielen Fällen anscheinend ausschließlich herrschen, treten hier in den Hintergrund. Die Bastarde der einzelnen Arten sind hier in der Regel intermediär zwischen ihren Eltern und sofort konstant, ohne Spaltungen. In einigen Fällen sind sie einförmig, in anderen sind die reziproken Bastarde einander ungleich, oder es treten Zwillinge auf, welche beide, obgleich deutlich verschieden, in ihren Eigenschaften zwischen den Eltern stehen. Bisweilen sind die Bastarde amphiklin[1]), indem sie zwei Gruppen bilden, deren eine dem Vater und deren andere der Mutter äußerlich gleicht.

Die Beziehungen der Mutationsvorgänge zu diesen Bastardierungserscheinungen wurden bisher vielfach verkannt. Sie treten am klarsten dort hervor, wo die letzteren am einfachsten sind. Wenn die Erfolge der Kreuzungen sich dem MENDELschen Gesetze in dessen einfachster Form fügen, kann über die gegenseitige Unabhängigkeit der Mutationen und der Kreuzungen überhaupt kein Zweifel bestehen. Ich wähle als Beispiel die Entstehung von Zwergen aus *Oenothera gigas*[2]). Seit dem ersten Jahre des Bestehens dieser Form bringt sie in jeder Generation etwa 1 bis 2 pCt. Zwerge durch Mutation hervor. Kreuzt man diese mit der

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[1]) Über amphikline Bastarde. Ber. d. d. bot. Ges. Bd. XXXIII, S. 461, 1915.

[2]) *Oenothera gigas nanella,* a Mendelian Mutant. Botanical Gazette. Bd. LX, Nov. 1915, S. 337—345.

Mutterart, so gelten die einfachen MENDELschen Regeln für monohybride Verbindungen, und die Prozentsätze, in denen sie aus Bastarden hervorgehen können, sind somit gründlich bekannt, weichen aber von den erwähnten Mutations-Koeffizienten in auffallender Weise ab.

Nimmt man an, daß die Mutationen vor der Befruchtung stattfinden, so müssen bei der Befruchtung bisweilen zwei mutierte Sexualzellen zusammentreffen, öfter aber werden mutierte Zellen mit unveränderten kopulieren müssen. Die ersteren Verbindungen liefern in unserem Beispiel die *Gigas*-Zwerge, die letzteren aber Hybrid-Mutanten, deren Nachkommenschaft sich nach der MENDELschen Regel spaltet. Solche Bastard-Mutanten oder halbe Mutanten sind in den reinen Linien von *O. gigas* keineswegs selten; sie können aber nur aus ihrer Nachkommenschaft erkannt werden. Sie sind von SCHOUTEN, GATES und mir selbst mehrfach gefunden worden. Zu der Fortsetzung meiner reinen Linie von *O. gigas* habe ich sie selbstverständlich niemals benutzt und in dem Hauptstamme dieser Kultur sind latente Zwergkreuzungen somit nicht vorgekommen. Die Zwerge, welche durch Mutation entstehen, haben deshalb nachweislich unter ihren Vorfahren, rückwärts bis zum Anfang des ganzen *Gigas*-Stammbaumes in 1895, keine Kreuzungen gehabt. Sie können somit auch aus diesem Grunde nicht als Folgen solcher hypothetischen Vorgänge betrachtet werden.

Sind somit die Mutationen Erscheinungen eigener Natur, so erscheint die Frage nach ihrer Abhängigkeit von äußeren Einflüssen als eine berechtigte. Dabei sind aber die einzelnen Stadien des Prozesses auseinander zu halten. Ich bezeichne sie, mit Bezug auf den vorliegenden Fall, als Prämutation, als eigentliche oder synaptische Mutation und als die Kopulation der mutierten Sexualzellen. Die Prämutation ist der Anfang des mutabelen Zustandes für jedes einzelne in diesem Zustande befindliche Merkmal. Sie ist bei den Oenotheren, wenigstens für die bis jetzt untersuchten Mutationen, ein historischer Vorgang, der sich als solcher unserem experimentellen Studium entzieht. Sie ist für die parallelen Mutationen wohl älter als die Arten selbst. Das Vermögen, Zwerge hervorzubringen, verdanken *O. biennis* und *O. Lamarckiana* vermutlich ihren gemeinschaftlichen Vorfahren, das Mutieren in *O. gigas* haben diese beiden Arten mit *O. stenomeres* Bartl. und *O. pratincola* Bartl. gemein.

Die Vorgänge bei der Kopulation mutierter Sexualzellen müssen offenbar denselben Gesetzen folgen, wie die künstlichen Kreuzungen der mutierten Rassen. Sie lassen sich somit aus den

Erfolgen dieser Versuche berechnen. Diese aber hängen nachweislich von äußeren Einflüssen ab. Im Falle der amphiklinen Bastarde zwischen *O. Lamarckiana* und ihrem Zwerge wechselt das numerische Verhältnis der beiden Typen zwischen fast 0 und fast 100 pCt.; in anderen Beispielen wechselt es in ähnlicher Weise, wenn auch innerhalb engerer Grenzen. Wenden wir dieses auf den betreffenden Mutationsvorgang an. Ist eine Eizelle von *O. Lamarckiana* in *O. nanella* mutiert worden, und wird sie von einem normalen Pollenkern befruchtet, so kann der betreffende Keim je nach Umständen zu einer hohen *Lamarckiana*-Pflanze oder zu einem Zwerge emporwachsen. Die Aussicht, Zwerg zu werden, wird aber um so größer sein müssen, je günstiger die Kulturbedingungen der elterlichen Pflanzen sind.[1] Oder mit anderen Worten, es werden die Mutations-Koeffizienten aus diesem Grunde durch die Lebenslage beeinflußt werden müssen.

Ob daneben auch die synaptische Mutation als solche eine analoge Abhängigkeit besitzt, habe ich bis jetzt nicht ermittelt.

Für meine Versuche wählte ich teils *O. Lamarckiana* selbst und teils *O. lata,* da diese bekanntlich höhere Koeffizienten aufzuweisen pflegt als die erstere. Die Befruchtung wurde auf die endständigen Rispen des Hauptstammes beschränkt, umfaßte aber jedesmal alle Blüten, welche sich im Laufe des ganzen Sommers auf der betreffenden Rispe öffneten. Sie geschah in einem Falle auf einigen Individuen mit dem eigenen Staub, auf anderen mit *O. nanella.* Ebenso wurden einige *Lata*-Pflanzen mit *O. Lamarckiana* und andere mit *O. nanella* befruchtet. Die zweite Gruppe (*O. Lamarckiana* × *O. nanella*) umfaßte dieselben Pflanzen, an denen ich den Einfluß der Lebenslage auf die Erfolge dieser Kreuzung studiert habe (a. a. O.). Ich untersuchte die Frage, ob der Mutations-Koeffizient sich auf einer Rispe im Laufe des Sommers ändert, und ob er auf verschiedenen Individuen gleicher Abstammung Verschiedenheiten zeigt. Für den ersteren Zweck wurden die Früchte in kleinen Gruppen geerntet, nachdem die Grenzen dieser Gruppen auf der Rispe während der Blütezeit markiert worden waren. Jede Gruppe enthielt die Früchte der an drei aufeinander folgenden Abenden geöffneten Blumen. Die einzelnen Samenproben wurden getrennt ausgesät und die Prozentsätze für ihre Mutanten einzeln berechnet, dann aber die Ergebnisse in zwölftägigen Perioden zusammengefaßt, als es sich ergab, daß feinere Differenzen sich nicht ermitteln ließen.

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1) Über amphikline Bastarde, a. a. O. S. 463.

Die Aussaat der Samen geschah in Holzkästen im Gewächshaus bei einer Temperatur von etwa 30° C. Die Samen wurden ausreichend weit gestreut, die Keimlinge nicht verpflanzt, aber gezählt und ausgerodet im Laufe mehrerer Wochen, sobald sie ihre Merkmale deutlich zeigten. Die übrig bleibenden erhielten dadurch jedesmal etwas mehr Raum zur Entfaltung ihrer Kennzeichen und auch die träge keimenden Exemplare konnten mitgezählt werden. Um aber eine ausreichende Genauigkeit und Zuverlässigkeit zu erreichen, ist es bei solchen Versuchen durchaus notwendig die Samen alle oder doch nahezu alle zur Keimung zu bringen. Dieses kann aber nur unter Anwendung der von mir beschriebenen Methode erzielt werden.[1]) Es werden die Samen nach vorheriger Durchweichung ihrer äußeren schlaffen Haut in Wasser einem Drucke von z. B. 8 Atmosphären während am besten 2 Tage ausgesetzt. Dadurch wird das Wasser in die feinen Risse der Hartschicht hineingepreßt und das rasche Aufschwellen der Keime fast in allen Samen ermöglicht. Durch die Anwendung dieses Verfahrens und durch die Verwendung einer sehr großen Anzahl von Keimlingen erhalten die Unterschiede in den gefundenen Prozentzahlen, obgleich sie verhältnismäßig klein sind, dennoch die erforderliche Zuverlässigkeit.

Für die Ermittelung der Mutationskoeffizienten habe ich mich auf das Zählen der häufigeren und leicht kenntlichen Mutationen beschränkt. Es waren diese: *O. albida*, *O. oblonga*, *O. nanella* und *O. lata*, die beiden letzteren offenbar nur da, wo sie nicht bereits unter den Eltern vertreten waren.

In dieser Weise erhielt ich die folgenden Prozentzahlen:

Befruchtung in 1914	Juli		August			Gezählte Mutanten
	1—11	12—23	24—4	5—16	17—28	
O. Lamarckiana S. . . .	2.2	1.7	2.1	1.9	—	A. O. L. N.
O. Lam. × *nanella* . . .	2.0	3.1	2.2	1.8	—	A. O. L.
O. lata × *nanella*	—	3.5	3.3	2.2	1.0	A. O.
O. lata × *Lamarck.* . .	—	5.0	7.3	5.3	4.3	A. O. N.

Die gezählten Mutanten, aus deren Summen diese Prozentzahlen berechnet sind, waren, wie bereits erwähnt: A. = *O. albida*, O. = *O. oblonga*, L. = *O. lata* und N. = *O. nanella*. Sie sind unter den Keimlingen, wenn die Blätter der *Lamarckiana*-Pflänzchen etwa 10 cm Länge erreichen, leicht und sicher kenntlich. Die befruchteten Individuen von *O. Lamarckiana* und *O. lata* waren sehr kräftige zweijährige Pflanzen. Die Zahl der befruchteten Pflanzen war im

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[1]) Über künstliche Beschleunigung der Wasseraufnahme in Samen durch Druck, Biol. Centralbl. XXXV, Nr. 4, S. 175, 1915.

ersten Versuch 10, und für die drei Kreuzungen 3, 2 und 3. Der Blütenstaub wurde in den beiden mittleren Fällen von einer reinen Kultur von *O. nanella* genommen, welche aus Samen einer einzigen Mutterpflanze erzogen worden war. Im letzten Versuch gaben die Hauptrispen von drei kräftigen zweijährigen Exemplaren von *O. Lamarckiana* den Pollen, jedes für eine andere der drei *Lata*-Pflanzen. Bei der Reife wurden die Früchte mit Kupferdraht geschlossen, um keine Samen zu verlieren, bis die ganzen Rispen geerntet werden konnten. Die Keimkraft war, nach dem Einpumpen des Wassers, eine sehr vollständige und hatte in den einzelnen Proben ausreichend denselben Wert. Es wurden im ganzen 25 000 Exemplare für den ersten Versuch und 8800—1500 und 3800 für die drei Kreuzungen ausgezählt. Pro Rispe also im Mittel 2500—2000—750 und 1260 Keimlinge. Über die einzelnen Proben ergaben sich die keimenden Samen sowie die einzelnen Mutanten als sehr gleichmäßig verteilt.

Wie man sieht, entsprechen die Ergebnisse unseren oben erörterten Erwartungen in genügender Weise. Bisweilen nehmen die Mutationskoeffizienten im Laufe des Sommers deutlich ab, bisweilen aber nicht (*O. Lamarckiana*). Am klarsten ist die Abnahme im letzten Versuch, wo die Prozentzahlen selber die größten sind. Das Ergebnis ist dem Verhalten der Erbzahlen bei den künstlichen Kreuzungen durchaus parallel und zweifelsohne durch dieselbe Ursache bedingt.[1])

Für die zehn selbstbefruchteten Rispen von *O. Lamarckiana* habe ich die mittleren Mutationskoeffizienten für die einzelnen Mutanten berechnet. Ich fand für *O. albida* 0.5 pCt., für *O. oblonga* 0.8 pCt., für *O. lata* 0.2 pCt. und für *O. nanella* 0.5 pCt. Vergleicht man diese Werte mit den früher gefundenen[2]) (0.2—0.7—0.4—0.5 pCt.) so findet man eine ausreichende Uebereinstimmung.

Berechnet man ferner die mittleren Mutationskoeffizienten für den ganzen Sommer für die einzelnen untersuchten Rispen, so treten individuelle Unterschiede deutlich hervor.

Ich führe nur die höchsten und niedrigsten Zahlen an:

Sommer 1914	Mutationskoeffizient pro Pflanze	
	Niedrigster	Höchster
O. Lamarckiana S.	1.5 pCt.	2.3 pCt.
O. Lam. × *nanella*	1.4 „	2.8 „
O. lata × *nanella*	1.9 „	3.6 „
O. lata × *Lamarck.*	4.8 „	6.7 „

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1) Über amphikline Bastarde a. a. O. S. 465.

2) Gruppenweise Artbildung S. 313.

Änhnliche Unterschiede habe ich auch früher in meinen Kulturen vielfach beobachtet.

Vergleichen wir zum Schlusse die mitgeteilten Zahlen mit den gleichzeitig und unter genau denselben Umständen, z. T. auf denselben Rispen ermittelten Verhältniszahlen der beiden amphiklinen Gruppen aus der Kreuzung *O. Lamarckiana* und *O. nanella.* Diese letzteren sind durch die zweijährige Kultur, durch frühes Auspflanzen und starkes Begießen, sowie durch die Wahl eines besonders günstigen Jahres (1914) von 0–50 pCt. Zwergen bis zu 90 pCt. und darüber, im Mittel auf etwa 65 pCt. Zwerge hinaufgeführt worden. Die Mutationskoeffizienten sind aber jetzt noch nahezu dieselben wie in den älteren Versuchen. Nur im Versuche mit *O. lata* und *O. Lamarckiana* sind die Zahlen deutlich höher (4.8 - 6.7 pCt. gegen 4.1 pCt. in 1901—1909.[1]) Diese kleinen Unterschiede geben nur eine geringe Aussicht, die Beziehung der Mutationskoeffizienten zu den äußeren Lebensbedingungen nach dieser Methode in weiteren Einzelheiten verfolgen zu können.

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[1] Gruppenweise Artbildung S. 314.

MASS MUTATION IN OENOTHERA PRATINCOLA

(WITH FIFTEEN FIGURES)

HARLEY HARRIS BARTLETT

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MASS MUTATION IN OENOTHERA PRATINCOLA[1]

HARLEY HARRIS BARTLETT

(WITH FIFTEEN FIGURES)

Introduction

Of the several small-flowered wild evening primroses thus far examined by the writer for mutability, no other has yielded as valuable data as *Oenothera pratincola*. Certain mutations of this species have been treated in a former article,[2] of which this one is in effect a continuation. To recapitulate very briefly, it may be recalled that *O. pratincola*, a species found wild at Lexington, Kentucky, gives rise in successive generations to a small proportion of mutations, belonging to several distinct types. Of these the most conspicuous in the young condition is mut. *nummularia*, which originates in every generation from seven of the eight independent strains which have been studied. The eighth strain, designated in the former article as Lexington E, shows the phenomenon which the writer has elsewhere designated as mutation *en masse*.[3] Mutant species in *Oenothera*, as typified by *O. Lamarckiana*, give rise to few mutations. The frequency of mutations in

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[1] From the Bureau of Plant Industry, U.S. Department of Agriculture, Office of Plant Physiological and Fermentation Investigations. Published by permission of the Secretary of Agriculture.

[2] BARTLETT, H. H., Additional evidence of mutation in *Oenothera*. BOT. GAZ. **59**:81–123. 1915.

[3] ———, Mutation *en masse*. Amer. Nat. **49**:129–139. 1915.

O. Lamarckiana is about 2 per cent. Some of its mutations are themselves mutable and give 4 per cent or even 6 per cent of secondary mutations.[4] The ordinary strains of *O. pratincola* produce about 2 per cent of mutations,[5] and the true *O. biennis*, of Holland, only about 0.45 per cent.[6] In strains which show mass mutability, however, the number of mutations rises to 50 per cent or even 100 per cent. This is the case with Lexington E.

Lexington E differs from all the other strains of *O. pratincola* (1) in that it gives rise to a characteristic group of four mutations, (2) in that these characteristic mutations occur in such large numbers as to justify the use of the designation mass mutation for the phenomenon, and (3) in that it does not give rise to mut. *nummularia* and certain other mutations which are characteristically produced by the strains which do not show mass mutation.

Turning now to resemblances, we find absolutely no morphological characteristics to indicate even the slightest difference between Lexington E and the other strains of *O. pratincola.* Moreover, Lexington E shows also the ordinary type of mutability, in that it gives rise to small numbers of some of the same mutations which the other strains produce. These mutations are in no wise distinguishable morphologically from the same forms occurring in the other strains, but all the evidence at hand shows that when derived from the strain showing mass mutation the non-characteristic mutations themselves show mass mutability. The mutations characteristic of mass mutability are themselves mutable and throw as secondary mutations other members of the characteristic group.

In view of the extraordinary interest of the phenomenon of mass mutation, it is hoped that the reader will pardon the presentation of this confessedly preliminary report. Many of the genetic relationships between the mutations and the parent species remain to be worked out, and, as will be very obvious, a cytological study of the whole subject is imperative.

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[4] DEVRIES, H., Gruppenweise Artbildung. pp. 312–315.

[5] An estimate based upon the results tabulated in BOT. GAZ. **59**:105–109. 1915.

[6] DEVRIES, H., The coefficient of mutability in *Oenothera biennis* L. BOT. GAZ. **59**:169–196. 1915.

The characteristic mutations of the mass mutating strain

The four mutations, which by occurring in such large numbers characterize the hereditary behavior of Lexington E, form a group with a common structural peculiarity which sets them apart from typical *O. pratincola* and from all the other mutations. This peculiarity lies in the narrow, strongly revolute, veiny leaves, of which the midrib is frequently but not always prolonged from a point below the apex as a setiform appendage. This appendage strongly resembles the infra-terminal calyx tips of certain species of *Oenothera*, and suggests the translocation of a character from one organ to another which does not typically display it. The setiform appendage is exceptionally a centimeter long but is entirely absent on some leaves of each individual mutation. It may be said that the four mutations are characterized by the possibility of manifesting the appendage under favorable conditions rather than by its invariable presence. The revoluteness, narrowness, and venoseness of the leaves, however, are characters which are always distinctive.

The four characteristic mutations may be contrasted as follows:

Plants as tall as *O. pratincola* f. *typica*, with a much-branched terminal inflorescence; fruiting freely by self-pollination and producing a normal number of viable seeds . . . . mut. *formosa*

Plants semi-dwarf; leaves whitish, broader and thicker than in the last; inflorescence often simple and bearing a few thick-tissued, usually cleistogamous flowers; producing by self-pollination large, apparently normal capsules which contain very few seeds . . . . mut. *albicans*

Plants semi-dwarf; leaves green, narrower than in mut. *formosa;* inflorescence densely branched and many-flowered; ovaries almost sterile, producing no capsules by normal self-pollination and only shriveled capsules with few seeds by artificial pollination . . . . mut. *revoluta*

More extreme dwarfs, with narrowly linear leaves; inflorescence-bearing branches with broader leaves than the rest of the plant, simple, with thick-tissued, usually cleistogamous flowers which produce large normal fruits but very few viable seeds by natural self-pollination . . . . mut. *setacea*

The four mutations do not form a linear series showing successive degrees of reduction. Mut. *formosa* and mut. *revoluta* are very similar and might be interpreted as successive reduction stages. They differ in size and fertility, but have many morphological characters in common. Before flowering they can be distinguished with certainty only when the environmental conditions are the same for both. Thus, mut. *revoluta* grown in a rich, moist soil is as large as mut. *formosa* grown in a dry, sandy soil. Under such conditions they might be indistinguishable until they flowered, when the latter would produce large capsules, filled with good seeds, and the former would produce few seeds or none in the shriveled ovaries. Grown under identical conditions, however, the two mutations differ at every stage of development. In some features mut. *setacea* also appears to be a reduction derivative in the same series with mut. *formosa* and mut. *revoluta*. In comparison with the latter, however, it shows a partial resumption of fertility. Its large, strong capsules are well filled, although the seeds are for the most part empty. In this characteristic, as also in its simple inflorescences and thick-tissued buds and flowers, it resembles mut. *albicans*. Mut. *setacea* is different from the other three mutations in its strong tendency to produce dimorphic foliage. The rosette leaves and young cauline plants have narrowly linear, grasslike leaves, which are succeeded above and on the inflorescence-bearing lateral branches by leaves much like those of mut. *revoluta*, which nearly always show the setiform terminal appendage. Like the latter mutation, mut. *setacea* responds greatly to environmental changes. In dry sandy soil it flowers and fruits when only 10 cm. high, but in moist loam it becomes 50 cm. high and has quite a different aspect. The comparatively broad-leaved mut. *albicans* is totally unlike the other mutations at every stage of development.

THE F_1, F_2, AND F_3 PROGENIES OF FORMA *typica*

The original wild mother plant designated as Lexington E did not give a progeny in any way peculiar when it was first grown in 1913. A casual inspection of the F_1 seedlings disclosed no mutations. The majority of the plants of this first culture were discarded as very young seedlings and only 30 were brought to maturity. These 30 plants were entirely typical. In 1914 the F_2 of the strain was found to show mass mutation. The remaining seeds of the original collection were therefore sown, in order to detect any mutability which, on account of the use of insufficiently rigorous experimental methods, might have been overlooked the year before. The results from the new F_1 cultures of 1914 are set forth in table I.

TABLE I

ANALYSIS OF THE F_1 SEEDLING CULTURES OF LEXINGTON E

Culture	Seeds planted	Total plants	Forma *typica*	Mut. *albicans*	Mut. *setacea*	Mut. *latifolia*	Mut. *graminea*
2........	200*	162	160†	0	1 (no. 35)	1 (no. 36‡)	0
3........	199*	175	172	1 (no. 34‡)	0	0	2 (nos. 32‡ and 33‡)
4........	203*	62	62	0	0	0	0
5........	185*	123	123	0	0	0	0
Total	787	522	517†	1	1	1	2

* Indicates seeds from one capsule.

† 25 plants of f. *typica* from culture 2, grown to maturity, were uniform. The remaining plants of f. *typica* were discarded in the rosette stage.

‡ Indicates that the mutation was grown to maturity.

It is clear from table I that the F_1 did not point to Lexington E as a specially mutant strain. There were only 5 mutations in a progeny of 522 plants. Moreover, 2 of the 4 types obtained, mut. *latifolia* and mut. *graminea*, were common to the other strains of *O. pratincola*.

In 1914, F_2 progenies were grown from 3 plants of *O. pratincola* f. *typica* belonging to strain E, and the progeny of a fourth was grown in 1915. The results are summarized in table II.

The F_2 shows a decidedly greater degree of variability than the F_1. One progeny only, that from Lexington E-5, shows mutations in excess of the number of typical plants; the other three progenies indicate a degree of mutability more comparable with that of certain derivatives of *O. Lamarckiana*, such as *O. scintillans*. The F_1, however, was, if anything, less mutable than *O. Lamarckiana* itself. Successive generations seem to show an increasing degree of mutability. Only one F_3 progeny from f. *typica* has been studied. The parent belonged to the progeny of Lexington E-5, that is, it was selected from the most mutable line. The analysis of the F_3 culture is shown in table III.

The salient fact shown by the data for the F_1, F_2, and F_3 progenies is that the number of mutations varies inversely with the number of seeds per capsule. The F_1 progeny, with few mutations, came from capsules with about 200 seeds. (Perhaps the capsules had dehisced at the apex and lost part of their seeds, as frequently happens. A normal capsule of *O. pratincola* contains 300 seeds,

TABLE II

ANALYSIS OF THE F_2 CULTURES OF LEXINGTON E, FROM 4 F_1 F. *typica* PARENTS

Parent	Culture	Seeds planted	Total plants	Forma *typica*†	Mut. *formosa*	Mut. *albicans*	Mut. *revoluta*	Mut. *setacea*	Other mutations	Total mutations	Percentage of mutations
Lex. E-5..	1	156*	131	109	0	0	3	17	2 (no. 208, *angustifolia*)	22	
" ..	2	96*	72	26	0	6	3	36	1 (no. 210, *chimaera*)	46	
" ..	3	106*	75	33	?	6	1	33	0	41	
" ..	4	75*	57	15	1	3	5	33	0	42	
" ..	5	104*	69	10	2	1	4	51	1 (no. 238, *gigas*)	59	
Total...	1–5	537	404	194	4	15	15	172	4	210	52
Lex. E-19..	1	340*	270	261	0	0	4	5	0	9	
" ..	2	350*	239	224	0	0	4	11	0	15	
" ..	3	219*	150	142	0	0	4	4	0	8	
" ..	4	299*	230	219	0	0	4	7	0	11	
" ..	5	378*	143	108	0	1 (no. 67)	7	27	0	35	
Total...	1–5	1586	1032	954	0	0	24	54	0	78	7.5
Lex. E-25..	1	187*	136	130	0	0	3	3	0	6	
" ..	2	225*	147	142	0	0	1	4	0	5	
" ..	3	186*	145	138	0	0	4	3	0	7	
" ..	4	180*	147	134	0	1	3	9	0	13	
" ..	5	144	72	66	0	0	1	4	1 (no. 34)	6	
Total...	1–5	922	647	610	0	1	12	23	1	37	5.7
Lex. E-43..	1	410‡	275	238	0	0	1	36	0	37	
" ..	2	424‡	362	328	0	2	4	27	1 (no. 70§)	34	
Total...	1 and 2	834	637	566	0	2	5	63	1	71	11

* Seeds from one capsule.

† Plants of f. *typica* were grown to maturity as follows: Lex. E-5, 49 plants from cultures 2, 3, 4, and 5, including all of the *typica* plants shown in figs. 1, 2, 3, 4, and 5; Lex. E-19, 18 plants from cultures 1 and 5; Lex. E-25, 23 plants from culture 5; Lex. E-43, 29 plants from culture 2. The remainder were classified in the seedling stage and discarded. The mutations were all retained and classified at maturity, except that some of the weaker specimens of mut. *setacea* died at various stages of development.

‡ Seeds of two capsules.

§ Lex. E-43-70 was a new mutation combining characters of mut. *nitida* and mut. *angustifolia*, two frequent derivatives of *O. pratincola*.

more or less.) The F_2 progenies of 3 mother plants whose capsules contained an average of about 250 seeds gave about 8 per cent of mutations, the upper limit of ordinary mutability, as far as experience goes. Another F_2 progeny from a mother plant with about 110 seeds to the capsule gave over 50 per cent of mutations. Turning to the very striking F_3 progeny, we find that a mother plant with only 90 seeds to the capsule gave almost 75 per cent of mutations. It would be necessary to have much more complete data to establish any exact relationship between progressive sterility and mutability. Nevertheless, it is beyond question that the decrease in the number of seeds has gone hand in hand with the increase in mutability.

TABLE III

ANALYSIS OF F_3 CULTURES OF LEXINGTON E, FROM LEX. E-5-229, F. *typica*

Culture	Seeds planted	Total plants	Forma *typica*	Mut. *formosa*	Mut. *albicans*	Mut. *revoluta*	Mut. *setacea*	Other mutations	Total mutations	Percentage of mutations
1	39	30	9	0	1	1	19	0	21	70
2	86*	56	6	2	4	4	39	1 (*angustifolia*)	50	89·3
3	91*	71	17	0	3	8	43	0	54	76·1
4	100*	74	22	0	3	5	42	2 (*gigas?*)	52	70·3
5	80*	48	20	3	3	4	18	0	28	58·3
6	97*	69	24	0	4	2	39	0	45	65·2
7	95*	51	19	0	3	1	28	0	32	62·7
8	104*	73	21	0	4	3	44	1(?)	52	71·2
9	105*	68	30	0	3	0	35	0	38	55·9
10	142*	102	8	0	0	5	89	0	94	92·2
11	59*	39	4	0	5	2	28	0	35	89·8
12	79*	65	13	0	5	3	43	1 (*gigas?*)	52	80·0
13	83*	65	8	1	4	6	46	0	57	87·7
14	85*	42	18	1	0	1	22	0	24	57·3
15	72*	59	19	2	6	2	30	0	40	67·8
16	73*	51	15	1	7	2	26	0	36	70·6
17	87*	73	13	0	2	5	53	0	60	82·2
Total	1477	1036	266	10	57	54	644	5	770	74·3

* Seeds from one capsule; the entire progeny was classified from the young seedlings; 30 plants of f. *typica* and all the mutations except the weaker individuals of mut. *setacea* were retained.

In *Oenothera pratincola*, therefore, the phenomenon which I have termed mutation *en masse* is associated with the failure of a large number of zygotes to develop, for the number of ovules in all capsules appears to be about the same. Probably the zygotes which fail to develop into embryos represent the weaker individuals of mut. *setacea*, or perhaps some still more reduced mutation which is incapable of development. The problem, however, must be attacked by cytological methods. It is interesting to observe that the F_3, with an average seed germination of 70 per cent, contained 75 per cent of mutations. If all the seeds had germinated, and the additional plants had all been f. *typica*, there would still have been more than 50 per cent of mutations. It seems far more likely, however, that the seeds which did not germinate were either empty or else that they were the weak mut. *setacea*.

A comparable degree of mutability to that of Lexington E is known only in the case of *O. Reynoldsii*, in which mass mutation was first described. In *O. Reynoldsii*, also, the great increase in mutability is associated with an enormously increased degree of sterility. The data in regard to the latter species will soon be published elsewhere.

A number of photographs were made to record the appearance of the mutations at various stages of growth. Figs. 1–5 show a portion of the F_2 progeny from F_1 parent Lexington E-5, recorded in table II. All of the characteristic mutations are shown, as well as several plants which became the parents of subsequent cultures. Fig. 6 shows 6 rosettes of mut. *setacea*, one of which will be found in fig. 3. Fig. 7 shows two mature plants of the same mutation, of which one is shown in fig. 5. Fig. 8 shows 4 rosettes of mut. *revoluta*, 3 of which are likewise shown in figs. 4 and 5. A mature plant is shown in fig. 9. Fig. 10 shows 6 rosettes of mut. *albicans*, 3 of which will be found in figs. 2, 3, and 4. Fig. 11 shows two cauline plants of the same form. The one on the left is just beginning to flower; the one on the right lingered in the rosette condition and would therefore have matured as a stronger plant than its sister. Rosettes of mut. *formosa* are shown in fig. 12. The main stem of the mature plant is shown in fig. 13, and the identical cross mut. *formosa*×f. *typica* in fig. 14. Fig. 15 shows young rosettes of f. *typica* and mut. *gigas*. The *gigas* plant was the particular individual in which E. G. ARZBERGER determined the chromosome number to be 28. For a figure showing the mature stem of f. *typica* the former article on *O. pratincola* in this journal[2] should be consulted.

FIG. 1.—Progeny of Lexington E-5, pan 5 (part of culture 2; see table II); the pan contained 23 rosettes which were classified, most of them at maturity, as follows:

Row	1	2	3	4	5
1....	typica	typica	setacea	setacea	setacea
2......	albicans	setacea	typica	setacea	setacea
3......	setacea	albicans (no. 187; see fig. 11)	typica	setacea	setacea
4......	typica	setacea	setacea	typica	setacea
5......	setacea	setacea	typica		

Mass mutability of the non-characteristic mutations

It has already been stated that Lexington E gives rise to certain mutations which are common to the other strains of *O. pratincola* from Lexington, and that these non-characteristic mutations, as

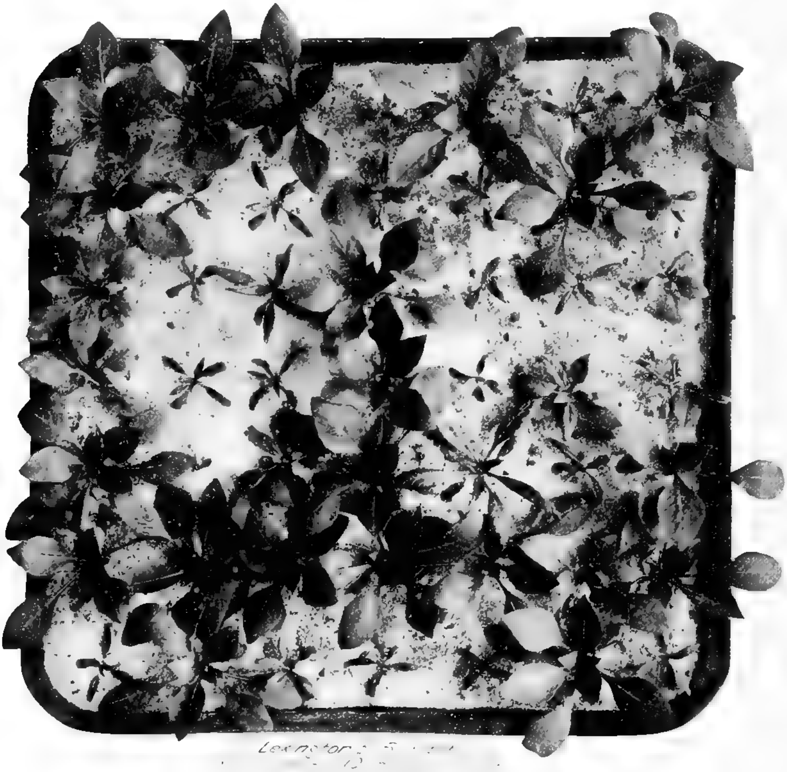

FIG. 2.—Progeny of Lexington E-5, pan 6 (part of culture 3; the remainder is shown in fig. 3; see table II); the pan contains 49 plants, classified as follows:

Row	1	2	3	4	5	6	7
1.	typica	typica	typica	setacea	typica	setacea	typica
2.	typica	setacea	setacea	setacea	setacea	typica	setacea
3.	typica	setacea	setacea	typica	setacea	setacea	albicans (no. 190; see fig. 10)
4.	typica	setacea	setacea	typica	setacea	albicans	setacea
5.	typica	setacea	setacea	typica	formosa	setacea	typica
6.	typica	typica	typica	typica	typica	typica	typica
7.	setacea	typica	albicans	setacea	setacea	typica	setacea

they may be called for convenience, exhibit mass mutability superposed upon their ordinary behavior in heredity. In order to present the data in regard to this point it will be necessary to anticipate somewhat the publication of the next article of this series.

Among the mutations of *O. pratincola* which have been obtained both from Lexington E and from the strains showing only ordinary

FIG. 3.—Progeny of Lexington E-5, pan 7 (part of culture 3; the remainder is shown in fig. 2; see table II); the pan contains 26 plants, which were classified at maturity as follows:

Row	1	2	3	4	5	6
1	formosa	setacea	albicans (no. 191; see fig. 10)	setacea	setacea	
2	typica	albicans	setacea	setacea	typica	
3	typica	setacea	setacea	albicans	typica	
4	typica	setacea	typica	typica	setacea	
5	setacea	setacea	setacea	setacea	setacea	setacea (no. 88; see fig. 6)

mutability, two, mut. *angustifolia* and mut. *latifolia*, have been carried into an F_1 generation from parent plants derived from both sources. A third non-characteristic mutation, mut. *gigas*, has appeared in Lexington E and also, apparently, in the other strains,

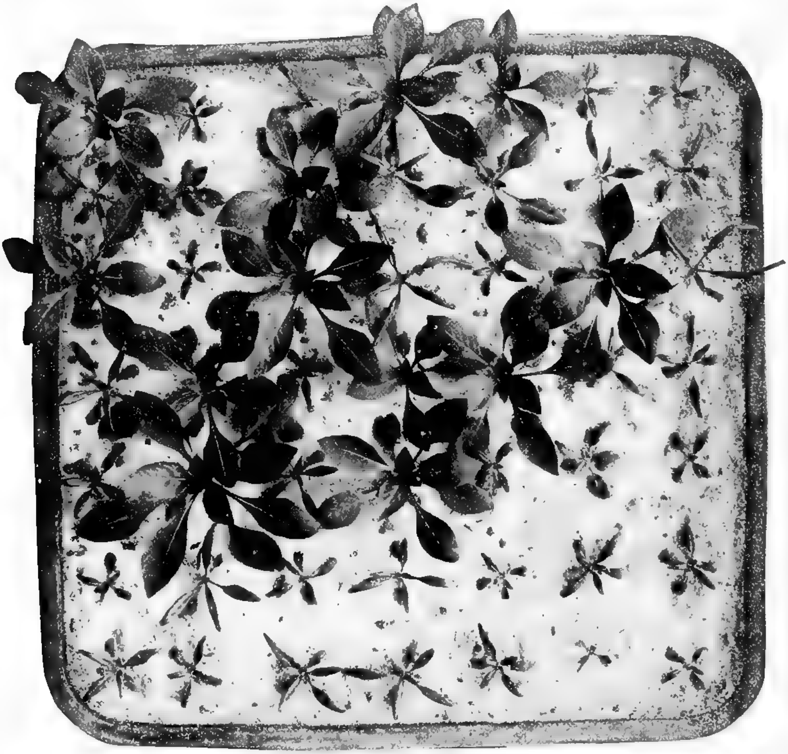

FIG. 4.—Progeny of Lexington E-5, pan 8 (part of culture 4; see table II); the pan contains 49 plants, which were classified (most of them at maturity) as follows:

Row	1	2	3	4	5	6	7
1...	typica	setacea	setacea	typica	typica	setacea	setacea
2...	setacea	albicans	typica	setacea	formosa	setacea	setacea
3...	typica	setacea	typica	revoluta (no. 203; see fig. 8)	setacea	typica	revoluta (no. 202; see fig. 8)
4...	setacea	typica	setacea	typica	typica	setacea	setacea
5...	setacea	typica	setacea	typica	setacea	albicans (no. 195; fig. 10)	setacea
6...	setacea	setacea	setacea	setacea	setacea	setacea	setacea
7...	setacea	revoluta	setacea	setacea	setacea	setacea	setacea

but no progenies have yet been grown or chromosome counts made, except in the case of one plant, belonging to the mass mutant strain.

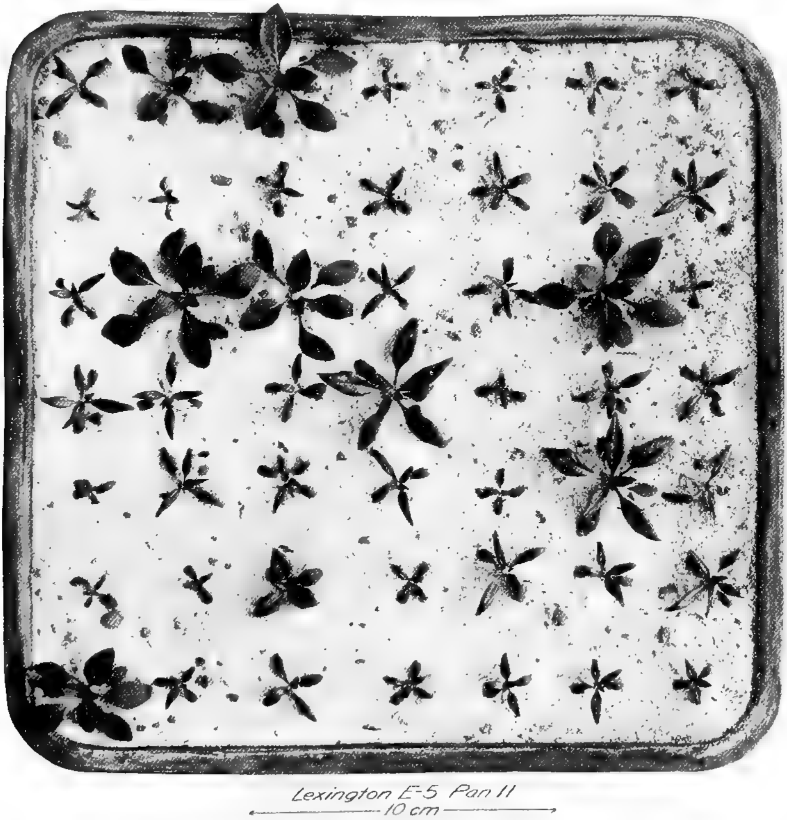

FIG. 5.—Progeny of Lexington E-5, pan 11 (part of culture 5; see table II); the pan contains 49 plants, which were classified (most of them at maturity) as follows:

Row	1	2	3	4	5	6	7
1	setacea	gigas (no. 238; see fig. 15)	typica (no. 239; see fig. 15)	setacea	setacea	setacea	setacea
2	setacea	setacea	setacea	setacea	setacea	setacea	setacea
3	setacea	typica	typica	setacea	setacea	typica	setacea
4	setacea	setacea	setacea	formosa (no. 206; fig. 12)	setacea	revoluta	setacea
5	setacea	setacea	setacea	setacea (no. 164; see fig. 7)	setacea	formosa (no. 207; see fig. 12)	revoluta (no. 172; see fig. 8)
6	setacea	setacea	albicans	setacea	setacea	revoluta	setacea
7	typica	setacea	setacea	setacea	setacea	setacea	setacea

(This plant is shown in figs. 5 and 14.) All three mutations are discussed here, but full data and illustrations are reserved for a paper entitled "Certain mutations and hybrids of *Oenothera pratincola*," to appear later in this journal.

Mut. *angustifolia*.—It has been found that mut. *angustifolia* from ordinary strains gives no descendants resembling itself; aside from the usual small proportion of other mutational types, the progeny consisting of f. *typica* only. The variation, although striking and entirely discontinuous, appears to be somatic. In this connection it is interesting to note that a perfect branch of f. *typica* has been observed as a bud sport on mut. *angustifolia*. As would be expected, mut. *angustifolia* crossed reciprocally with f. *typica* gives f. *typica* together with the usual few mutations. The hereditary behavior may be stated:

mut. *angustifolia* × mut. *angustifolia* → f. *typica*
mut. *angustifolia* × f. *typica* → f. *typica*
f. *typica* × mut. *angustifolia* → f. *typica*

The behavior of mut. *angustifolia* from Lexington E is most remarkable. The parent plant was a sister of the *typica* plant whose progeny is analyzed in table III, but the degree of mutability proved to be much more extreme than in the case of the *typica* sister. Only two plants in the progeny, out of a total of 505, were f. *typica;* the other 503 plants, 99.6 per cent of the progeny, were mutations belonging to the group characteristic of Lexington E. The results are summarized in table IV.

The cross mut. *angustifolia* × f. *typica* and the reciprocal gave respectively 100 per cent and 91.5 per cent of mutations. By comparison with table III it will be seen that each of the reciprocal crosses tends to show the same degree of mutability as the female parent. To be sure, there would seem to be a considerable discrepancy between 74.3 per cent, representing the mutability of f. *typica*, and 91.5 per cent, representing the mutability of f. *typica* × mut. *angustifolia*. No significance can be urged for this discrepancy, however, when we consider that one of the cultures from a single capsule of f. *typica* contained 92.2 per cent of mutations among 102 plants, as compared with 91.5 per cent of mutations

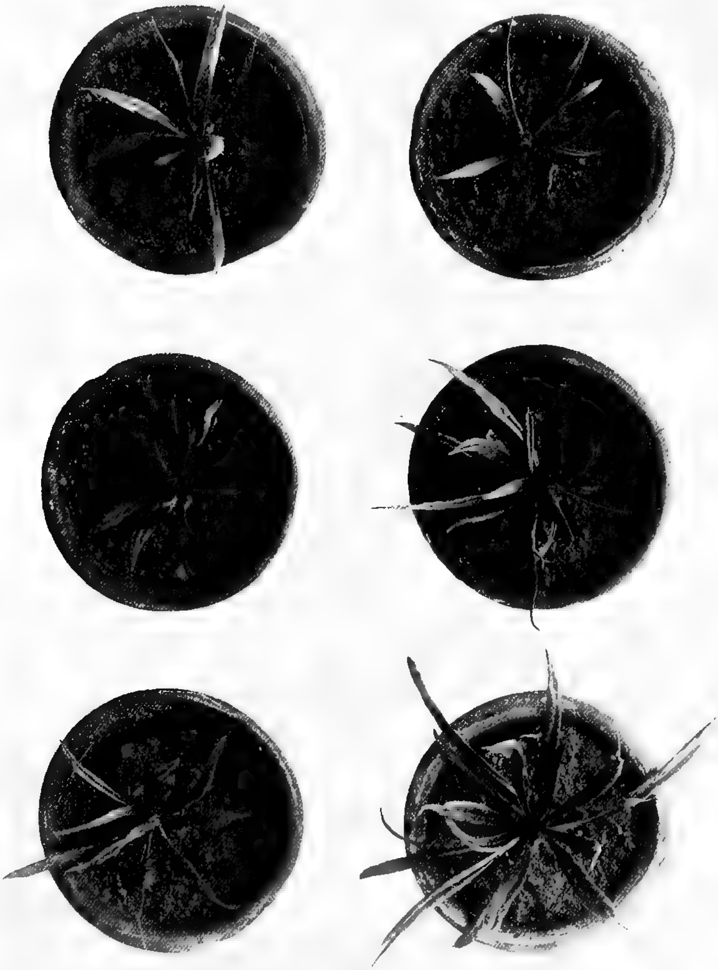

FIG. 6.—Mut. *setacea:* 6 rosettes of the F_2 progeny of f. *typica,* from F_1 parent Lexington E-5; the plant in the upper left-hand corner, Lexington E-5-88, is shown also in fig. 3.

among 118 plants of the cross. As a matter of fact, the significance of ratios in *Oenothera* can be maintained only with great caution, in view of the enormous elimination of gametes during maturation and the subsequent failure of large classes of zygotes to develop. Nevertheless, the absence or almost complete absence of a strong zygote such as f. *typica* in the progenies of mut. *angustifolia* and mut. *angustifolia*×f. *typica* is strong evidence for the view that the composition of the progeny among the mass mutating strains is conditioned by the female gametes. The failure of a class of strong zygotes to appear has much greater evidential value than any fluctuation in the proportion of weak zygotes. From other sources the evidence is unusually strong that the female and male gametes of *O. pratincola* are not equivalent, and that many characters are not carried by the male gametes.

TABLE IV

ANALYSIS OF F_1 CULTURES OF MUT. *angustifolia*, LEXINGTON E-5-208, SELF-POLLINATED AND RECIPROCALLY CROSSED WITH F. *typica*, LEXINGTON E-5-229 (THE PLANT WHOSE PROGENY IS ANALYZED IN TABLE III)

The mutation was a sister plant of the *typica* plant with which it was crossed; for position in pedigree see table II, culture 1 from Lexington E-5

Parent	Seeds planted	Total plants	Forma *typica*	Mut. *formosa*	Mut. *albicans*	Mut. *revoluta*	Mut. *setacea*	Other mutations	Total mutations	Percentage of mutations
Mut. *angustifolia*..	651*	505	2	4	2	21	475	1 (no. 1)	503	99.6
Mut. *angustifolia* ×f. *typica*......	199†	173	0	0	0	4	168	1 (no. 1)	173	100
F. *typica*×mut. *angustifolia*.....	182‡	118	10	0	1	4	99	4	108	91.5

* The 651 seeds were from 11 capsules, containing respectively 51, 75, 53, 62, 44, 59, 82, 101, 46, 33, and 45 seeds.

† The 199 seeds were from 3 capsules, containing respectively 73, 47, and 79 seeds.

‡ The 182 seeds were from 2 capsules, containing respectively 79 and 103 seeds.

In conclusion: mut. *angustifolia* ordinarily gives a progeny containing nearly 100 per cent of f. *typica;* in a strain exhibiting mass mutation many of the *typica* plants are replaced by mutations of the characteristic group. Presumably other individuals of mut. *angustifolia* could be found which would be less mutable than the one tested, just as different individuals of f. *typica* show widely varying degrees of mutability. The progenies of crosses indicate that mass mutability is conditioned by the female gametes.

Mut. *latifolia*.—In contrast with mut. *angustifolia*, mut. *latifolia* reproduces itself in part of its progeny. Its descendants include roughly 50 per cent f. *typica* and 50 per cent mut. *latifolia*, the proportion varying within rather wide limits. Moreover, mut. *latifolia* gives progenies of the same type whether self-pollinated or cross-pollinated with f. *typica*. The reciprocal cross, with f. *typica* as the pistillate parent, consists only of f. *typica*, aside from the usual low proportion of mutations, among which mut. *latifolia* may or may not happen to occur. These relations are as follows:

FIG. 7.—Mut. *setacea:* 2 mature plants from the F_2 progeny of f. *typica*, from F_1 parent Lexington E-5; the right-hand plant, Lexington E-5-164, is shown also in fig. 5; note particularly the dimorphic foliage.

mut. *latifolia* × mut. *latifolia* → f. *typica* + mut. *latifolia*
mut. *latifolia* × f. *typica* → f. *typica* + mut. *latifolia*
f. *typica* × mut. *latifolia* → f. *typica*

The type of heredity here exemplified is shown by several mutations from *O. Lamarckiana*. *O. lata* DeVries provides the classic case. The heredity of *O. scintillans* DeVries and *O. oblonga*

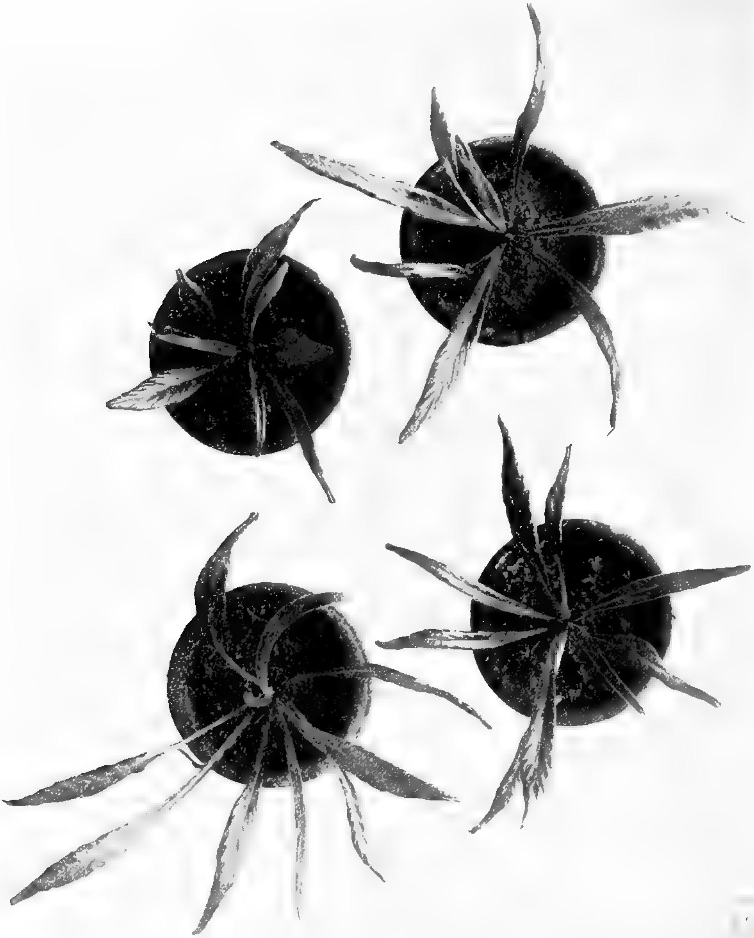

FIG. 8.—Mut. *revoluta:* 4 rosettes of the F_2 progeny of f. *typica*, from F_1 parent Lexington E-5; the upper right-hand plant, Lexington E-5-172, will be found in fig. 5; the two lower plants, nos. E-5-202 and 203, will be found in fig. 4.

DeVries is in essentials the same.[7] Another case is provided by *O. stenomeres* mut. *lasiopetala.*[8] HERIBERT-NILSSON[9] has recently described several new mutations from *O. Lamarckiana* ("heterogame Kombinanten" *dependens*, *undulata*, *stricta*, etc.) which probably show the typical *lata* type of inheritance, although he erroneously concludes that the repeated segregation of *O. Lamarckiana* from these mutations in each generation is due to the existence of two types of functioning gametes on the male rather than on the female side.

It must not be inferred from the similarity of the names that mut. *latifolia* is a parallel variation to *O. lata* DeVries. Such is not the case. Its characters are quite different. Both mut. *latifolia* and mut. *angustifolia* will be described and illustrated in a future article.

As in the case of mut. *angustifolia*, the progeny of mut. *latifolia* from the mass mutating strain contained the expected types, f. *typica* and mut. *latifolia*, together with the characteristic mutations. The latter did not show differences among themselves which would enable one to classify them as modified *typica* or modified *latifolia*, as the case might be. The mother plant belonged to the F_1 generation from Lexington E, and showed about the same degree of mutability as the *typica* sister plant, Lexington E-5 (see table II). The data for mut. *latifolia* are summarized in table V.

Mut. *gigas.*—E. G. ARZBERGER'S discovery that this mutation has 28 chromosomes has already been announced.[10] The count has been made only in one plant, Lexington E-5-238 (figs. 5 and 14), belonging to the mass mutant strain. An apparently identical mutation in one of the other strains has appeared this summer (1915), but its heredity is unknown. Mut. *gigas* is treated, therefore, as a non-characteristic mutation. Only 196 seeds were

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[7] For the latest treatment of these mutations see DEVRIES, Gruppenweise Artbildung. pp. 244–267.

[8] BARTLETT, H. H., The mutations of *Oenothera stenomeres.* Amer. Jour. Bot. **2**: 100–109. 1915.

[9] HERIBERT-NILSSON, N., Die Spaltungserscheinungen der *Oenothera Lamarckiana.* Lunds Universitets Arsskrift. N.F. Avd. 2. **12**: no. 1. pp. 132. 1915.

[10] BARTLETT, H. H., The experimental study of genetic relationships. Amer. Jour. Bot. **2**:132–155. 1915 (see p. 143).

obtained from 15 capsules of the primary mutation, Lexington E-5-238. The progeny consisted of 25 plants, only 16 of which survived transplanting from the seed pan. None of the progeny resembled the parent. All were extreme dwarfs which resembled, but were not identical with, mut. *revoluta* and mut. *setacea*. They differed mainly in the thicker leaves, which in 4 plants were narrow but not markedly revolute. Although a very nondescript lot, differing much among themselves, 5 most resembled mut. *revoluta*, and 7 mut. *setacea*. The result of this culture might almost have been predicted. The mass mutability was inherited by mut. *gigas* from f. *typica*. In view of the dependence of the *gigas* characters upon the double complement of chromosomes, which would in general be handed on to any secondary mutations, it follows that the mutations occurring *en masse* would not be identical with those from f. *typica*. Furthermore, chance irregularities in chromosome distribution might increase the polymorphism of the progeny. In such a highly modified germ plasm irregularities would be expected.

TABLE V

ANALYSIS OF AN F_1 CULTURE FROM SELF-POLLINATED MUT. *latifolia*, LEXINGTON E-36

The parent plant belonged to the F_1 from Lexington E, f. *typica;* see table I, culture 2, for position in pedigree

Parent	Seeds planted	Total plants	Forma *typica*	Mut. *latifolia*	Mut. *albicans*	Mut. *revoluta*	Mut. *setacea*	Other mutations	Total mutations‡	Percentage of mutations‡
Lex. E-36, mut. *latifolia*........	375*	182	95	48	5	2	29	3†	87	47.8

* Seeds from 7 capsules, containing respectively 54, 72, 49, 30, 38, 70, and 62 seeds.

† Nos. 32 and 43, a new mutation; no. 51 mut. *gigas (?)*, morphologically identical with Lexington E-5-238 which had 28 chromosomes; see table II, culture 5 from Lexington E-5, for position of latter plant in pedigree.

‡ Excluding, of course, mut. *latifolia*.

The cross mut. *gigas*×f. *typica* yielded 160 seeds in a single capsule, of which 10 germinated. The plants were all extreme dwarfs, of the most nondescript nature, hardly any two alike. All had thick leaves, some plane, others revolute. No mutation of

f. *typica* could be identified among them. The reciprocal cross yielded no seeds.

Inheritance and mutability of the characteristic mutations

Of the group of characteristic mutations, including mut. *formosa*, mut. *albicans*, mut. *revoluta*, and mut. *setacea*, only the first is both normally fertile and vigorous. The second is vigorous, but produces few good seeds. The third is almost sterile, and the fourth is not only difficult to cultivate, but like mut. *albicans* gives very few good seeds. All of the forms were self-pollinated and reciprocally crossed with f. *typica* in 1914, but, except in the case of mut. *formosa*, the resulting F_1 cultures were very fragmentary or entire failures. The other three forms bloomed in September, when only a few weak, belated flowers of f. *typica* were available for the crosses. The results of the cultures are summarized in table VI.

FIG. 9.—Mut. *revoluta:* a mature plant, Lexington E-19-21 (for position in pedigree see table II).

Mut. *formosa*.—The entirely satisfactory cultures of this form show that it is constant in the sense that it gives no reversions to f. *typica* in its progeny. Moreover, there is no

TABLE VI

ANALYSIS OF F_1 CULTURES IN THE GROUP OF MUTATIONS CHARACTERISTIC OF MASS MUTABILITY

Parentage culture	Seeds planted	Total plants	Forma *typica*	Mut. *formosa*	Mut. *albicans*	Mut. *revoluta*	Mut. *setacea*	Other mutations	Total mutations
Mut. *formosa* Lex. E-5-199 1	244*	196	0	171	0	1	24	0	25
2	269*	163	0	137	0	0	26	0	26
3	201*	177	0	149	0	2	26	0	28
4	216*	174	0	130	1	0	43	0	44
5	217*	193	0	150	0	1	42	0	43
6	224*	179	0	146	0	0	33	0	33
Total 1–6	1371	1082	0	883	1	4	194	0	199
Mut. *formosa* Lex. E-5-199 × f. *typica* Lex. E-5-217	365†	309	0	218	0	0	91	0	91
Mut. *formosa* Lex. E-5-206	177‡	146	0	130	2	0	14	0	16
Mut. *formosa* Lex. E-5-206 × f. *typica* Lex. E-5-229	233§	177	0	151	0	3	23	0	26
F. *typica* Lex. E-5-229 × mut. *formosa* Lex. E-5-206	246‖	133	7	0	1	0	121	4	126
Mut. *albicans* Lex. E-19-67 (seeds of 4 capsules)	386	265	0	0	36	3	226	0	229
Mut. *albicans* Lex. E-5-182 (seeds of 4 capsules)	173	69	0	0	7	3	59	0	62
F. *typica* Lex. E-5-229 × mut. *albicans* Lex. E-5-182	22*	14	1	0	0	1	12	0	13
Mut. *revoluta* Lex. E-5-190 (seeds of 14 capsules)	85	23	0	0	1	17	5	0	6
Mut. *setacea* Lex. E-5-17 (seeds of 4 capsules)	625	140	0	0	0	0	140	0	0
Mut. *setacea* Lex. E-5-20 (seeds of 16 capsules)	1997	8	0	0	0	0	8	0	0
Mut. *setacea* Lex. E-5-66	114*	31	0	0	0	0	31	0	0
Mut. *setacea* Lex. E-5-135 (seeds of 3 capsules)	463	14	0	0	0	0	14	0	0

* Seeds from one capsule.

† Seeds from 2 capsules; 215+150.

‡ Seeds from 2 capsules; 48+129.

§ Seeds from 2 capsules; 64+169.

‖ Seeds from 2 capsules; 115+131.

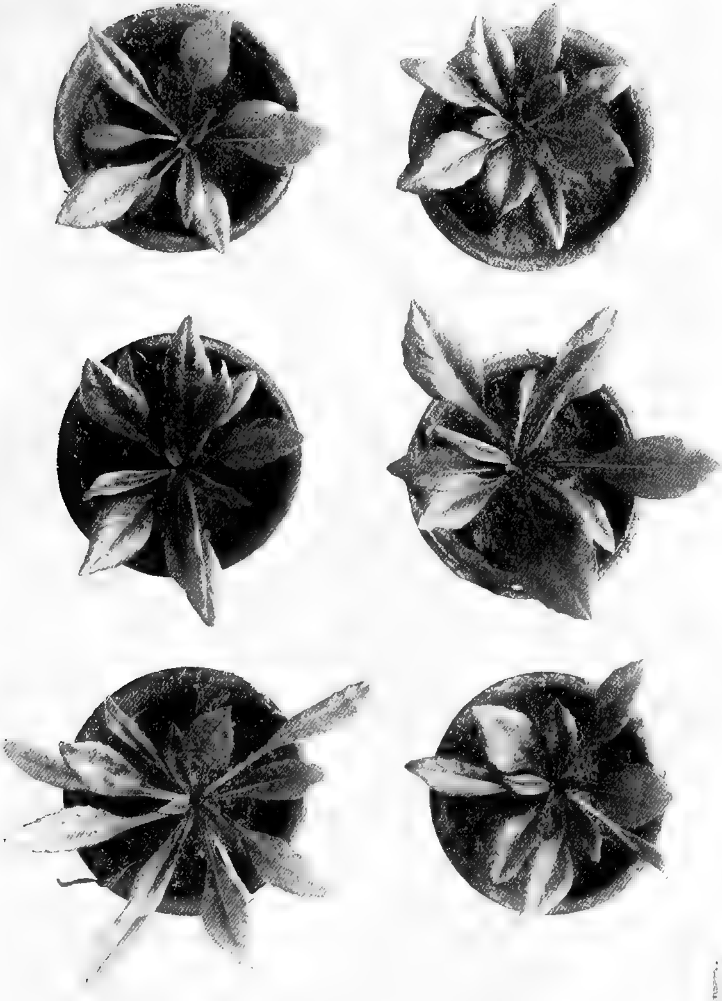

FIG. 10.—Mut. *albicans:* 6 rosettes of the F_2 progeny of f. *typica*, from F_1 parent plant Lexington E-5; the right-hand plant in the middle row, Lexington E-5-190, will be found in fig. 2; the two plants in the lower row, E-5-191 (left) and 195 (right), will be found respectively in figs. 3 and 4.

difference between the progenies resulting from self-pollination and those resulting from pollination with f. *typica*. In other words, mut. *formosa* is dominant over f. *typica* if it enters the cross as a female gamete, but is not even dominant over the weak mut. *setacea* when the *formosa* gamete is male. The scheme of heredity is:

mut. *formosa*×mut. *formosa* → mut. *formosa*
mut. *formosa*×f. *typica* → mut. *formosa*
f. *typica*×mut. *formosa* → f. *typica*

It would have been instructive to cross mut. *formosa* reciprocally with f. *typica* from a non-mass mutant strain. (Such crosses have been made this year and will be grown next year.) From the data at hand, concerning only crosses within the mass mutant strain, it appears clear that the external features of all the characteristic mutations are determined by the female gametes. The female and male gametes are not equivalent. Thus, the progeny obtained from f. *typica*, Lex. E-5-229, by pollination with mut. *formosa* is not significantly different from the progeny obtained by self-pollination (cf. tables III and VI). The characteristic mutations occur with their usual frequency regardless of which pollen is used. We know that this particular individual of f. *typica* gave about 1 per cent mut. *formosa* when grown in large cultures from self-pollinated seeds. That pollination with pollen of mut. *formosa* does not increase the proportion of this mutation in the progeny is strikingly shown by the absence of even a single individual among the 133 plants of the cross. In a culture of this size from self-pollinated seed the chances are about even that an individual of mut. *formosa*, with a frequency of 1 per cent, would or would not turn up. If the use of *formosa* pollen had appreciably increased the frequency of this form in the progeny, a culture of 133 plants might have been expected to show it. The results can be interpreted in only one way, that is, the female gamete carries all the factors which determine the visible characters of the several forms, not only of the 4 mutations, but of f. *typica* as well.

Both parent plants of mut. *formosa* showed a high degree of mutability themselves, and gave rise to the other 3 characteristic mutations. As in the case of progenies from f. *typica*, mut. *angustifolia*, and mut. *latifolia*, the predominating form among the mutations was mut. *setacea*.

FIG. 11.—Mut. *albicans:* 2 cauline plants, Lexington E-5-196 (left) and 187 (right), from the F_2 progeny of f. *typica;* no. 187 is shown also in fig. 1.

Mut. *albicans*.—This mutation reproduces itself in only a small proportion of its progeny, but can be said to come true in the sense that it gives no reversions to f. *typica*. All of the aberrant plants in the cultures, both from self-pollination and from pollination with f. *typica*, are mutations belonging to the characteristic group. As in the case of mut. *formosa*, most of the secondary mutations were mut. *setacea*.

The small culture of f. *typica*×mut. *albicans* emphasizes the fact that the composition of the culture is conditioned by the female gamete. As in the case of the analogous cross f. *typica*×mut. *formosa*, the progeny is just what we should expect from self-pollination of the *typica* parent.

FIG. 12.—Mut. *formosa:* 2 rosettes, Lexington E-5-206 and 207, from the F_2 progeny of f. *typica;* both are shown in fig. 5.

Mut. *revoluta*.—Only one small progeny was obtained from this nearly sterile mutation. It showed that the form reproduces itself except for throwing other mutations of the characteristic group. None of the crosses made with mut. *revoluta* were successful, but there can be little doubt, from collateral evidence, that mut. *revoluta*, as well as mut. *albicans*, follows the same type of inheritance as mut. *formosa*.

Mut. *setacea*.—So far as can be determined, this form comes entirely true from seed, and represents the most extreme modification which can take place in the direction followed by the group of characteristic mutations. Although the crosses with f. *typica* have so far not been successful, it is probable that this extreme reduction phase would also be dominant when introduced into the cross as the female gamete.

The numerical data for mut. *setacea* in all cultures have had to be based largely on the determination of very young plants, for many weak plants do not succeed in forming new roots after being transplanted. There is no difficulty in growing to maturity practically every individual of mut. *formosa* that germinates, and most of those of mut. *albicans* and mut. *revoluta*. It is the rule rather than the exception, however, to lose three-fourths or more of the *setacea* plants. They show some variation among themselves which may possibly indicate that mut. *setacea* is itself mutable and that more than one type is covered by this name. If so, only one type survives in the part of the cultures which reaches maturity.

FIG. 13.—Mut. *formosa* (Lexington E-5-206-51): the setiform leaf appendages show very clearly; the position of the plant in the pedigree may be determined from table VI.

The phenomenon of mass mutation

From the results of the crosses between f. *typica* and muts. *formosa* and *albicans*, as well as from the insignificant variation in the composition of cultures showing mass mutation regardless of the source of the pollen, it appears clear that the factors responsible for the mutational characters are carried in the female gametes. So far, there is no evidence that the pollen of any of the characteristic mutations differs from that of f. *typica*. It follows that mass mutation in *O. pratincola* must be due to the wholesale modification of female gametes. The relations have not been worked out in the case of *O. Reynoldsii*, which also shows mass mutability.

FIG. 14.—Mut. *formosa*×f. *typica* (Lexington E-5-206×E-5-229, one of the F_1 progeny): this cross is identical with mut. *formosa* itself (cf. fig. 13); the constitution of the F_1 progeny is given in table VI; the progenies resulting from self-pollination of the parent plants are recorded in tables III and VI.

There can be no doubt that mass mutation is not Mendelian segregation, although the two phenomena have points of resemblance. HERIBERT-NILSSON'S hypothesis to account for the mutability of *O. Lamarckiana* depends upon the segregation of plural factors for the same character, and involves such complications as the elimination of all zygotes which are homozygous with regard to the presence of any of the numerous plural factors. Needless to say, he has also relied upon the doctrine of the equivalence of male and female gametes. His last paper bears evidence that his faith in the equivalence of gametes is beginning to waver, although he has formerly trusted so implicitly that he has made crosses only one way. If he had studied the reciprocals of his crosses it is safe to assume that he would never have advanced his Mendelian explanation of mutability. As far as his results extend, his derivatives of *O. Lamarckiana* fall, for the most part, into two classes, which conform in hereditary behavior to the two main classes of mutations which have been obtained from *O. pratincola.*

Class I.—The mutation breeds true, in the sense that it gives no reversions to the parent form. The reciprocal crosses with the parent species are matroclinic. The progeny conforms to the type which supplies the female gamete.

Class II.—The mutation gives a progeny consisting of the parental and mutational types in greatly varying proportions. The progenies from reciprocal crosses are mixed if the mutation supplies the female gametes, but consist of the parental type only if the mutation supplies the male gamete.

FIG. 15.—Mut. *gigas* (above) and f. *typica* (below): rosettes from the F_2 progeny of f. *typica;* the rosette of mut. *gigas*, Lexington E-5-238, had a darker color and more conspicuous pubescence than the sister plant of f. *typica*, but the difference does not appear in the photograph; both plants are shown in fig. 5.

Several mutations of each class have been studied by the writer in more or less detail, and the results will soon be published. As already announced,[11] the interesting mut. *nummularia* belongs to class I, as do also all of the mutations characteristic of Lexington E. Mut. *latifolia* is a typical member of class II. There are mutations, of course, which show neither type of behavior, but they need not be involved in the present discussion.

Heribert-Nilsson's hypothesis demands the recessiveness of mutations of class I, regardless of which way they are crossed with the parent. This condition is not fulfilled. It demands that the female gametes of the mutations of class II should be of one kind, and the pollen of two kinds. Neither is this condition fulfilled. His hypothesis makes no provision for the appearance of mutations in excess of one-third of the progeny. In this respect it is quite inadequate. On Mendelian grounds it is as difficult to account for too many mutations as for too few. His assumption is that after a homozygous and recessive condition has been attained in *O. Lamarckiana*, except for one of the plural factors which produce the *Lamarckiana* phaenotype, monohybrid splitting will take place. The one-fourth of dominant homozygotes will be eliminated, and therefore the progeny will consist of heterozygotes and recessives (mutations) in a 2:1 ratio. He has not attempted to explain how more than one-third of a progeny can consist of mutations, although he states in a vague and general way that the discovery of highly mutable strains is an argument in favor of his thesis. Nothing, he says, has made the mutation phenomena appear so exceptional as the low frequency of mutations. In his opinion, the high mutability of *O. Reynoldsii* has rendered the mutation fiction an absurdity.

Further comment on this opinion is rendered unnecessary by the serious discrepancies between Heribert-Nilsson's hypothesis and the facts. It can do no harm to point out, however, that even if mutations appeared through the operation of Mendelian segregation, as no one denies may sometimes be the case, it is still necessary to account for the origin of heterozygosis in the parent strain. The writer believes that mutations may often appear as a result of segregation, but that the antecedent heterozygosis has its origin in a mutative change. To attempt to account for the hetero-

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[11] Amer. Jour. Bot. 2:146. 1915.

zygosis by hybridization leads to such absurdities as the denial that new forms have ever originated except by hybridization and recombination.

It is perhaps unwise to hazard even a guess at the nature of the modification of the female gametes which results in mass mutation. At one time the writer was inclined to believe that the modification had involved the cytoplasm rather than the nucleus, and that cytoplasmic inheritance might account for the matroclinic crosses. However, there are now adequate data at hand to show that similar matroclinic crosses in other cases cannot be explained by cytoplasmic inheritance. The reason for discarding this hypothesis will be explained in a future paper, since it involves data which cannot be touched upon here.

Mendelian expectations require that the largest class in a progeny showing mutation shall consist of the parent phaenotype. No explanation of the high mutability of mass mutating strains can be accepted which requires the elimination of zygotes of this phaenotype, which according to all other experience are strong and viable. If a deficiency in any class of zygotes were to be expected in a mass mutant strain, it would be the class of weakest mutations; in the case of *O. pratincola*, for example, it would be mut. *setacea*. Yet this mutation is the very one which occurs in the largest numbers.

Mass mutation is neither more nor less easily explained than ordinary mutation. It seems to be due to sudden mutative transformations of certain female gametes, and to be apparent in the zygotes without the necessity of subsequent segregation because of the fact that the factors involved have no counterparts in the male gametes. There is no real distinction between mass mutation and ordinary mutation except that in the former type large numbers of gametes may be simultaneously affected, whereas in the latter only a few are affected.

Summary and conclusions

1. Mass mutation consists in the production of unexpectedly large numbers of mutations, in some cases amounting to 100 per cent of the progeny.

2. The phenomenon is known in two species of *Oenothera: O. Reynoldsii*, in which it was first described, and *O. pratincola*, the subject of this paper.

3. It cannot be explained by HERIBERT-NILSSON'S Mendelian hypothesis.

4. The mutations of the mass mutant strain of *O. pratincola* are: (A) common to other strains of the species; the non-characteristic mutations are not produced in unexpected numbers and show mass mutability superposed upon their ordinary behavior in heredity; (B) characteristic of the mass mutant strain.

5. The characteristic mutations are constant in that they do not throw the type form of the species, but, except in the case of the most reduced member of the group, are themselves highly mutable.

6. As far as tested, the characteristic mutations adhere to the following scheme of inheritance:

mutation×mutation → mutation
mutation×parent → mutation
parent×mutation → parent

7. They belong to a group with certain structural characters in common, but do not seem to form a linear reduction series.

8. They seem to result from the mutative modification in the female gametes of factors which have no counterparts in the male gametes.

9. Mass mutation is associated with a high degree of sterility, which manifests itself in the production of a greatly reduced number of seeds or in the production of many empty seeds.

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[From the Bulletin of the Torrey Botanical Club, 39: 519–533, pls. 37–39. 16 Nov. 1912]

Was Lamarck's evening primrose (*Oenothera Lamarckiana* Seringe) a form of Oenothera grandiflora Solander ?

Bradley Moore Davis

(with plates 37–39)

This paper will present evidence which in the writer's opinion clearly indicates that the *Oenothera* grown in the gardens of the Muséum d'Histoire Naturelle at Paris about 1796, described by Lamarck (?1798) under the name *Aenothera grandiflora* and renamed by Seringe (1828) *Oenothera Lamarckiana*, was a form of *Oenothera grandiflora* Solander (1789), introduced into England in 1778 from Alabama. If this identification is correct it follows that the name *Oenothera Lamarckiana* Seringe becomes a synonym of *Oenothera grandiflora* Solander (*O. grandiflora* "Aiton").

The evidence in the light of recent studies shows that Professor De Vries made an incorrect determination of the material of his cultures when he identified it with Lamarck's plant of 1796 or earlier. The material of De Vries's cultures is very different from this plant and can only be allowed to keep the name *Lamarckiana* when written "*Oenothera Lamarckiana* De Vries"; it is not *Oenothera Lamarckiana* Seringe.

My attention was first directed to this matter on seeing in the herbarium of the New York Botanical Garden tracings of Lamarck's plant, the type of *Oenothera Lamarckiana* Seringe, which is preserved in Lamarck's herbarium at the Muséum d'Histoire Naturelle. The resemblance of these tracings to the material of *Oenothera grandiflora* Solander from Alabama, now assembled in my own collections and at the New York Botanical Garden, was unmistakable. Miss Alice Eastwood, who kindly looked up various matters for me during her recent trip abroad, examined last winter in Paris this sheet which stands for the type of *Oenothera Lamarckiana* Seringe and reported to me her belief that it is identical with *O. grandiflora* Solander. As a result of this report I obtained through the courtesy of M. François Gagnepain negatives of this and other herbarium sheets at the Muséum d'Histoire Naturelle bearing upon the problem. M. Gagnepain further has most kindly answered a number of specific enquiries concerning the history of the specimens and certain characters of the plants not shown in the photographs. The following descriptions of these herbarium sheets are then in part from the photographs here published and in part from the notes of Miss Eastwood and M. Gagnepain, to whom I am greatly indebted.

The three sheets, to be described, were examined by Professor De Vries, who has given his interpretation (1901) in footnotes to Die Mutationstheorie, Vol. I, pp. 316, 317. De Vries believed that the first two sheets agreed with his cultures of *Lamarckiana*. The specimens on the third sheet he referred to *Oenothera grandiflora* Aiton (*O. suaveolens* Desfontaines) = *O. grandiflora* Solander. The conclusions of the present paper are (1) that the first sheet (PLATE 37), the type of *Oenothera Lamarckiana* Seringe, shows a remarkably well preserved and characteristic specimen of *Oenothera grandiflora* Solander, (2) that the specimen on the second sheet (PLATE 38) is neither *O. grandiflora* Solander nor "*O. Lamarckiana* De Vries" but a plant that is close to certain forms of *O. biennis*, and (3) that the two plants on the third sheet (PLATE 39), obviously stunted in growth, are so imperfect that an opinion of their identity can hardly be more than a guess. Our interest in this herbarium material centers upon the first two sheets.

SHEET 1. LAMARCK'S PLANT, WHICH STANDS AS THE TYPE OF *Oenothera Lamarckiana* Seringe

This specimen (PLATE 37) is in the herbarium of Lamarck, acquired by the Muséum d'Histoire Naturelle in 1886. The sheet bears in the handwriting of Lamarck: "Oenothera . . . [grandiflora] . . . nova spec. flores magni lutei, odore grato, caulis

3 pedalis." The spelling of the word Oenothera is not clear; it might be interpreted "Onothera" or possibly "Aenothera." This note designating a new species, *grandiflora*, in the handwriting of Lamarck establishes the specimen as what we would now designate as the type of his species *Aenothera grandiflora* described in the Encyclopédie Méthodique Botanique **4**: 554. ?1798. This description agrees with the specimen. It seems unlikely that we shall ever know the exact date at which the description was published. Authors usually give it as 1797, but Sherborn and Woodward (1906), from evidence presented by extraneous matter bound in with certain copies of the volume concerned, place the year as ?1798. I can find no evidence that Poiret wrote the description, as was believed by De Vries, but he is known to have written later volumes of the encyclopedia.

Seringe in his diagnosis of *Oenothera Lamarckiana* (De Candolle, Prodromus **3**: 47. 1828) gives *O. grandiflora* Lamarck as a synonym together with the comment that the species is not the *grandiflora* of Aiton. This was of course his reason for renaming the plant. The diagnosis of Seringe, as will appear later, is virtually a copy of a portion of Lamarck's description.

The following is the description of the species written by Lamarck in the Encyclopédie Méthodique Botanique; it should be noted that the abbreviation (V.S.) at the end of the diagnosis shows that the description was based on dried material.

> "12. Onograire à grandes fleurs. *Ænothera grandiflora* (n). *Ænothera foliis integerrimis, ovato-lanceolatis; petalis integris, capsulis glabris.*
>
> "Cette espèce paroît se rapprocher, par son port, de l'*ænothera longiflora;* mais elle en diffère par plusieurs caractères frappans, sur-tout par ses tiges rameuses, ses pétales entiers, ses fruits lisses & courts.
>
> "Ses tiges s'élèvent à trois ou quatre pieds de hauteur. Elles sont cylindriques, munies de quelques poils rares, d'un rouge brun, divisées en rameaux nombreux, étalées. Les feuilles sont vertes, alternes, ovales, lancéolées, lisses & glabres des deux côtés, très-entières; les feuilles du bas sont pétiolées & munies de quelques dents à peine sensibles. Celles qui accompagnent les fleurs sont plus étroites, plus aiguës & sessiles.
>
> "Les fleurs sont terminales, & forment, par leur disposition, une panicule étalée; elles sont axillaires, solitaires, mais très-

> rapprochées. Le calice est jaune, muni d'un tube un peu plus long que la corolle, qui se divise en quatre folioles lancéolées, élargies à leur bâse, aiguës à leur sommet, terminées par un filet court, sétacé. La corolle est jaune, composée de quatre pétales ovales, très-grands, entiers, arrondis, presque aussi longs que le tube calicinal, retrécis à leur bâse en forme de coin. Les anthères sont longues, linéaires. Le fruit est une capsule courte, cylindrique, glabre, tronquée, légèrement quadrangulaire, n'ayant qu'environ le tiers de longueur du tube calicinal. Cette espèce est originaire de l'Amérique septentrionale. On la cultive au jardin du Muséum d'Histoire naturelle. (V.S.)"

An interesting point has been brought to my notice by Mr. H. H. Bartlett. Poiret has this note in the Encyclopédie Méthodique Botanique, Suppl. 4: 141. 1816: "L'Oenothera grandiflora, no. 11, est la même plante que celle d'Aiton, Hort. Kew., 2, pag. 2." The designation "no. 11" instead of "no. 12" must have been a slip of the pen on Poiret's part. Although Poiret was correct in considering *O. grandiflora* Lamarck as a synonym of *O. grandiflora* Solander, he could not have had a clear conception of this plant since he kept *O. suaveolens* Desfontaines, which is also a synonym, as a distinct species.

We will give also the short diagnosis by Seringe (1828) of *Oenothera Lamarckiana* for comparison with the longer description of Lamarck.

> "OE. Lamarckiana (Ser. mss.) caule ramoso, *foliis integerrimis ovato-lanceolatis*, *petalis integris* magnis, *capsulis glabris* cylindrico-tetragonis brevibus. ② in Americâ sept. OE. grandiflora Lam. dict. 4. p. 554. *non Ait. Fl. flavi."

I have italicized phrases that are the same as those in the brief introduction in the description of Lamarck, showing that Seringe had little or nothing to add to the original description.

Certain points should be noted in these descriptions of Lamarck and Seringe before we compare Lamarck's plant (PLATE 37) on the one hand with *O. grandiflora* Solander and on the other with the material of De Vries's cultures ("*O. Lamarckiana* De Vries"). The description of the petals as entire must not be emphasized, for while there may not be in these species a conspicuous notch at the tip of the petals there is usually at least a shallow indentation; the character is not one easily determined in dried specimens and presents so much variation as to have no taxonomic value. The leaves of these species are not strictly entire but serrulate, the teeth being small and in dried material inconspicuous; the teeth are, however, shown on some of the leaves on Lamarck's plant (PLATE 37). The glabrous fruits agree best with the seed capsules of *grandiflora*, which are almost smooth, while those of De Vries's *Lamarckiana* are decidedly puberulent and pilose. Mature capsules are not shown on the specimen of Lamarck's plant, and no importance can be attached to their description as short. The reddish brown stem with occasional hairs agrees with *grandiflora*; there is no mention of numerous hairs arising from red papillae, a striking characteristic of the plants in the cultures of De Vries. The description of the leaves as glabrous is not strictly true either of *grandiflora* or of De Vries's *Lamarckiana*, both having a minute pubescence, which is more evident in the latter form. Mr. Bartlett has called my attention to the word "sétacé" in Lamarck's description of the sepal tips; this has been translated by De Vries (1901, p. 317) as "dicke." The French is, however, from the late Latin word "setaceus," derived from "seta," a stiff hair or bristle. The meaning is, then, exactly the opposite of that given by De Vries and refers to the much attenuated sepal tips, as shown in PLATE 37, a striking characteristic of *grandiflora;* the sepal tips of De Vries's *Lamarckiana* are in contrast much shorter and thicker.

It is surprising how little information is contained in the descriptions of Lamarck and Seringe that is of value in a comparison of Lamarck's original plant with *O. grandiflora* Solander and "*O. Lamarckiana* De Vries." The most important points in the writer's opinion are the description of the attenuated sepal tips and the absence of all reference to the remarkable stem coloration which is characteristic of the material of De Vries's cultures. De Vries's *Lamarckiana* invariably, so far as I am aware, presents a green stem punctate with red papillae from which long hairs arise among a short glandular pubescence. This is not noted by Lamarck, who describes the stem in agreement with *grandiflora* as reddish brown with occasional hairs.

We may now take up the consideration of the herbarium sheet of Lamarck's plant (PLATE 37) preserved in the herbarium of the

Muséum d'Histoire Naturelle. First, however, it should be noted that Buchet (1912) in a recent paper gives his opinion that this sheet agrees with *Oenothera suaveolens* Desfontaines, which he recognizes as synonymous with *Oenothera grandiflora* Solander, an older name. Buchet also regards the sheet shown on PLATE 38 from the collection of Abbé Pourret as the same form as Lamarck's plant and identifies it also with *O. suaveolens*. On this point I cannot agree, since, as will be shown later, the specimen of Abbé Pourret has important characters that distinguish it both from Lamarck's plant (*O. suaveolens* Desfontaines = *O. grandiflora* Solander) and from the material in the cultures of De Vries.

In the following account of the sheet which stands for the type of *Oenothera Lamarckiana* Seringe, are included not only the characters shown by the photograph (PLATE 37) but also others of equal or perhaps greater importance from the notes of Miss Eastwood and M. Gagnepain. In order to obtain direct comparisons with respect to the pubescence I furnished M. Gagnepain with specimens of stems and buds from both *grandiflora* and the *Lamarckiana* of De Vries's cultures, asking him to compare the specimens with Lamarck's plant but not informing him of their source.

1. STEM AND FOLIAGE. The specimen of Lamarck's plant (PLATE 37) exhibits the rather dense branching characteristic of certain forms of *grandiflora* in sharp contrast to the long sparsely branched stems of De Vries's *Lamarckiana*. The stem, according to M. Gagnepain, does not have long hairs from red papillae, as is so characteristic of De Vries's *Lamarckiana;* the pubescence is short and the stem subglabrous. The leaves are broadly elliptical or lanceolate with serrulate margins and with short but distinct petioles as in *grandiflora;* they are not sessile or almost sessile nor so broad as are the leaves of the *Lamarckiana* of De Vries. This herbarium sheet may be readily matched in the form of the branching and in the foliage by numerous specimens of *grandiflora* collected in Alabama; it represents neither the broader- nor the narrower-leaved forms in the range of variation in this species but is nearest to the intermediate condition.

2. INFLORESCENCE. The inflorescence does not present the close spike with broad-based, sessile bracts, which are so character-

istic of the younger flowering shoots of De Vries's *Lamarckiana*. On the contrary the bracts are narrow and short-petioled and the inflorescence is more open, in agreement with *grandiflora*.

3. BUDS. The buds are not stout as in the *Lamarckiana* of De Vries and the sepal tips are much more attenuate, a distinctive character of *grandiflora*. The form of the buds is exactly as in *grandiflora*, and this character is one of the most important points of agreement with this species. The pubescence on the sepals, as described by M. Gagnepain, is short; there are not present the numerous long hairs from papillae, which are characteristic of De Vries's *Lamarckiana*.

4. FLOWERS. The flowers have the very long and delicate hypanthium characteristic of *grandiflora*. Miss Eastwood reports that the petals in a bud dissected by her are entire. This is a character typical of neither *grandiflora* nor the *Lamarckiana* of De Vries, but as stated before, the petals of these forms vary so greatly in the degree of their indentation that the character has little if any taxonomic value. The length of the petals, between 3 and 4 cm., is that of *grandiflora* and also of certain forms of De Vries's *Lamarckiana*. The style extends beyond the tips of the anthers so that the lobes of the stigma (*s*, in PLATE 37) are above the latter and could not be pollinated in the bud. In these respects the flower agrees with both *grandiflora* and the large-flowered types of *Lamarckiana* in De Vries's cultures.

5. CAPSULES. There are apparently no mature capsules on the specimen, so direct comparisons are impossible. Since the size and form of a capsule depends upon the development of the ovules, i. e. upon whether or not the stigma has been fully pollinated, it is unsafe to accept statements of size unless there is evidence that sufficient material has been examined. Lamarck's statement that the capsules are short was probably based on immature or partially pollinated capsules. His description of the capsules as glabrous points to *grandiflora;* as stated before, the capsules of De Vries's *Lamarckiana* are decidedly puberulent and pilose.

The characters of *Oenothera grandiflora*, which appear on the herbarium sheet of Lamarck's plant, and those of the *Lamarckiana* of De Vries's cultures may be more readily contrasted in the following statement.

O. grandiflora Solander AND LAMARCK'S PLANT	*O. Lamarckiana* FROM THE CULTURES OF DE VRIES
Flowering stems generally with numerous approximate branches.	Flowering stems sparsely branched or not at all.
Stems green above, reddish brown below, the papillae at the base of long hairs colored like the stem.	The papillae at the base of the long hairs colored red so that the green stem appears punctate with red dots.
Leaves of upper foliage lanceolate, rarely broad, with distinct petioles.	Leaves of upper foliage ovate-lanceolate, sessile or almost sessile.
Inflorescence more open, with narrow, petioled bracts.	Inflorescence more close, with sessile bracts broad at the base.
Buds not stout, with much attenuated sepal tips. Sepals puberulent, sometimes sparsely pilose.	Buds stout, with shorter sepal tips, Pubescence of sepals a heavy puberulent and pilose covering.
Flowers with a long delicate hypanthium. Petals 3–3.5 cm. long. Stigma lobes above the tips of the anthers.	Flowers with a stouter hypanthium. Petals in some races 4–4.5 cm. long, in others 2.5–3 cm. long. Stigma lobes in the large-flowered types above the tips of the anthers, in the smaller-flowered forms at about the level of of the anther tips.

There is another sheet in the herbarium of the Muséum d'Histoire Naturelle which is without a name but bears in the handwriting of Lamarck: "d'Amérique sept. Tige rameuse, haute de 3 à 4 pieds." Both M. Gagnepain and Miss Eastwood report that this sheet is similar to that of Lamarck's plant which we have described above and shown on PLATE 37. The history of the sheet is apparently not known and I have no evidence that it can safely be associated with the specimen upon which Lamarck undoubtedly based his description. Nevertheless, this sheet may be closely related to or even a duplicate of the specimen that served as the type for the descriptions of Lamarck and Seringe.

In summary it may be said that the specimen, which we must consider the type of *Oenothera Lamarckiana* Seringe, presents no characters in clear form that are not those of *O. grandiflora* Solander. In not one of the contrasted characters discussed above does the specimen agree with the *Lamarckiana* of De Vries's cultures. The only points in which De Vries's *Lamarckiana* may be said to resemble this specimen are the size of the petals and the position of the stigma, which in the large-flowered forms of *Lamarckiana* is above the tips of the anthers; these are characters which *grandiflora* and De Vries's *Lamarckiana* have in common.

It is exceedingly fortunate that the plant which serves as the type of *Oenothera Lamarckiana* Seringe should have come down to us so well preserved that there is scarcely a doubt of its identity with *Oenothera grandiflora* Solander, introduced into England in 1778.

SHEET 2. A SPECIMEN OF *Oenothera* FROM THE COLLECTION OF ABBÉ POURRET

This specimen (PLATE 38) is of interest for the reason that De Vries (1901, footnote to p. 317) believed that it as well as Lamarck's plant agreed with the material of his cultures ("*Oenothera Lamarckiana* De Vries"). Buchet (1912) has recently referred the specimen to *Oenothera suaveolens* Desfontaines = *O. grandiflora* Solander. I am unable to agree with either of these opinions and shall present evidence that the plant was close to certain forms of *Oenothera biennis*.

The sheet bears the label HERB. MUS. PARIS. with the statement at the bottom "Collection de l'Abbé Pourret, extraite de l'Herbier légué par M. le Dr. Barbier. 1847." On this label, in the handwriting of Spach are the names "*Onagra vulgaris* Spach" and "*Oenothera biennis* Linné." At the left is a list of old names representing synonymy, copied by Abbé Pourret, and below this list his clerk wrote the name *Oenothera biennis* L.

De Vries states that the plant was probably collected by Abbé Pourret in the garden of the museum at the time of his visit to Paris in 1788. M. Gagnepain, however, is not satisfied with the evidence for this view and writes that the history of the sheet is unknown to him.

An examination of the specimen itself (PLATE 38) shows the following characters.

1. STEM AND FOLIAGE. The long unbranched stem bears elliptical, petioled leaves very different from the sessile or almost sessile, broad-based leaves of De Vries's *Lamarckiana*. The absence of approximate flowering branches is against any relationship to *grandiflora*. The appearance of the small buds in the axils of the lower leaves is characteristic of some forms of *Oenothera biennis*. The pubescence of the stem is described by M. Gagnepain as very like the specimen of *grandiflora* and not at all like the specimen of De Vries's *Lamarckiana* sent for comparison.

2. INFLORESCENCE. The bracts of the inflorescence are not broad at the base and sessile as in the *Lamarckiana* of De Vries. They are narrow-elliptical and short-petioled.

3. BUDS. The size and form of the buds present perhaps the most important characters on the sheet. They are short and stout, and these characters alone make it impossible that the plant could have been *O. grandiflora* Solander. (Compare PLATE 38 with PLATE 37.) Forms of *O. biennis* frequently show these peculiarities. The sepals have a greater pubescence than those of *grandiflora*.

4. FLOWERS. The flowers are medium-sized, petals probably between 2 and 2.5 cm. long. They are not large enough for *grandiflora* or for the large-flowered forms of De Vries's *Lamarckiana*. The stigma (*s*, PLATE 38) appears to be at about the level of the anthers, the style not extending well beyond as in the types mentioned above. The flowers, in size and in the relation of the stigma to the anthers, agree with forms of *biennis*.

5. CAPSULES. The capsules appear to be of the *biennis* type, which is similar to that of De Vries's *Lamarckiana*.

In conclusion, the forms of the leaves and bracts distinguish this plant of Abbé Pourret from the *Lamarckiana* of De Vries's cultures. The size and form of the buds, the size of the flowers, and the position of the stigma distinguish it from *O. grandiflora* Solander as well as from the larger-flowered forms of De Vries's *Lamarckiana*. All of the characters described above are represented in the assemblage of forms included under the name *Oenothera biennis*. Since we know nothing of the rosette, general habit, and lower foliage of this plant, it is quite impossible to follow its determination further.

SHEET 3. SPECIMENS REFERRED BY DE VRIES TO *Oenothera grandiflora*

The specimens on this sheet (PLATE 39) are so imperfect and their form so abnormal that a satisfactory determination of their identity is probably impossible. De Vries (1901, footnote to p. 316) considered them to be *Oenothera grandiflora* Aiton = *O. grandiflora* Solander (*O. suaveolens* Desfontaines).

The sheet bears a label of Michaux with "Ameriq. sept." On this label in the handwriting of Desfontaines is "*Oenothera suaveolens* Hort. Paris." Above this name has been written "*Oenothera grandiflora* Poiret Encycl.," and below, Spach wrote "*Onagra vulgaris grandiflora* Spach." A second label bears the name "*Oenothera grandiflora*," probably in the handwriting of André Michaux. M. Gagnepain states that the specimens were imported as dried plants from North America. The chief interest in this sheet lies in the fact that Desfontaines evidently considered the specimens to be his own species *Oenothera suaveolens*.

Both specimens are entire plants, the smaller about 3.5 dm., the larger about 5 dm. in height. They are unbranched and obviously dwarfed. The leaves are petioled as in *grandiflora*, but those of the smaller plant are much below the average size for this species. The stigma (*s*, PLATE 39) shown in the flower of the smaller plant seems to be above the tips of the anthers as in *grandiflora*. The pubescence of the stems and sepals, from notes of M. Gagnepain, appears to be somewhat similar to *grandiflora*; it is not that of De Vries's *Lamarckiana*.

There appear to be no characters on these plants that might not have been those of *O. grandiflora* Solander under very unusual or abnormal conditions. There is, however, little or nothing in these specimens that is typical of *grandiflora*, and apparently nothing that determines a relationship to any other *Oenothera*. It is hardly possible that plants so different from one another grew together in the same environment and it seems more probable that they were quite unrelated. They remain to us as the flotsam of the herbarium, plants of whose precise origin and parentage we know nothing.

DISCUSSION

The reader will have noted that throughout this paper the name *Lamarckiana* has been kept strictly for the plant that has come down to us from the cultures of De Vries, a plant well known to scores of botanists and grown in numerous botanical gardens. If this paper has shown that Lamarck's plant in the gardens of Paris at about 1796 or earlier, the type of *Oenothera Lamarckiana* Seringe (1828), was a form of *Oenothera grandiflora* Solander (1789) the former name becomes a synonym of the latter. The *Oenothera* of De Vries's cultures is left without a name or at least without the authority of Seringe. I propose, however, that the name "*Oenothera Lamarckiana* De Vries" be kept for this plant, which has been the subject of such extensive experimental study by De Vries and whose origin and behavior is a matter of such great interest to the geneticist.

The name when written "*Oenothera Lamarckiana* De Vries" is clear to all who have knowledge of the relation that this plant bears to the mutation theory. If there were evidence that "*O. Lamarckiana* De Vries" is or ever was a component of the American flora as a native species, there might be some reason to change its name. However, the evidence indicates that *Lamarckiana* has come to us greatly modified, that its parentage is far from pure, that it is in fact of hybrid origin. We are dealing with the product of the garden, and as such the plant may reasonably be exempt from a change of name that would carry endless confusion through the literature of experimental morphology. Should any taxonomist contemplate the introduction of a new name let him first ponder the inscription over the grave of William Shakespeare.

The introduction of *Oenothera grandiflora* Solander into England in 1778 marked a very important date in the development of the *Oenothera* flora over parts of Europe. This species undoubtedly holds the key to many puzzling herbarium sheets and records. Botanists do not yet realize how definite is our knowledge of this native American species and how clear is our information on its history. (See MacDougal, 1905, p. 7.)

Oenothera grandiflora Solander was discovered by William Bartram in 1776 near Tensaw, Alabama, on an expedition undertaken at the request of John Fothergill, M.D. Solander's original description in Aiton's Hortus Kewensis, 1789, from material grown at Kew, states that *O. grandiflora* was introduced by John Fothergill in 1778. A herbarium specimen in the British Museum from "Hort. Fothergill 1778" makes it evident that Bartram must have sent seed to Fothergill. The species still occupies its original station in Alabama, where it was rediscovered in 1904, and there is abundant herbarium material from this source; also, there are strains under cultivation by myself and others. As striking an American novelty as this large-flowered species would naturally become widely distributed, which explains its presence in Paris somewhat earlier than ?1798, when Lamarck's description was published. Escaping from the gardens, the plant has been reported as growing wild at various stations in England and France. Following in the wake of its distribution to European botanical centers came the inevitable description as new species of forms derived from the original. *Oenothera suaveolens* Desfontaines and Lamarck's plant, *Oenothera Lamarckiana* Seringe, were undoubtedly such derivatives and must be considered as forms of *Oenothera grandiflora* Solander.

The identification of Lamarck's plant with *Oenothera grandiflora* Solander has very greatly modified the problem of the origin of "*Oenothera Lamarckiana* De Vries." The problem has become far more tangible. I have recently (Davis, 1911, p. 226, and 1912, p. 379) criticized adversely the evidence that has been offered to show that *Lamarckiana* was known previous to 1778 when *grandiflora* was introduced into England. With Lamarck's plant assigned to *grandiflora* we pass from the eighteenth century to periods when we may hope for more direct evidence than that furnished by the old accounts and figures.

We know that as a cultivated plant handled by seedsmen *O. Lamarckiana* first appeared about 1860, when it was placed on the market by the firm of Carter and Company of London, who state that their seed came from Texas. The identification by Lindley of these plants with *O. Lamarckiana* Seringe was undoubtedly incorrect. I have recently described and figured (Davis, 1912, p. 417) certain well preserved specimens of an *Oenothera* in the Gray Herbarium from a plant grown at Cambridge, Massachusetts, by Dr. Asa Gray in 1862. Evidence is there given which indicates that this plant held a close genetical relationship to these same cultures of Carter and Company, perhaps not more than one or two generations removed from the original plants. These specimens show characters in part those of De Vries's *Lamarckiana* and in part like *grandiflora*. If this plant grown by Dr. Gray was representative of the cultures of Carter and Company their plants must have differed from the *Lamarckiana* of today in a number of important particulars. I regard this herbarium sheet as the most important now known bearing on the problem of the origin of *Oenothera Lamarckiana*. Its relation to the writer's working hypothesis that

Lamarckiana arose as a hybrid between *biennis* and *grandiflora* has been fully discussed in the paper mentioned above.

Although Carter and Company state that they received their seed from Texas, it must be borne in mind that we have at present no confirmatory evidence that such a plant as they describe or as that represented on the sheet in the Gray Herbarium is native in the southern or southwestern United States. Here is a problem that well deserves the attention of botanists in these regions, who should make every effort to bring such a type to light that seed may be sent to the workers in the experimental gardens. If such a form grew in Texas no further back than 1860 it may surely be expected there today.

It is possible that the cultures of Carter and Company arose in England and that their association with a Texan source may have been some mistake on the part of the seedsmen. We have several accounts of large-flowered Oenotheras in England at dates previous to 1860. The most important and the earliest is that in Smith's English Botany (**22**: 1534. 1806) with the excellent figure of Sowerby. This account describes at this early date (1806) very extensive growths of an interesting form on the sand banks along the coast a few miles north of Liverpool. At the present day "*Oenothera Lamarckiana* De Vries" and variants from this type are established and flourishing over extensive tracts in the same region north of Liverpool through the sand hills of Lancashire. It is not impossible that the *Lamarckiana* of Carter and Company may have come from such regions.

The problem of the origin of "*Oenothera Lamarckiana* De Vries" must be approached from two sides. The English botanists have the problem of the history of such an *Oenothera* flora as that of the Lancashire sand hills, and collections should be searched with the greatest thoroughness for herbarium sheets that may be of assistance in tracing its development. American botanists have the problem of the discovery and isolation by cultures of the large-flowered Oenotheras throughout the south and west, which might have a direct relationship to *Lamarckiana* or which might be one of the parents of a possible hybrid. A good beginning was made in the rediscovery of *Oenothera grandiflora* Solander but the search should be pushed further.

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REFERENCES CITED

Buchet, Samuel. Le cas de l'*Oenothera nanella* de Vries. Bull. Soc. Bot. France IV. **12**: 18. 1912.

Davis, B. M. Some hybrids of *Oenothera biennis* and *O. grandiflora* that resemble *O. Lamarckiana*. Amer. Nat. **45**: 193. 1911.

Davis, B. M. Further hybrids of *Oenothera biennis* and *O. grandiflora* that resemble *O. Lamarckiana*. Amer. Nat. **46**: 377. 1912.

De Vries, Hugo. Die Mutationstheorie. Leipzig, vol. I, 1901.

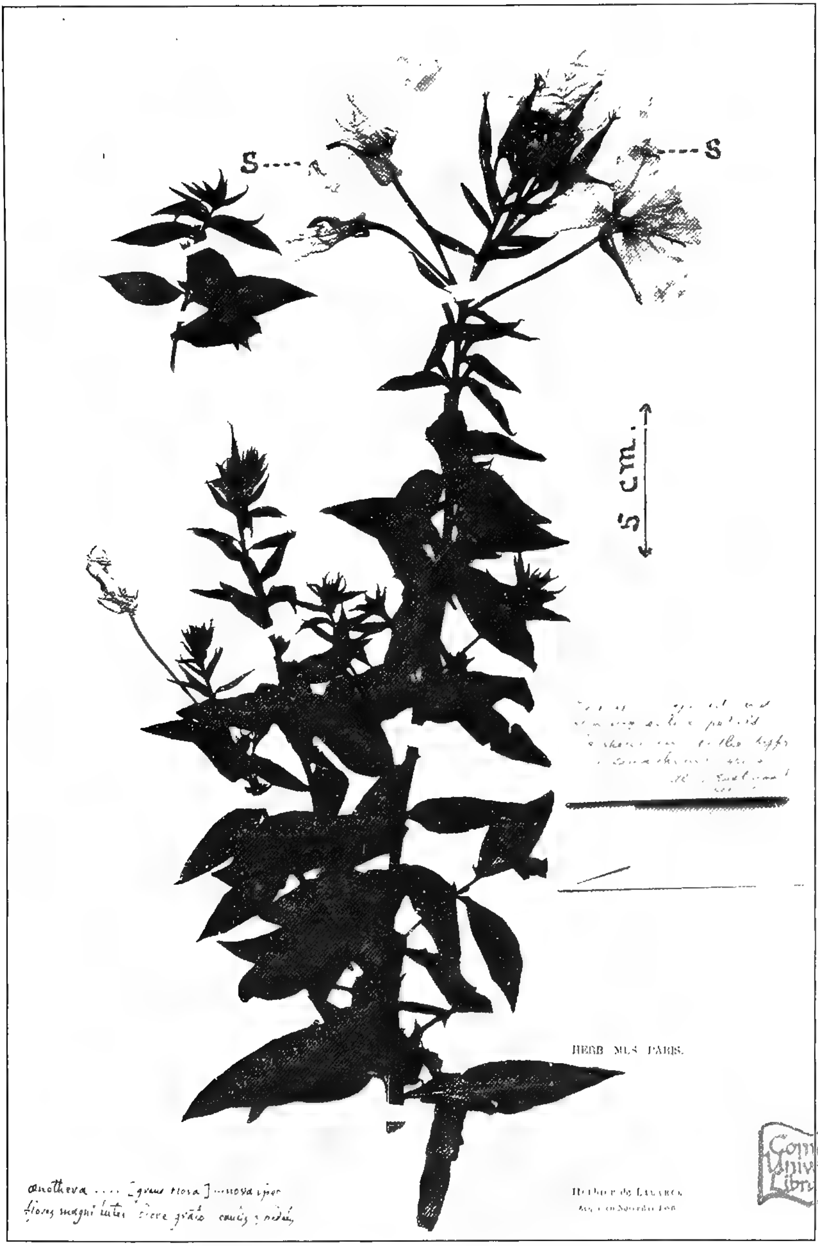
Lamarck. Encyclopédie Méthodique Botanique **4**: 554. ? 1798.

MacDougal, D. T., Vail, A. M., Shull, G. H., & Small, J. K. Mutants and hybrids of the Oenotheras. Carnegie Institution Pub. 24. 1905.

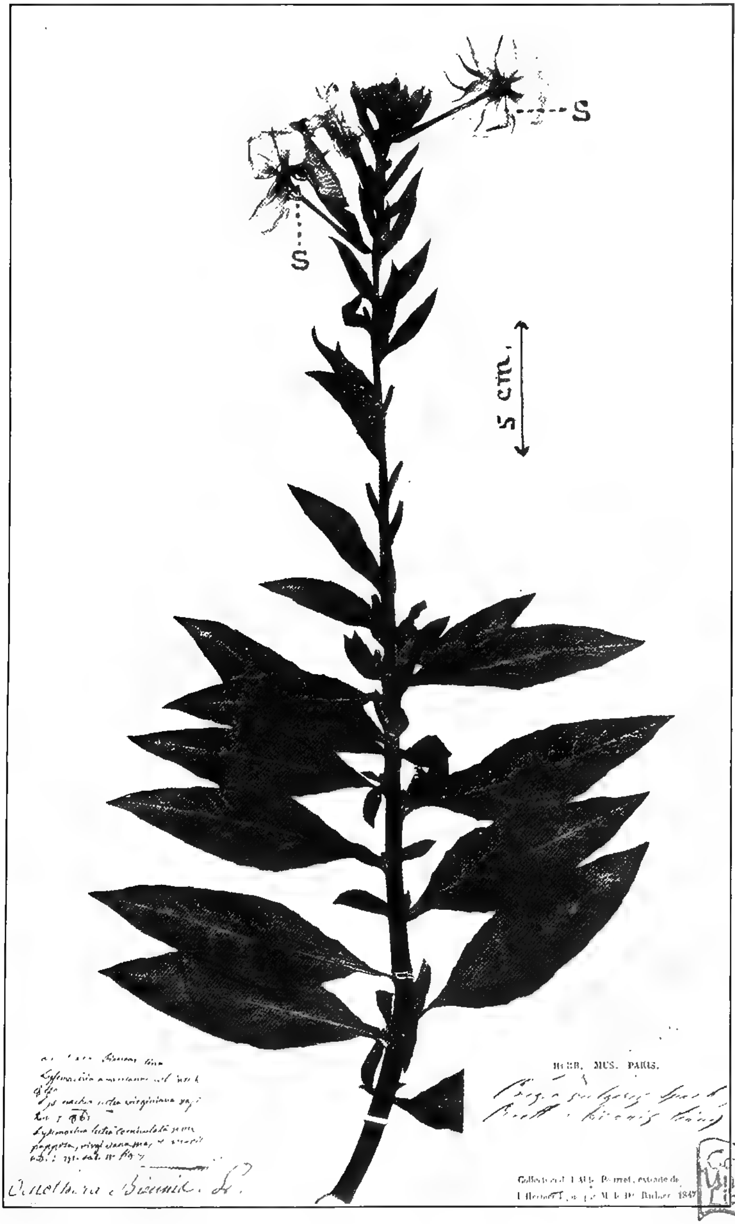
Seringe, N. C. De Candolle, Prodromus **3**: 47. 1828.

Sherborn, C. D., & Woodward, B. B. On the dates of publication of the natural history portions of the "Encyclopédie Méthodique." Ann. and Mag. Nat. Hist. VII. **17**: 577. June 1906.

Solander, D. Aiton, Hortus Kewensis **2**: 2. 1789.



LAMARCK'S PLANT, TYPE OF OENOTHERA LAMARCKIANA SERINGE



OENOTHERA FROM THE COLLECTION OF ABBÉ POURRET

SPECIMENS REFERRED BY DE VRIES TO OENOTHERA GRANDIFLORA

THE PROBLEM OF THE ORIGIN OF *ŒNOTHERA LAMARCKIANA* DE VRIES.

By Bradley Moore Davis,

University of Pennsylvania.

[*Reprinted from* The New Phytologist, *Vol. XII, No. 7,*
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[With One Figure in the Text].

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I am led to write this paper partly for the reason that the problem of the origin of *Œnothera Lamarckiana* De Vries has in the past few months became far more tangible than formerly, but chiefly because it seems probable that certain phases of the problem can be solved only by studies on the development of certain English *Œnothera* floras. I have then the hope that a brief outline of the situation, as it now appears to me, will be of some assistance to British botanists interested in the subject.

Recent studies[1] clearly indicate that the *Lamarckiana* of the cultures of De Vries cannot be identified with the plant described by Lamarck[2] under the name *Ænothera grandiflora* from material grown in Paris at about 1796 or earlier and renamed by Seringe[3] *Œnothera Lamarckiana.* The evidence is very strong that Lamarck's plant (*Œnothera Lamarckiana* Seringe), was a form of *Œnothera grandiflora* Solander[4] (*O. grandiflora* "Aiton") introduced into England in 1778 from Alabama.

This disposition of *Œnothera Lamarckiana* Seringe as a form of *O. grandiflora* Solander relieves our problem from association with the early date of 1796 and allows us to pass to later periods when we may hope for more direct evidence than that furnished by old descriptions and figures. The attempts to establish the presence

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[1] Davis, B. M. "Was Lamarck's evening primrose (*Œnothera Lamarckiana* Seringe) a form of *Œnothera grandiflora* Solander?" Bull. Torrey Bot. Club, vol. 39, p. 519, 1912.

[2] Lamarck. Encyclopédie Méthodique Botanique, vol. 4, p. 554, ? 1798.

[3] Seringe, N. C. De Candolle, Prodromus, vol. 3, p. 47, 1828.

[4] Solander, D. Aiton, Hortus Kewensis, vol. 2, p. 2, 1789.

of *O. Lamarckiana* De Vries in Europe at dates previous to 1796 are, to the writer, not convincing and have been discussed in previous papers.[1] In a recent contribution Gates[2] abandons his former views and admits (pp. 17-19) that the presence of *Lamarckiana* in Europe previous to 1760 is not established.

Since *Œnothera Lamarckiana* Seringe becomes a synonym of *O. grandiflora* Solander, I have proposed that the plant of De Vries retain the name under which it is known in the extensive literature of experimental morphology, but the name must be written *Œnothera Lamarckiana* De Vries. In making the above suggestion it should be noted that *O. Lamarckiana* De Vries has come down to us as the product of the garden through a long history of cultivation and that there are good reasons for believing it to be of hybrid origin. We have no evidence that the plant is present as a native species of any flora. As a garden plant we are apparently justified in giving it the name *Œnothera Lamarckiana* De Vries by Article 50 of the nomenclatorial code formulated by the International Botanical Congress held in Vienna in 1905.

There is little doubt that the material of De Vries's cultures was derived, possibly greatly modified, from certain plants placed upon the market by the seedsmen Carter and Company of London at about 1860. These plants were considered by Lindley to be *Œnothera Lamarckiana* Seringe, but we cannot accept this identification as correct. However, this opinion of Lindley gave the name *Lamarckiana* under which seedsmen are to this day selling a somewhat heterogeneous mixture of forms.

The description of the cultures of Carter and Company,[3] accompanied by an obviously inaccurate figure, gives us very little information on the plants. We are told that they were 3-4 feet high, very hardy biennials, and with flowers 4 inches in diameter. Carter and Company state that their plants came from seed received unnamed from Texas.

The problem of the origin of *Œnothera Lamarckiana* De Vries at present largely centers on the probable composition of the cultures of Carter and Company, and every effort should be made to bring forward evidence on the characters of these plants. The only information so far at hand apart from the unsatisfactory description

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[1] See Davis, American Naturalist, vol. 45, pp. 226-227, 1911, and vol. 46, pp. 379-380, 1912.

[2] Gates, R. R. "A Contribution to a Knowledge of the Mutating Œnotheras." Trans. Linnean Society, Botany, vol. 8, Part I, 1913.

[3] The Floral Magazine, vol. 2, plate 78, 1862.

and plate in "The Floral Magazine" is that furnished by a very important sheet in the Gray Herbarium of Harvard University. This sheet I shall again describe and figure in the hope that it may lead botanists to make a persistent search for herbarium material that may throw further light on the problem.

Fig. 1. Sheet in the Gray Herbarium of Harvard University. An *Œnothera* grown by Dr. Asa Gray at Cambridge, Massachusetts, in 1862 and probably derived directly or indirectly from the cultures of Carter and Company, of London, which were distributed under the name *Lamarckiana*. This plant differed from *Œnothera Lamarckiana* De Vries in the longer internodes of the inflorescence, in the larger and more leaf-like bracts, in the more slender form of the buds, in the more attenuated sepal tips, and in the longer seed-capsules.

The sheet in the Gray Herbarium (Fig. 1) holds specimens of a plant "*Oe. Lamarckiana*" grown in Cambridge, Massachusetts, in 1862 by Dr. Asa Gray. From records upon the sheet[1] it appears quite certain that Dr. Gray received seeds from William Thompson

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[1] See Davis, American Naturalist, vol. 46, p. 417, 1912.

of Ipswich, England, a seedsman who probably obtained from Carter and Company their novelty. It is then possible that the plant grown by Dr. Gray was not more than one or two generations removed from the original cultures of Carter and Company. The following is a description of the sheet in the Gray Herbarium illustrated by Fig. 1 :—

I. *Stems and Foliage.*—The stem bears long hairs arising from papillæ which are colored red as in *Lamarckiana* and are about as numerous as in that species. The large detached leaf, about 18·5 cm. long with sinuate margins, slightly lobed below, and with some evidence of former crinkles, suggests by its shape (although too small) the basal leaves of *Lamarckiana*. The leaves of the upper foliage, short petioled, are not so nearly sessile as those of *Lamarckiana*.

2. *Inflorescence.*—The inflorescence has longer internodes than in *Lamarckiana* and consequently is not so compact. The bracts are broad at the base, slightly toothed, and persistent, becoming large, lanceolate leaves on the fruiting branches: those of *Lamackiana* remain much smaller.

3. *Buds.*—The buds are about 9·5 cm. long, not stout and 4-angled as in *Lamarckiana*. The sepal tips are more attenuate than in *Lamarckiana*, projecting 1 cm. beyond the folded petals. The pubescence upon the sepals consists of long hairs arising from papillæ among much shorter hairs as in *Lamarckiana*.

4. *Flowers.*—The petals are about 4·5 cm. long, as long as those of the largest forms of *Lamarckiana*. The stigma lobes are about 8 mm. long, and close to 5 mm. above the tips of the anthers, in these respects agreeing with large-flowered forms of *Lamarckiana*.

5. *Capsules.*—The capsules, about 3 cm. long, are longer than those of *Lamarckiana* and not so stout.

From the above it will be noted that the plant grown by Dr. Gray differed from the *Lamarckiana* of the cultures of De Vries in the longer internodes of the inflorescence, in the larger more leaf-like bracts, in the more slender form of the buds, in the more attenuated sepal tips, and in the longer seed capsules. It would profit little to discuss at present whether or not this plant was truly representative of the cultures of Carter and Company and whether or not their plants became greatly modified during the quarter century before the time when De Vries began his studies, at about 1886, and isolated the form that we know to-day as *Œnothera Lamarckiana* De Vries.

What we desire is further information on the composition of the cultures of Carter and Company through the discovery of other herbarium material of about the same date (1862) as that of the sheet in the Gray Herbarium. It will be strange if Dr. Gray proves to the only botanist who preserved specimens of the " Lamarckiana " placed on the market by Carter and Company. There should be made a persistent search through herbaria to bring forward any specimen that may throw light upon the problem. This is a matter in which it would seem that the British botanists can render a great service.

Another feature of the problem concerns the development of some remarkable *Œnothera* floras in parts of England composed in greater part of *O. Lamarckiana* or variants from this type.

It is surprising how common have become *Lamarckiana*-like forms in England. During the past three years several English botanists have kindly replied to my request for seed of broad-leaved forms of *Œnothera biennis* with green stems bearing red papillæ at the base of long hairs. From the seed sent to me I have grown eleven different cultures in the hope of finding a type of *biennis* which in the past I have greatly desired as a parent for a cross with *O. grandiflora*. All of these cultures have proved to be forms essentially *Lamarckiana* as to habit, foliage and stem coloration, but with smaller flowers than is usual for De Vries's plant. They correspond very closely and some of them are indistinguishable from the small-flowered races of *Lamarckiana* which I have differentiated from material of De Vries.[1] They were not at all the forms of *biennis* that I hoped to obtain, and could not be used in my experimental work.

The type of *biennis* that I wish should agree closely in morphology with the *biennis* of the sand dunes of Holland, but it should have the stem coloration characteristic of *Lamarckiana*, i.e., the green portions of the stems should be punctate with red papillæ at the base of the long hairs. The Dutch *biennis* has as far as we know a clear green stem above, but it would not be surprising if a form should be found with the stem coloration of *Lamarckiana*, since races of American *biennis* occur differing only in the presence or absence of red coloration in the stem papillæ. Seeds of a type agreeing with the Dutch *biennis* have been sent to me from the botanical garden of Cambridge University and presumably the plant

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[1] See Davis, American Naturalist, vol. 46, p. 383, 1912.

is not uncommon in England. De Vries[1] reports (p. 32) that it is present on the sand hills of Lancashire.

This plant which I have referred to as the Dutch *biennis*, so well known through the studies of De Vries, is perhaps the most important type in the *biennis* assemblage of races and should be familiar to all students of œnotheras. It is very old having apparently been on the sand dunes of Holland since pre-Linnean times. Bartlett[2] has recently brought forward strong reasons for regarding the plant as the form known to Linnæus as *Œnothera biennis* and consequently to be regarded as the type-form of the species. It is very important that British botanists should endeavour to trace the history of this species in England and its relations to the present *Œnothera* floras. I shall be glad to supply seeds of the plant to anyone interested in the study.

To return to the specific problems of the origin and development of *Lamarckiana* floras in England the most important and historically the most interesting flora seems to be that of the Lancashire sand hills north of Liverpool. From the studies of several botanists it appears that over an extensive area *O. Lamarckiana* De Vries occurs mixed with variants from the type proper. It is reported by Gates (l.c. 1913) that *O. grandiflora* is also present with the *Lamarckiana* and we have De Vries's statement (l.c. 1912) that the Dutch *biennis* (*O. biennis* Linnæus) is in the same region. The studies of Gates (l.c. 1913) clearly show that among the types there is a large amount of hybridization and consequently a very complex mixture of forms differing among themselves in many respects.

We know that a conspicuous *Œnothera* flora was present on the sand hills of Lancashire before 1806,[3] and the problem is briefly the determination of its original character and the tracing of its modification or development down to present times. The account by Smith in the "English Botany" (1806) together with the accompanying figure of James Sowerby's indicate a biennial plant, 2-3 feet high, a stem "rough with minute tubercles," leaves broad and the lower decidedly crinkled, flowers with petals about 3 cm. long (if drawn natural size), and stigma lobes slightly above the tips of the anthers. There is no mention of red coloration in the stem tubercles which suggests a plant with green stems as in the Dutch

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[1] De Vries H. "Die Mutationen in der Erblichkeitslehre." Berlin, 1912.

[2] Bartlett, H. H. "The Delimitation of *Œnothera biennis* L." Rhodora, vol. 15, p. 48, 1913.

[3] English Botany, vol. 22, p. 1543 1806.

biennis and if the petals were really no more than 3 cm. long the flower size was also closer to this species than to the large-flowered forms of *Lamarckiana*. On the other hand the stigma lobes figured somewhat above the tips of the anthers are in a position more like that in *Lamarckiana* than in the Dutch *biennis* where the stigma lobes lie below the tips of the anthers and pollination takes place before the opening of the bud.

In the third edition of the "English Botany" Syme[1] gives a description of "*Œnothera biennis* Linn." and states it to be "now perfectly established on the Lancashire coast, at Crosbie, near Liverpool, and occuring occasionally throughout Britain, but generally an outcast from gardens." The description of this plant is accompanied by a somewhat different figure from that in the edition of 1806, but the two figures agree in all essentials of structure. The figure and description indicate a plant 2-3 feet high, rosette leaves oblanceolate-elliptical 6 inches to 1 foot long, stem leaves elliptical 3-6 inches long, all leaves short petioled and with thick white midribs, repand denticulate; flowers with petals 1¼ to 1½ inch or more across (about 3-4 cm.), stigma lobes figured somewhat above the tips of the anthers; "plants dull green, sub-glabrous, with the stem, calyces, petioles, midribs, and margins of the leaves more or less hairy." In this account, also, as in that of the first edition (1806) there is no mention of that stem coloration characteristic of *Lamarckiana*, i.e., red papillæ on green portions of the stem. This point together with the statement that the plant is dull green suggests the Dutch *biennis* but the large petals and the position of the stigma indicate a plant with flowers more like those of *Lamarckiana*.

It ought at least to be possible to determine through herbaria whether or not the "*Œnothera biennis*" described in the different editions of the "English Botany" is the same form or one similar to the Dutch *biennis* which probably represents the *Œnothera biennis* of Linnæus. It ought to be possible to obtain evidence through herbaria for or against the possibility of the presence in England of *O. Lamarckiana* De Vries at a date as early as 1806 or at least previous to 1860. There should be some direct evidence whether or not *O. Lamarckiana* was first introduced into England through the cultures of Carter and Company at about 1860 and whether or not its appearance on the sand hills of Lancashire is of an earlier or a later date.

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[1] English Botany, Third Edition, vol. 4, p. 24, 1865.

I have certain views on the subject but my purpose is not to present them at this time but to plead that a strong effort be made to fix the approximate date of the appearance in British *Œnothera* floras of the *biennis* of Linnæus (probably represented by the Dutch plant) and of *O. Lamarckiana* De Vries. The characters that are likely to be most helpful in distinguishing these species on herbarium sheets are:—

1. The presence in *Lamarckiana* and absence in the Dutch *biennis* (so far as is known) of red in the stem papillæ. It must be borne in mind, however, that some races close to the *biennis* of Linnæus have the stem coloration of *Lamarckiana.*

2. The size of the petals, 4-4·5 cm. long in the large-flowered forms of *Lamarckiana* and 2-2·5 cm. long in the Dutch *biennis.* There are small-flowered races of *Lamarckiana* the petals of which are of about the same size as those in the Dutch *biennis.*

3. The position of the stigma 5-7 mm. above the tips of the anthers in the large-flowered *Lamarckiana* (open pollinated) and well below in the Dutch *biennis* (close pollinated in the bud). The small-flowered races of *Lamarckiana* sometimes present the stigma in a lower position more like that of the Dutch *biennis.*

4. The coloration of the sepals, sometimes streaked with red in *Lamarckiana* but normally green in the Dutch *biennis.*

De Vries has suggested that what I have termed the small-flowered forms of *Lamarckiana* may be hybrids between the large-flowered type and *biennis*, but it is also possible that they are variants from *Lamarckiana*, itself a hybrid. It seems most unlikely that Great Britain has no herbarium sheets that can throw light on these problems.

Most interesting from my standpoint is the problem of the first appearance in England of the progenitors of *O. Lamarckiana* De Vries. Were they certainly first introduced through the cultures of Carter and Company, about 1860, or were they in England and perhaps on the sand hills of Lancashire previous to this date? Is it possible that the plants of Carter and Company came not from Texas but from some part of England, perhaps from the very sand hills of Lancashire? There certainly should be in British herbaria some evidence on these questions.

It seems to be impossible to determine with exactness what are the forms under consideration in some of the descriptions published at dates of great importance to our problem, and that is why I have laid so much importance upon herbarium material.

Thus Don[1] described in 1832 "*Œ. biennis*" from "sand banks on the coast of Lancashire" and noted that it "is common in gardens and often escapes from thence into rich waste ground," but the statements "flowers large" and "delicately fragrant" are relative matters and we cannot be certain from this or other parts of the account whether the plants were nearest to *Lamarckiana* De Vries or to forms of *biennis* such as that from Holland (the *biennis* of Linnæus). Lindley[2] in 1833 gave an account of "*Œnothera biennis* var. *grandiflora*" and stated it to be "not uncommon in gardens." The figure of this plant shows petals drawn about 3.5-4 cm. long, as large as those of *Lamarckiana* De Vries, but a basal or perhaps a rosette leaf is too narrow for *Lamarckiana,* nor will it do for the Dutch *biennis* or for *grandiflora.* The bracts are figured broad at the base and sessile as in both *Lamarckiana* and *biennis,* but the inflorescence with long internodes is not as in those species but is more like that of *grandiflora*; the bracts, however, are not those of *grandiflora.* These contradictions are most puzzling, but may there not be specimens preserved at this period which will clear the obscurity.

I am aware that the *Œnothera* floras in other parts of England offer opportunities for investigation that should not be overlooked in the study of the problems presented in this paper. I have, however, confined my suggestions to the remarkable assemblage on the sand hills of Lancashire for the reason that this region seems to be best known and to have been under observation for the longest period.

[1] Don, George. A General System of Gardening and Botany, vol. 2, p. 685, 1832.

[2] Lindley, John. *Œnothera biennis*; var. *grandiflora.* Edwards's Botanical Register, vol. 6, p. 1604, 1833.

UNIVERSITY OF PENNSYLVANIA.

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A MUCH DESIRED OENOTHERA

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This paper is written to bring to the attention of botanists in the southwestern part of the United States a problem of importance and great interest. It is the problem of the origin of *Oenothera Lamarckiana* De Vries.

It seems clear from evidence recently brought forward[1] that the *Lamarckiana* of De Vries's cultures is not the same plant as that described by Lamarck[2] under the name *Aenothera grandiflora* from material grown in Paris at about 1796 or earlier, and renamed by Seringe[3] *Oenothera Lamarckiana.* The plant of Lamarck seems to have been a form of *Oenothera grandiflora* Solander[4] (*O. grandiflora* "Aiton") introduced into England in 1778 from Alabama.

The material of De Vries's cultures which I have proposed shall bear the name *Oenothera Lamarckiana* De Vries (since *O. Lamarckiana* Seringe passes into the synonymy of *O. grandiflora* Solander) has with little doubt come down to us, possibly greatly modified, from certain plants placed upon the market by the seedsmen Carter and Company of London at about 1860.

The description of the cultures of Carter and Company is not sufficiently detailed to allow us to form a picture of their plants further than that they were 3 to 4 feet high, very hardy, and with flowers 4 inches in diameter. The figure published with the description[5] is of an impossible *Oenothera.* Carter and Company

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[1] Davis, B. M., Was Lamarck's evening primrose (*Oenothera Lamarckiana* Seringe) a form of *Oenothera grandiflora* Solander? Bull. Torr. Bot. Club, **39**: 519, 1912.

[2] Lamarck, Encyclopédie Méthodique Botanique, **4**: 554,? 1798.

[3] Seringe, N. C., De Candolle, Prodromus, **3**: 47, 1828.

[4] Solander, D., Aiton, Hortus Kewensis, **2**: 2, 1789.

[5] The Floral Magazine **2**: pl. 78, 1862.

report that their cultures came from seeds received unnamed from Texas.

Now we have no evidence to dispute the statement that these seeds came from Texas and we certainly have reason to feel hopeful that if these plants grew in Texas further back than 1860 they will still be present in the southwest. It is of course possible that the seedsmen made some mistake and that their seeds came not

Fig. 1. Sheet in the Gray Herbarium of Harvard University. An *Oenothera* grown by Dr. Asa Gray at Cambridge, Massachusetts, in 1862, and probably derived directly or indirectly from the cultures of Carter and Company of London, which were distributed under the name of *O. Lamarckiana*.

from Texas but from some part of England where large-flowered oenotheras were recorded at dates much earlier than 1860. That, however, is a problem for the English botanists. It is plainly the responsibility of American botanists to make every effort to bring forward any form that may throw light on the source of the cultures of Carter and Company.

There is fortunately in the Gray Herbarium a sheet (fig. 1) which contributes much more information on the probable composition of the cultures of Carter and Company than the brief description and obviously inaccurate plate of the Floral Magazine. The specimens on the sheet are from a plant grown in Cambridge, Massachusetts in 1862 by Dr. Asa Gray. From the records upon the sheet[6] it appears quite certain that Dr. Gray received the seeds from William Thompson of Ipswich, England, a seedsman who probably obtained from Carter and Company their new novelty. It is then possible that the plant grown by Dr. Gray was not more than one or two generations removed from the original cultures of Carter and Company.

The following is a brief description of the specimens on the sheet in the Gray Herbarium illustrated by figure 1.

1. *Stems and Foliage.* The stem bears long hairs arising from papillae which are colored red as in *Lamarckiana* and are about as numerous as in that species. The large detached leaf, about 18.5 cm. long with sinuate margins, slightly lobed below, and with some evidence of former crinkles, suggests by its shape (although too small) the basal leaves of *Lamarckiana.* The leaves of the upper foliage, short petioled, are not so nearly sessile as in *Lamarckiana.*

2. *Inflorescence.* The inflorescence has longer internodes than in *Lamarckiana* and consequently is not so compact. The bracts are broad at the base, slightly toothed, and persistent, becoming large lanceolate leaves on the fruiting branches; those of *Lamarckiana* remain much smaller.

3. *Buds.* The buds are about 9.5 cm. long, not stout and 4-angled as in *Lamarckiana.* The sepal tips are more attenuate than in *Lamarckiana,* projecting 1 cm. beyond the folded petals. The pubescence upon the sepals consists of long hairs arising from papillae among much shorter sessile hairs as in *Lamarckiana.*

4. *Flowers.* The petals are about 4.5 cm. long, as long as those of the largest forms of *Lamarckiana.* The stigma lobes are about 8 mm. long, and close to 5 mm. above the tips of the anthers, in these respects agreeing with large-flowered forms of *Lamarckiana.*

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[6] See Davis, Am. Nat. **46**: 417, 1912.

5. *Capsules.* The capsules about 3 cm. long, are longer and not so stout as those of *Lamarckiana.*

The plant grown by Dr. Gray differed from the Lamarckiana of the cultures of De Vries in the longer internodes of the inflorescence, in the larger more leaf-like bracts, in the form of the buds, in the much attenuated sepal tips, and in the longer seed capsules. There would be little profit in discussing at present whether or not this plant was truly representative of the cultures of Carter and Company and whether or not their plants became greatly modified during the quarter century before the time when De Vries began his studies at about 1886, and isolated the form we know today as *O. Lamarckiana* De Vries.

What we desire is information on all of the tall oenotheras of the south and west that have large flowers (petals 3 to 4 cm. long) and broad leaves. We wish to know whether any of them resemble the *Lamarckiana* of De Vries's cultures. We wish to know whether any of them resemble the specimens of the plant grown by Dr. Gray. One species of the south, *Oenothera grandiflora,* from Alabama is fairly well understood; does this species grow in Texas? In California and Arizona are forms usually designated *O. Hookeri*; do any of these grow in Texas?

A few words to the field botanist will not be out of place. For this problem the mere observation or collection of an herbarium specimen without seeds is worse than useless. We can have no certainty as to the characters of an individual plant unless its seeds have been grown in large cultures; it may be a chance hybrid. Preferably flowers should be hand pollinated and then protected by paper bags until withered. When this is not possible ripe capsules should be gathered always from the same plant upon which observations are made.

A recent experience of the writer will illustrate the reason for the cautions expressed above. In January, 1912, Mr. H. H. Bartlett sent me seeds of an *Oenothera* which he had in cultivation and which seemed to be very close to *Lamarckiana* De Vries, if not identical with it. His cultures came from seeds of a plant which grew near Boulder Creek, Santa Cruz County, California and was collected by Prof. C. P. Smith (No. 2320). Prof. Smith had written "my 2320 was taken at the edge of a vacant, unkempt lot in town (Santa Cruz) and may very well have escaped from cultivation, though none of the plant was in evidence in cultivation roundabout as far as I noticed."

The writer grew in 1912 a culture of 106 plants from this Santa Cruz material. As young rosettes the culture presented a diverse assemblage; about $\frac{1}{3}$ of the rosettes were *Lamarckiana*-like, about $\frac{1}{5}$ had leaves much narrower and more loosely clustered than in *Lamarckiana* and between these types was a wide range of intermediates. The differences became more conspicuous as the culture matured and finally the following types were distinguished in a careful analysis made by Mr. Bartlett:

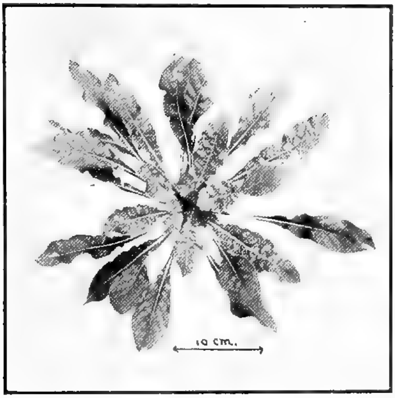

Fig. 2

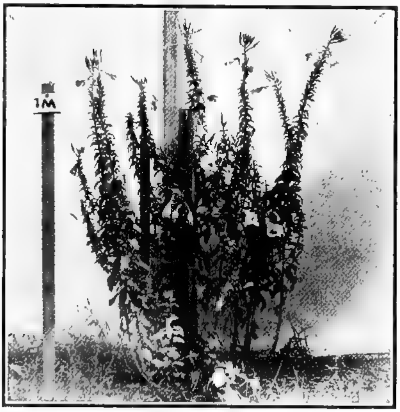

Fig. 3

Fig. 2. Mature rosette of *Oenothera Lamarckiana* De Vries. There are also forms with broader leaves more closely clustered.

Fig. 3. Mature plant of a large-flowered form of *Oenothera Lamarckiana* De Vries.

Type I. *Oenothera Lamarckiana.* Leaves crinkled, stems green with red papillae at the base of long hairs, buds both viscid-pubescent and pilose. 44 plants.

Type II. Differed from Type I in that the longer flowering side branches were red above, although the main stem was clear green. 5 plants.

Type III. Differed from Type I only in having red stem coloration. 6 plants.

Type IV. Differed from Type I only in the intensely red sepals (a character of *O. rubrinervis*). 2 plants.

Type V. Differed from Type I in having the red stem coloration of Type III and the intensely red sepals of Type IV. 1 plant, *rubrinervis*-like.

Type VI. Differed from Type I in having plane leaves. 1 plant.

Type VII. Differed from Type I in its narrow, plane leaves with red veins. 2 plants.

Type VIII. Similar to Type VII except for intensely red sepals. 1 plant.

Type IX. Leaves crinkled, stems clear green (papillae at the base of long hairs not red as in Type I). 4 plants.

Type X. Leaves crinkled, stem clear green as in Type IX, buds viscid-puberulent only, not pilose. 38 plants.

Type XI. Differing from Type X in that the lower leaves were red-veined. 1 plant.

Type XII. Differed from Type X in having a red stem and the lower leaves red-veined. 1 plant.

To one familiar with hybrids of *Oenothera* the behavior of the plant from Santa Cruz in this culture can have but one interpretation. The plant could not have been representative of a pure species. It must have had a germinal constitution of mixed parentage (heterozygous), or, in other words, it must have been of hybrid origin. No plant of an approximately uniform germinal constitution (homozygous) would have thrown off such a variety of types differing in such clear cut characters.

This culture thus illustrates the necessity of testing experimentally any plant which may be supposed to present evidence that *Oenothera Lamarckiana* occurs in the American flora as a native species. The discovery of the Santa Cruz plant suggested the possibility that *Lamarckiana* grows wild in California. The culture from its seeds showed that the plant was hybrid in character and consequently was not representative of a native species. Its history is not known but we suspect that the plant was a garden escape from *Lamarckiana* (frequently grown for ornamental purposes) which had hybridized with some other species of the neighborhood. It was certainly not pure *Lamarckiana* because of the very great number and variety of the different types thrown off in the culture.

A brief description of *Oenothera Lamarckiana* De Vries together with some photographs illustrating its most important characters will be given for those who are not familiar with the plant.

1. *Rosettes.* The mature rosette (fig. 2), 4 to 5 dm. broad, consists of broadly elliptical or spatulate leaves with sinuate margins, irregularly toothed below, and very strongly crinkled. There are forms of *Lamarckiana* with broader leaves,

shorter petioled, and more closely clustered than in the example shown by the photograph.

2. *Mature plant.* The mature plant (fig. 3), about 1.5 m. high, has normally a strong central stem from the base of which grow long side branches, about 1 m. long, and shorter branches are usually present about midway up the central stem. Flowering portions of the stem are usually unbranched. Red papillae at the base of long hairs give the upper green portions of the stem a very characteristic coloration. The foliage on upper portions of the plant (fig. 4) consists of ovate-lanceolate leaves, short petioled or almost sessile, and crinkled.

Fig. 4. Side branch of a large-flowered form of *Oenothera Lamarckiana* De Vries, with a leaf from the lower portion of the main stem.

3. *Inflorescence.* The close inflorescence (fig. 4) has sessile bracts, broad at the base, early in the season equalling or exceeding the length of the young buds; later in the season the bracts may be much shorter.

4. *Buds.* The buds in the largest-flowered forms of *Lamarckiana* (fig. 4) are 8 to 9 cm. long. The cone is stout and 4-angled. The sepals are green, in some forms streaked with red; sepal tips thick or not markedly attenuate. The pubescence on sepals, a heavy pilose and puberulent covering, consists of long hairs arising from papillae among numerous short sessile hairs. In the smaller-flowered forms the buds are from 7 to 8 cm. long and correspondingly smaller in their parts.

5. *Flowers.* The largest-flowered forms have petals 4 to 4.5cm. long, and stigma lobes 5 to 7 mm. above the tips of the anthers. The smaller-flowered forms have petals 2.5 to 3 cm. long and frequently the stigma lobes are about on a level with the tips of the anthers. The ovaries bear red papillae at the base of long hairs.

6. *Capsules.* The capsules vary in shape, in some forms being stout and relatively short, about 2 cm. long; in other forms more attenuate and about 3 cm. long.

Some remarks will not be out of place on the reason why the problem of the origin of *Oenothera Lamarckiana* is a matter of such great interest. As is well known the evidence for the mutation theory of De Vries rests chiefly upon the behavior of *Lamarckiana* in throwing off marked variants ("mutants") in successive generations. De Vries assumed that *Lamarckiana* was a native American species and interpreted its behavior as the giving rise to new species through the sudden appearance of wide variations (saltations). Many botanists are critical of the interpretation of De Vries and hold that Lamarckina is not representative of a wild species but is, on the contrary, of hybrid origin, and that its behavior illustrates the phenomenon of the splitting of a hybrid into diverse forms. So far no clear evidence has been presented that *Lamarckiana* is or ever was the component, as a wild species, of any native flora, but it is only fair to state that the southern and western United States have not been thoroughly explored. This is why we hope that botanists of these regions will push the search with vigor.

For the view that *Lamarckiana* is hybrid in character there is evidence from experimental studies upon the plant itself, the latest and best of which are described in a recent paper of Heribert-Nilsson.[7] There are also the experimental studies of the writer[8]

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[7] Heribert-Nilsson, N., Die Variabilität der *Oenothera Lamarckiana* und das Problem der Mutation. Zeitsch. ind. Abstam. u. Vererbungslehre, **8**: 89, 1912.

[8] See Davis, Am. Nat. **45**: 193, 1911, and **46**: 377, 1912.

on hybrids between O. *grandiflora* and forms of O. *biennis* which show points of resemblance to *Lamarckiana* and behave in a manner similar to *Lamarckiana* when grown through second and third generations. If forms resembling *Lamarckiana* are found growing wild in any part of America the mere record of their observation will be in no sense conclusive that the plant represents a wild species. Its progeny must be tested through experimental cultures, and their behavior alone will determine the character of the original plant as in the case of the cultures just described from the Santa Cruz plant. This is why we emphasize the importance of checking field observations by experimental studies and emphasize the necessity of collecting seed from any plant under observation.

In conclusion the writer expresses the hope that botanists will coöperate with him in the study of the problems outlined above. He hopes that observations will be promptly reported and specimens sent to him and above all that seeds will be collected from any plant that resembles *Lamarckiana* or the specimens on the sheet in the Gray Herbarium. I shall be very glad to furnish seed of *Lamarckiana* to anyone who wishes to grow the plant and thus to become familiar with its characters.

ADDITIONAL EVIDENCE OF MUTATION IN OENOTHERA

14

(WITH SEVENTEEN FIGURES)

HARLEY HARRIS BARTLETT

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ADDITIONAL EVIDENCE OF MUTATION IN OENOTHERA[1]

HARLEY HARRIS BARTLETT

(WITH SEVENTEEN FIGURES)

Introduction

Much of the advance which has been made in genetics and practical breeding during the last decade has been a direct result of the promulgation by DE VRIES of the theory of the origin of species and varieties by mutation. That recessive Mendelian variations originate singly by mutation has been shown by several investigators, notably by MORGAN, who has observed the origin of more than 150 such variations in his cultures of *Drosophila.* Many opponents of the mutation theory deny, however, that progressive mutations ever occur in homozygous strains, or that true species, differing from the parent in several independent characters, have ever been observed to originate at a single step by mutation. DAVIS,[2] for example, is in accord with the mutationists in regarding *Oenothera gigas* as a marked progressive mutation of specific rank, but he denies that *Oenothera Lamarckiana*, the parent form of *O. gigas*, is homozygous. The facts (1) that *O. Lamarckiana* is not known as a native component of any flora, (2) that its known history has been that of a cultivated plant or an escape from cultivation,

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[1] Published by permission of the Secretary of Agriculture.

[2] DAVIS, B. M., Cytological studies on *Oenothera.* III. A comparison of the reduction divisions of *Oenothera Lamarckiana* and *O. gigas.* Ann. Botany **25**:941–974. 1911. "*Oenothera gigas* is a progressive mutant, its peculiarities being clearly associated with the changes in its germ plasm incident upon the doubling of its chromosome number" (*op. cit.* p. 974).

and (3) that its habit of throwing off marked germinal variations is paralleled by the behavior of certain interspecific hybrids in the F_2 and F_3 generations seem to DAVIS[3] a sufficient indication that this plant is of comparatively recent hybrid origin, and that its mutations are due to germinal instability resulting from hybridization. He holds that the germinal variations of *O. Lamarckiana* and of various hybrids which he has studied show marked progressive evolution which seemingly cannot be accounted for on a Mendelian basis. Although he does not deny that slight discontinuous variations may occur in homozygous strains (and he insists that the term mutation ought to be used only for such variations), he is of the opinion that variations large enough to be of evolutionary significance occur rarely if at all except in heterozygous lines.

GATES[4] does not believe that *O. Lamarckiana* is a recent interspecific hybrid, but does ascribe its mutations to germinal instability caused by occasional random crossing with other types. In their main conclusion, that when germinal variation occurs it usually follows crossing, DAVIS and GATES appear to agree. GATES, however, is more emphatic than DAVIS in his conclusion that mutation in *Oenothera* is not merely a result of Mendelian redistribution of unit characters, but is a distinct type of variation. He believes, moreover, that mutation sometimes takes place in pure as well as in hybrid lines. Since the phenomena are identical in the two cases, he has laid especial stress on the fact that there is no excuse for confusing mutation, when it occurs in hybrids, with any type of Mendelian segregation.[5]

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[3] DAVIS, B. M., Genetical studies on *Oenothera*. II. Amer. Nat. **45**:193–233. 1911; III. *Ibid.* **46**:377–427. 1912; IV. *Ibid.* **47**:449–476, 547–571. 1913.

[4] GATES, R. R., Mutation in *Oenothera*. Amer. Nat. **45**:577–606. 1911.

———, A contribution to a knowledge of the mutating *Oenotheras*. Trans. Linn. Soc. Lond. II. Bot. **8**:1–67. 1913.

———, Tetraploid mutants and chromosome mechanisms. Biol. Centralbl. **33**:92–99, 113–150. 1913.

[5] In this author's last paper he says: "The cytological evidence shows that germinal changes may and do occur which are independent of all the laws of hybrid combination and hybrid splitting. This generalization is of more fundamental significance than might at first appear; for it shows that mutation in *Oenothera* is a process *sui generis*, and that no amount of hybrid combination and splitting, Mendelian or otherwise, is sufficient to account for it." GATES, R. R., Breeding experiments which show that hybridization and mutation are independent phenomena. Zeitschr. Ind. Abstammungs- u. Vererbungslehre **11**:209–279. 1914.

Heribert-Nilsson[6] has made the first serious effort to explain the variations of *Oenothera Lamarckiana* on a strictly Mendelian basis. He does not hold with Davis that this species is necessarily of hybrid origin, but rather that it is a collective species, embracing a number of different strains which constantly cross among themselves. Consequently he assumes that the mutation phenomena do not exemplify progressive and regressive species formation, but merely the synthesis of new combinations from factors already existing within the species.

Although it is by no means true, as some critics seem to imply, that the mutation theory must stand or fall on the evidence derived from *Oenothera*, it must nevertheless be admitted that failure to find a parallel among other more fortunately chosen species of this genus to the mutation phenomena shown by *O. Lamarckiana* would discredit, if not invalidate, much of the direct evidence of mutation which has been so laboriously won by De Vries. Davis[7] has said that "it is evident that the adherents of the mutation theory are sensitive to the doubts freely expressed concerning the status of *Oenothera Lamarckiana*, the behavior of which in throwing off marked variants is cited as the most important evidence for the origin of species by mutations. . . . . Consequently, mutationists are likely to bring forward as rapidly as possible any evidence that may seem to indicate the appearance of clear inheritable variations of a marked character in forms of pure germinal constitution, i.e., in homozygous material."

It is the object of this paper to present additional evidence of mutation in *Oenothera*, derived from one of the small-flowered, self-pollinating wild American types. Before proceeding farther, however, it should be stated that a considerable body of similar evidence has already been obtained.

De Vries[8] and Stomps[9] have twice observed the origin of a dwarf variety of *O. biennis* by mutation, once in a pure line of

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[6] Heribert-Nilsson, N., Die Variabilität der *Oenothera Lamarckiana* und das Problem der Mutation. Zeitsch. Ind. Abst. u. Vererb. **8**:89–231. 1912.

———, *Oenothera* Problemet. Svensk. Bot. Tidskr. 7^1: pp. 16. 1913.

[7] Davis, B. M., Mutations in *Oenothera biennis* L? Amer. Nat. **47**:116–121. 1913.

[8] De Vries, H., Die Mutationen in der Erblichkeitslehre. pp. 28–30. 1912.

———, Gruppenweise Artbildung. pp. 299–306. 1912.

[9] Stomps, Theo. J., Mutation bei *Oenothera biennis* L. Biol. Centralbl. **32**:521–535. 1912.

O. biennis var. *leptomeres*,[10] and once in a cross between this variety and typical *Oenothera biennis*, from which var. *leptomeres* itself doubtless arose by mutation. STOMPS has also described *O. biennis* mut. *semigigas* from the same culture of *O. biennis* var. *leptomeres*×*O. biennis* which gave rise to the dwarf. A recent letter from Professor DE VRIES (dated May 16, 1914) states that mutations from *O. biennis* are still being obtained at Amsterdam.

STOMPS[11] has just published a second report on mutations in *O. biennis*. He records the origin by mutation, in a pure line, of *O. biennis* var. *sulfurea* De V. (long known as a wild component of the Dutch flora), together with mut. *nanella* and mut. *semigigas*. GATES[12] has likewise announced the discovery of mutations (*O. biennis lata*, *O. biennis laevifolia*, *O. biennis rubrinervis*) from *O. biennis*, but has not yet published a full account of his cultures.[13] Finally, DE VRIES has obtained two different mutations, *O. salicifolia* and *O. salicastrum*, from wild seed of a strain of the self-pollinating *O. biennis* "Chicago" which he collected near Courtney, Missouri; and the writer[14] has given a preliminary account of *Oenothera stenomeres* mut. *lasiopetala*,[15] a hairy-petaled derivative of one of the small-flowered cruciate Onagras.

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[10] *Oenothera biennis* var. *leptomeres* Bartlett. Amer. Jour. Bot. **1**:242. 1914= *Oenothera biennis* var. *cruciata* De Vries, not T. & G.

[11] STOMPS, THEO. J., Parallele Mutationen bei *Oenothera biennis* L. Ber. Deutsch. Bot. Gesells. **32**:179–188. 1914.

[12] GATES, R. R., Parallel mutations in *Oenothera biennis*. Nature **89**:659–660. 1912.

[13] Since the above was written, an account of the cytology of *O. biennis* mut. *lata* has been received. See GATES, R. R., and THOMAS, NESTA, A cytological study of *Oenothera* mut. *lata* and *O.* mut. *semilata* in relation to mutation. Quar. Jour. Micr. Sci. **59**:523–571. 1914.

[14] BARTLETT, H. H., An account of the cruciate-flowered *Oenotheras* of the subgenus *Onagra*. Amer. Jour. Bot. **1**:226–243. 1914.

[15] By an unfortunate oversight this name was published in Amer. Jour. Bot. as *O. stenopetala* mut. *lasiopetala*. The writer had originally used the name *O. stenopetala* for the species which was described as *O. stenomeres*. After the manuscript had been submitted to the editor, a change was made necessary by the publication of *O. stenopetala* Bicknell, Bull. Torr. Bot. Club **41**:79. 1914. In one place the original name escaped notice and was not corrected. It is hoped that the error will not lead to any confusion.

It is shown in this paper (1) that the phenomena of mutation are as characteristic and as easily observed in one of the wild small-flowered self-pollinating Onagras as in *Oenothera Lamarckiana;* (2) that the mutations show characters unlike those of any other form with which the parent could have crossed; and (3) that the mutations cannot be ascribed to Mendelian segregation as at present understood. It therefore seems in the highest degree probable that mutation is a phenomenon which is independent of hybridization, and that the evidence of mutation which DE VRIES has found in *Oenothera Lamarckiana* is just as valid as though that species were known as a wild plant and not suspected of having had a horticultural origin.

Differential germination

Several of the most interesting mutations which were observed during the season of 1913 were found quite by chance. One lot of potting soil, in which the seeds of several strains were sown, proved to be a very stiff clay on which a hard crust formed. Germination was so poor that in several cases less than a dozen seedlings resulted from sowing perhaps a thousand or more seeds. It was afterward found that the seeds showed the usual percentage of germination when sown in good soil. In three different species the small progenies obtained when the seeds were planted under unfavorable conditions disclosed striking mutations, which had survived as a result of differential or selective germination. These mutations might easily have been overlooked in a seed pan containing several hundred seedlings, of which only a few were to be retained and grown to maturity.

The three mutant species were from widely separated localities. The seeds of one, from Plymouth, Massachusetts, were sent by Professor B. M. DAVIS; the others were collected by the writer at White Sulphur Springs, W.Va., and Lexington, Ky., respectively. The mutations of the two former species were lost before they matured. It will be useless, therefore, to give an account of their characters or of the cultures in which they appeared until they shall have been found again. In the case of the third species, *O. pratincola*, the mutations were brought to maturity and have yielded a second generation. This species, therefore, has been systematically examined for variations, with the results recorded in this paper.

The Oenothera population at Lexington, Kentucky

During a brief visit in October 1912, the writer was able to find only two species of *Oenothera*×*Onagra* at Lexington, Ky. They are both new and are referred to below under the names *O. pratincola* and *O. numismatica.* If any other species occur within two or three miles of the city, they must be very scarce. Of course, in October many plants were through blooming and not in such condition that any differences among them would show to the best advantage. Nevertheless, it is believed that no common species could have been overlooked. Nine seed collections were made from individual plants, which showed as great a range of variation as possible. These plants, and the strains descended from them, have been designated by letters from A to I. Eight of the strains proved to be taxonomically identical and are referred to as *O. pratincola.* Lexington A, B, and C were collected in a pasture near Town Creek, 2 miles west of Lexington, where they grew within 200–300 feet of each other. Lexington E, F, G, H, and I were collected at random in vacant lots and within a mile of the city on the west. Lexington D is the only strain of the 9 which is referred to *O. numismatica.* The parent plant grew by a roadside about 2 miles east of Lexington. In addition to the seed collections, many rosettes were collected which flowered in Washington in 1913. Thirteen plants from the same general region as plants E to I proved on flowering to be typical *O. pratincola*, as were also 26 plants from the edge of a field near the reservoir east of the city. It thus appears that *O. pratincola* constitutes the bulk of the *Oenothera* population at Lexington. *O. numismatica* is much scarcer; it did not occur at all among the rosettes which were collected, and was seen in flower only east of Lexington.

The salient characters of the two evening primroses obtained at Lexington are the following:

In *O. pratincola*	In *O. numismatica*
A well-grown plant, is 1.5 m. high, and loosely branched.	A well-grown plant, is about 1 m. high, and densely branched.
The basal branches are frequently simple.	The basal branches bear tertiary branches and resemble the main stem.
The flowering time lasts about six weeks.	The flowering time lasts only about two weeks.
The lax terminal spike often becomes 5–6 dm. long (see fig. 1).	The dense terminal spike is about 2 dm. long in fruit (see fig. 2).
The lateral branches below the terminal spike are few in number and become 4–5 dm. long.	The lateral branches below the terminal spike are numerous and are seldom over 2 dm. long.
The lowest bracts of the upper lateral spikes are ovate, and grade upward to lanceolate.	The lowest bracts of the upper lateral spikes are nearly orbicular and grade upward through oblong to lanceolate (see fig. 2).
The calyx segments are so sparsely pilose as to appear practically glabrous.	The calyx segments are closely and finely pubescent.
The hairs of the calyx segments are about 1 mm. long, thick-walled, acute, with multicellular tuberculate bases.	The hairs of the calyx segments are less than 0.5 mm. long, and belong to two types: (1) an acute thick-walled type without tuberculate bases, and (2) a thin-walled, round-ended, clavate or cylindrical type.

Technical diagnoses of these two species, together with a discussion of their possible relationships, have been published elsewhere.[16] *O. pratincola* appears to be a frequent plant in the North Central States. *O. numismatica*, on the contrary, is known only from Lexington and may well be a local species, possibly derived by mutation from *O. pratincola*. Its close resemblance in certain characters to one of the mutations of *O. pratincola* is pointed out elsewhere in this paper.

The mutations of "Lexington C"

Seeds from four of the parent plants of *O. pratincola* which had been selected at Lexington were planted early in the spring of 1913.

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[16] Bartlett, H. H., Twelve elementary species of Onagra. Cybele Columbiana 1:37–56. 1914.

FIG. 1.—*Oenothera pratincola*, sp. nov.: upper part of main stem of Lexington C-30; leaves from middle of stem; flowers and buds; ×⅓.

FIG. 2.—*Oenothera numismatica*, sp. nov.: upper part of main stem of Lexington D-29; leaves from middle of stem; lateral branches from just below the terminal spike; characteristic foliage of such a lateral branch; in contrast with fig. 1, note the denser shorter spikes, which are only in flower a short time, the much closer branching, and the characteristic suborbicular leaves of the uppermost lateral branches; $\times\frac{1}{3}$.

Lexington A, B, and E germinated readily. Since no variation was noticed among the hundreds of seedlings of these three strains, all were discarded except 30 of each, which were potted off for the field cultures. The seeds of Lexington C, however, had been planted too deeply in unsuitable clay soil, and, although the seed pan received the same treatment as the rest, weeks passed before any seedlings appeared. At length 9 plants were obtained which were potted off. Almost from the first, they showed remarkable variation among themselves. Six (nos. 3, 4, 5, 6, 8, and 9) were typical *O. pratincola*, and agreed in all characters with the seed-

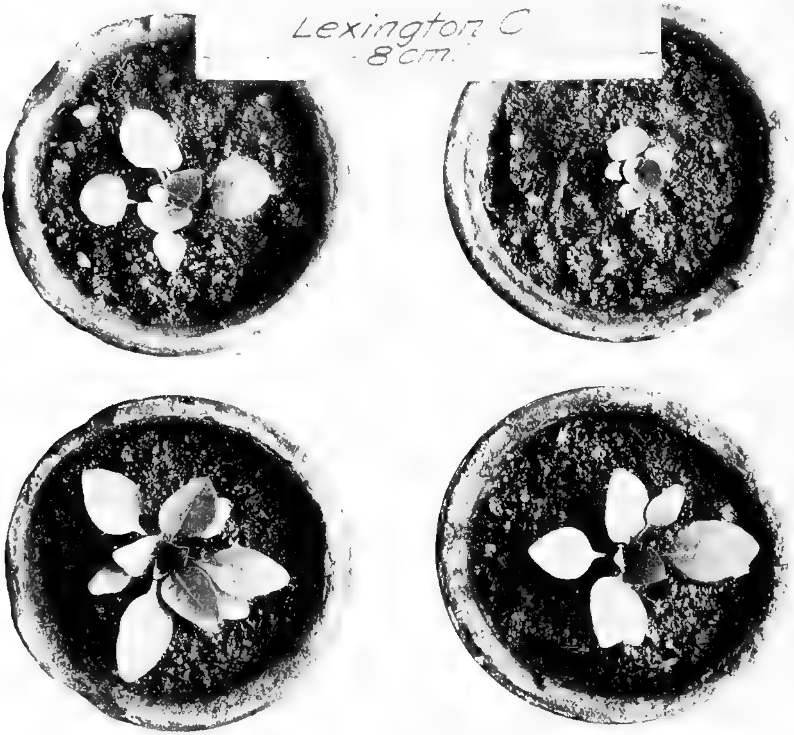

FIG. 3.—F_1 progeny of *Oenothera pratincola:* four of the 9 seedlings which constituted the first culture of Lexington C; the 2 upper plants, Lexington C-1 and C-2, are mut. *nummularia;* the latter bore seeds which gave rise to the F_1 culture referred to in table I; the 2 lower plants are typical *O. pratincola*.

lings of Lexington A, B, and E; one (no. 7) was of a darker green color than the type, the leaves were somewhat narrower, and the petiole and midrib below the middle of the blade were particularly broad and white; two (nos. 1 and 2) had almost orbicular leaves, and constituted the most striking deviation from the expected form that the writer had ever observed in a seedling of *Oenothera*. In fig. 3 the two upper plants are the round-leaved variations, nos. 1 and 2; the two lower are typical *O. pratincola*, nos. 3 and 4. In fig. 4 the same 4 plants are shown when a month older. The reader will observe that the orbicular seedling leaves of nos. 1 and 2 have

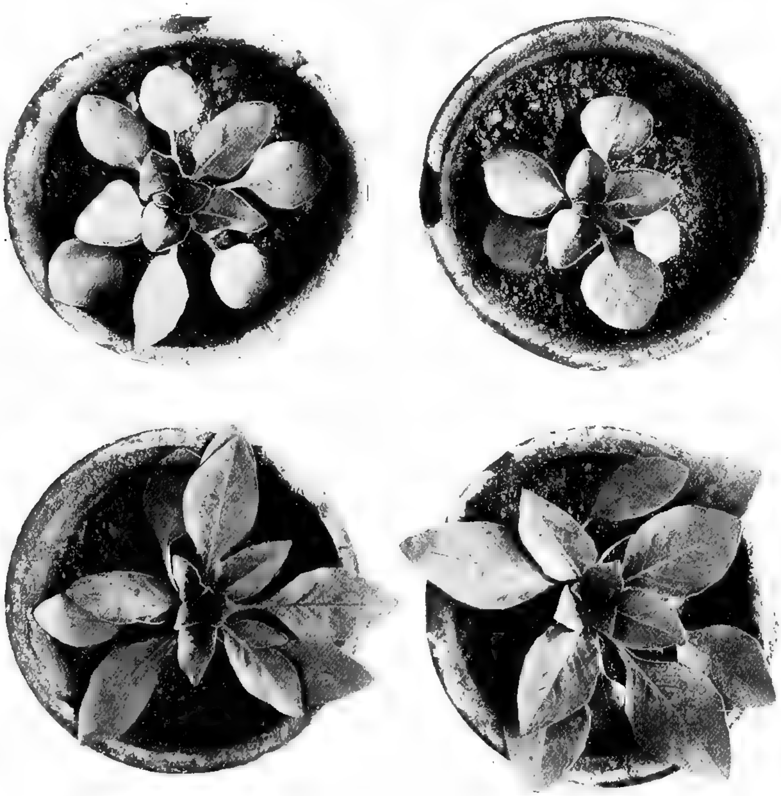

Fig. 4.—F_1 progeny of *Oenothera pratincola*, Lexington C: the same plants shown in fig. 3, but a month older.

been superseded in the more mature rosette by leaves of a different form, but that the sharp distinction between the variation and the typical form has not been obscured. The occurrence of so interesting a variation in Lexington C led to a careful examination of the strain for evidence of mutability.

A second sowing of the same seed on good soil resulted in a progeny of 720 seedlings from 1000 seeds. As soon as the seedlings were well rooted, they were transplanted to square seed pans in which they were widely enough spaced to allow of unimpeded growth for a month or six weeks. This system was followed in all subsequent work. Of course, the seeds were invariably sown on sterilized soil. After the seedlings were transplanted, the pans were frequently examined for mutations, and all plants which were noticeably divergent from the mass of the culture were marked for preservation. Among the 720 seedlings of the second sowing, there were only 4 round-leaved plants. Since the mass of the culture was uniform, and the round-leaved plants constituted an absolutely discontinuous variation from both the typical form and one other pronounced variant which occurred in the culture, it was concluded that they were probably mutations. In the following pages the round-leaved type is called *O. pratincola* mut. *nummularia*.[17]

In order to show the discontinuity between typical *O. pratincola* and mut. *nummularia*, photographs of two of the seed pans in which this mutation occurred are reproduced as figs. 5 and 6. At the time the pans were photographed, the plants were about as far advanced as nos. 1–4 in fig. 3. Comparison of the figures will

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[17] The writer has suggested (Amer. Jour. Bot. 1:237. 1914) that mutations of experimental origin be given trinomial names such as *O. pratincola* mut. *nummularia*, in order to avoid confusion with names which must be given consideration in floristic works. A trinomial nomenclature has the advantage over the binomial system proposed by GATES (Trans. Linn. Soc. London II. Bot. **8**:10. 1913) in that the parallelism of mutations occurring in different species may be indicated by the use of the same mutational designation. For example, a convenient way to show the parallelism between the mutations of *O. Lamarckiana* and those of *O. biennis* would be to call them *O. Lamarckiana* mut. *semigigas*, *O. biennis* mut. *semigigas*, etc. The trinomial used in this way need imply nothing as to the specific, varietal, or formal rank of a mutation, but only the manner of its origin. Nevertheless, for the sake of avoiding confusion, it would be well not to give any mutation a name which had previously been used in any subspecific category within the species which had given rise to the mutation.

show the complete identity, at this stage of growth, of different individuals of mut. *nummularia*, and also the great uniformity of the typical plants of the culture.

FIG. 5.—F$_1$ progeny of *Oenothera pratincola*, Lexington C, pan 1: the only mutation shown is Lexington C-10, mut. *nummularia;* the other plants are typical *O. pratincola;* about the same age as the plants shown in fig. 3.

In addition to the 4 plants of mut. *nummularia* which were discovered in the second sowing, there were solitary specimens of each of two other mutations, one plant (no. 12) like no. 7 of the first planting, and another (no. 18) unlike anything else in the culture. No. 18 had exceedingly narrow, red, subulate seedling leaves and was called on this account mut. *subulata*. There were also 7 plants (nos. 13–16, 19, 20, and 22) which developed very slowly and were retained in the expectation that they might prove to be dwarfs, although there was no character but size to distinguish them from typical sister plants. The solitary plant of mut. *subulata* died, but the type has since been found to be one of the most frequent mutations of *O. pratincola*. The type represented by nos. 7 and 12 was designated as mut. *pusilla*. Its rosettes were about 4 cm. in diameter at maturity. The stem leaves were

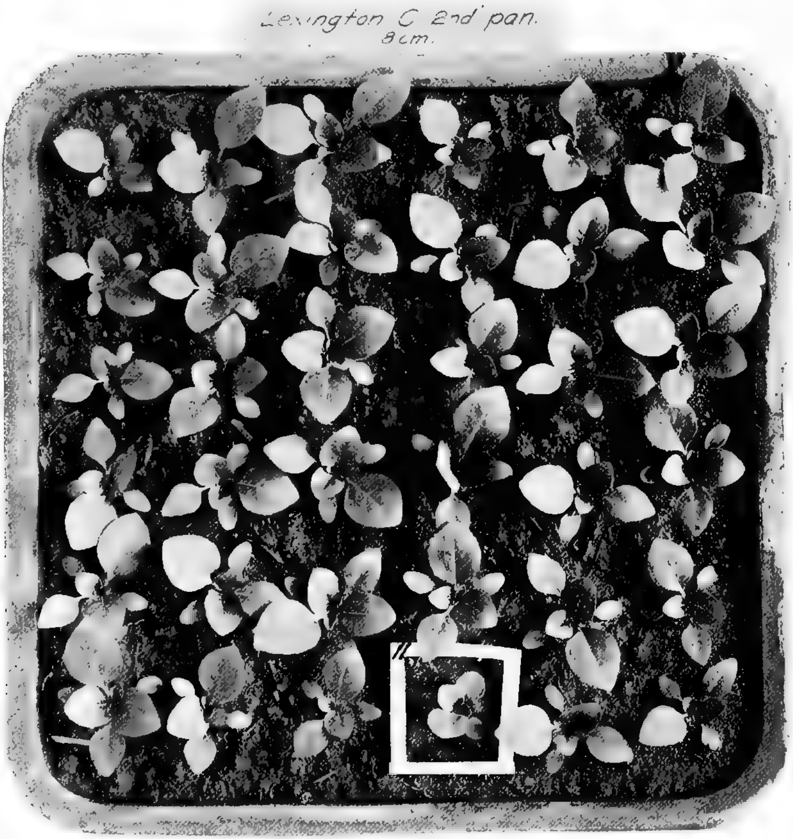

FIG. 6.—F_1 progeny of *Oenothera pratincola*, Lexington C, pan 2; the only mutation shown is Lexington C-11, mut. *nummularia;* the other plants are typical.

linear-lanceolate. The stems were simple. No. 7 died just before flowering, when only 7 cm. high. No. 12 flowered at a height of 10 cm. The ovary was 7 mm. long; hypanthium 10 mm. long; calyx segments 4 mm. long, excluding the distant free tips, which were 1 mm. long. The calyx differed from that of the typical form not only in having distant calyx tips, but also in being densely soft-pubescent. Unfortunately, this plant was sterile and produced no seeds. As far as the writer is aware, mut. *pusilla* represents the extreme of nanism in the subgenus *Onagra*.

With a single exception, the 7 suspected dwarfs developed as quite normal plants, indistinguishable from the mass of the culture. One plant, no. 19, differed from the rest in that it had stiff, distant calyx tips 5 mm. long which were continued on the angles of the squarish bud as a marked carina. The buds were almost glabrous, as in the type form of the culture, but in marked contrast to some of the other mutations. This plant was self-sterile, but produced abundant seeds when pollinated with typical *O. pratincola*.

The Lexington C culture which was grown to maturity in 1913 included, besides the 9 plants from the first sowing and the mutations and suspected mutations of the second sowing, all the plants from two pans in which there appeared to be no variation. There were 72 of these plants, nos. 23–94.[18] When they matured two mutations were found which had not been detected in the early seedling stages. With these two exceptions, the plants were absolutely uniform among themselves, and exactly the same as Lexington A, Lexington B, and Lexington E. (Of each of these three strains 30 plants were grown to maturity.) The two mutations were not alike and were different from any of the other new types which had been obtained. Both, however, were almost

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[18] The culture numbers of these plants are all given here in order to avoid lengthy repetition in subsequent papers which will deal with the same strains. It may be well to explain that every plant in the writer's garden is designated by the name of the strain (for which a number has often been substituted) followed by a succession of numbers which indicate the pedigree and number in the culture of each individual. Subscripts are used when it is wished to distinguish between sister plants grown in different years, or to indicate the years in which the successive generations were grown. "Lexington C-11_{13}," for example, would be the complete designation of the plant of mut. *nummularia* which is shown in fig. 6. Plants of the F_2 generation, grown in 1914, would be "Lexington C-11_{13}–1_{14}," "Lexington C-11–2," etc.

self-sterile. No. 28 was half as high as typical plants of the culture; the leaves were broader and white-margined; the buds were smaller and closely viscid-puberulent with a hair type which does not occur in the typical form; the branching differed in that there were numerous inflorescence-bearing tertiary branches. No. 57 (mut. *nitida*) was slightly taller than no. 28, almost simple, with leaves narrower than in the typical form, upwardly rolled parallel to the mid-vein, very glistening, nearly twice as thick as in normal

FIG. 7.—A, *Oenothera pratincola* mut. *nummularia*, Lexington C-21; B, *Oenothera pratincola* (typical), Lexington C-16; the 2 plants are of the same age and were grown under identical conditions; note particularly the difference in the branching.

plants, and very brittle. A few seeds were obtained from this plant by self-pollination, but they did not germinate.

The 729 plants of Lexington C which were grown in 1913 yielded in all 6 different mutations. All of them except mut. *nitida* and mut. *nummularia* were infertile or nearly so to their own pollen. The latter type, in spite of the fact that it was unwittingly subjected to very unfavorable conditions, produced seeds from which a second generation has been grown. For fear of losing the 6 original plants, they were planted in the center bed of the greenhouse when the rest of the culture was transferred to the garden. Before it was realized how much their development was being retarded by the extreme heat in the greenhouse, it was too late to move them again with any prospect of success. Three plants died after they had begun to flower, but before any seeds were ripe.

The characters of mut. nummularia

A few plants of typical *O. pratincola* which were kept in the greenhouse with the mutation served to show that there are distinct differences in the habits of growth of the two types, when they are grown under identical conditions. This fact will be apparent from fig. 7, in which two sister plants of the same age are shown. It will be noticed that the stature of the mutation is less than that of the parent type, but that the lateral branches are more numerous and more densely leafy. A thoroughgoing comparison of the two types cannot be made until the cultures of 1914 shall have grown to maturity out of doors. The more striking contrasting characters, however, are the following:

In *O. pratincola*	In mut. *nummularia*
The early seedling leaves are ovate.	The early seedling leaves are orbicular.
The stem leaves are reflexed.	The stem leaves are involute.
The lower leaves of the lateral branches are ovate-lanceolate.	The lower leaves of the lateral branches are broadly ovate.
The ovary and calyx are sparsely pilose (sometimes almost glabrous).	The ovary and calyx are closely and finely pubescent.

In *O. pratincola*	In mut. *nummularia*
The hairs of the calyx segments and hypanthium are about 1 mm. long and all belong to the thick-walled, acute type with multicellular, tuberculate bases.	The hairs of the calyx segments and hypanthium are less than 0.5 mm. long and belong to two types: (1) acute, thick-walled hairs without multicellular, tuberculate bases, and (2) thin-walled, round-pointed clavate or cylindrical hairs.
The calyx segments separate in pairs.	The four calyx segments remain united when the flower opens.

The difference in the rupture of the calyx is shown in fig. 8. The writer is inclined to believe that the clear-cut qualitative distinction between the calyx pubescence of the parent form and that of the mutation will provide an absolute criterion for determining whether or not mut. *nummularia* marks an evolutionary advance over *O. pratincola.* A priori it seems to be a safe prediction that mut. *nummularia* will prove to be a progressive mutation of even more striking individuality than *O. gigas.*

It is unfortunate that data on reciprocal crosses between *O. pratincola* and mut. *nummularia* will not be available until next year. The first flowers of the original mutations were, of course, self-pollinated, and further work was prevented by the loss of the plants. This year (1914) the writer has numerous plants of mut. *nummularia* (primary mutations as well as F_1 plants) with which to make the necessary crosses.

The heritability of mut. nummularia

The three individuals of mut. *nummularia* which bore seeds were nos. 2, 17, and 21. Even these, however, wilted and dried up while still in flower, so that very few capsules were obtained. As in the case of many somewhat self-sterile Oenotheras, the capsules were small and contained few good seeds. From each of several capsules only one or two seeds were obtained, and the best had but 30, whereas a large capsule of typical *O. pratincola* contains well over 300. Until plants of the mutation shall have developed under more favorable conditions than those to which the first season's plants were subjected, it will be impossible to say whether or not mut. *nummularia* is really as nearly self-sterile as this comparison would indicate. At any rate, only 403 seeds, many of them obviously too unripe to germinate, were obtained from 3 plants of the mutation. The seeds have given an F_1 progeny of 135 plants which is now (April 1914) in the early seedling stage.

The F_1 generation from mut. *nummularia* consists in part of plants which exactly reproduce the parental type and in part of secondary mutations. At the time this article is being written the plants are still young, but it is nevertheless clear (1) that the F_1 generation includes no typical *O. pratincola;* (2) that the secondary mutations (with one possible exception) are narrower leaved than *O. pratincola* and therefore even more sharply distinguished from mut. *nummularia* than the latter is from *O. pratincola;* and (3) that all of the secondary mutations (again with the single exception noted above) appear to be quite identical with certain primary mutations which have appeared simultaneously with mut. *nummularia* in various cultures of typical *O. pratincola.*

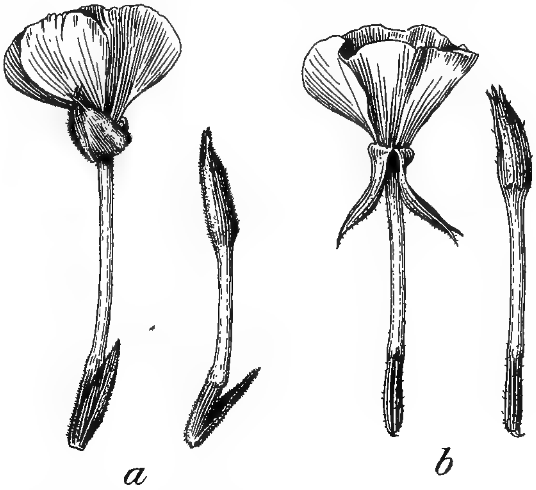

FIG. 8.—Flowers and buds of (*a*) *Oenothera pratincola* mut. *nummularia*, and (*b*) typical *O. pratincola*, showing especially the difference in the rupture of the calyx.

The secondary mutations fall into three well marked groups which have been called mut. *tortuosa*, mut. *rubricentra*, and mut.

subulata. It is of course impossible to establish absolute identities among seedling plants of types which have not yet been seen in flower. Consequently the F_1 progeny of mut. *nummularia* are classified either as true to type or as secondary mutations in table I, which shows the composition of the cultures now under observation.

TABLE I

COMPOSITION OF F_1 GENERATION OF MUT. *nummularia* (SEEDLING STAGE)

Parent	Number of seeds	Total plants	Mut. *nummularia*	Secondary mutations
Lex. C-2	15*	8	6	2
"	15*	6	5	1
"	30*	15	15	0
"	65	9	7	2
Lex. C-2 Total	125	38	33	5
Lex. C-17	39	14	12	2
Lex. C-17×C-21	20*	10	8	2
"	24*	2	2	0
"	11*	5	3	2
"	18*	5	5	0
"	64	25	15	10
Lex. C-17×C-21 Total ...	137	47	33	14
Lex. C-21	102	36	31	5
Grand total	403	135	109	26

* Indicates that the seeds were from one capsule.

Table I shows that only 34 per cent of the seeds of mut. *nummularia* germinated. In order to obtain as many plants as possible, a large number of seeds were counted into the seed pans which seemed too immature to germinate; 65 such seeds, planted by themselves, produced 9 plants. Part of the seeds planted were obtained from self-pollinated capsules, others from capsules which had been cross-pollinated. Table I shows that the progeny from the self-pollinated seeds includes secondary mutations and typical *nummularia* plants in the ratio 1:6. The same ratio for the progeny from cross-pollinated seeds is about 1:3.2. Although the difference in the ratio seems very marked, it may be due to the fact that the germination was poor and the cultures small.

Some of the progeny of two of the parents from which F_1 plants were obtained (Lexington C-17 and Lexington C-21) are shown in figs. 9–11. In fig. 9, no. 3 is a young specimen of mut. *tortuosa*, as yet only vaguely suggesting the characters which give this mutation its name. The other 5 plants are typical mut. *nummularia*, comparable in state of development with nos. 1 and 2 in fig. 3, and nos. 10 and 11 in figs. 5 and 6. Fig. 10 shows three of the types which are included in the F_1 cultures from mut. *nummularia*. Nos. 8 and 15 are characteristic plants of mut. *tortuosa;* nos. 13 and 16 are mut. *rubricentra;* nos. 35 and 36 are typical mut. *nummularia*. In order to show the striking uniformity of the *nummularia* plants 6 more of them are shown in fig. 11.

The frequency of mut. nummularia

In order to determine the frequency with which *O. pratincola* gives rise to mut. *nummularia*, large cultures were grown in the greenhouse during the winter of 1913–14. As usual, the seeds were sown on sterilized soil and transplanted to seed pans as soon after germination as circumstances permitted.[19] Remaining wild seeds of the original collections gave additional F_1 cultures of Lexington C, A, B, and E. F_1 cultures were also grown from the wild seeds of Lexington F, G, H, and I, which had not been previously planted. It will be remembered that mutations had been detected during the first year of cultivation only in Lexington C, and in this strain only because of the accidental application of the method of selective germination. The other strains were found to be quite as mutable as Lexington C when all of the seedlings were retained until old enough to show their distinctive characteristics. In addition to the F_1 cultures, F_2 cultures were grown from seeds of 8 self-pollinated F_1 sister plants of Lexington C, 1 self-pollinated plant of Lexington A, and 2 self-pollinated plants of Lexington B. These F_2 progenies from guarded seeds were found to contain approximately the same proportion of mutations as the F_1 progenies from unguarded wild seeds.

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[19] The writer wishes to express here his appreciation of Mr. MARTIN BILON'S painstaking and efficient care of the germination pans and the young seedlings.

FIG. 9.—F_1 progeny of *Oenothera pratincola* mut. *nummularia*, Lexington C-17; the plant in the upper left-hand corner, Lexington C-17-3, is *O. pratincola* mut. *tortuosa*, here occurring as a secondary mutation, but seemingly the same as one of the very rarest primary mutations of *O. pratincola;* the other plants are typical examples of mut. *nummularia*.

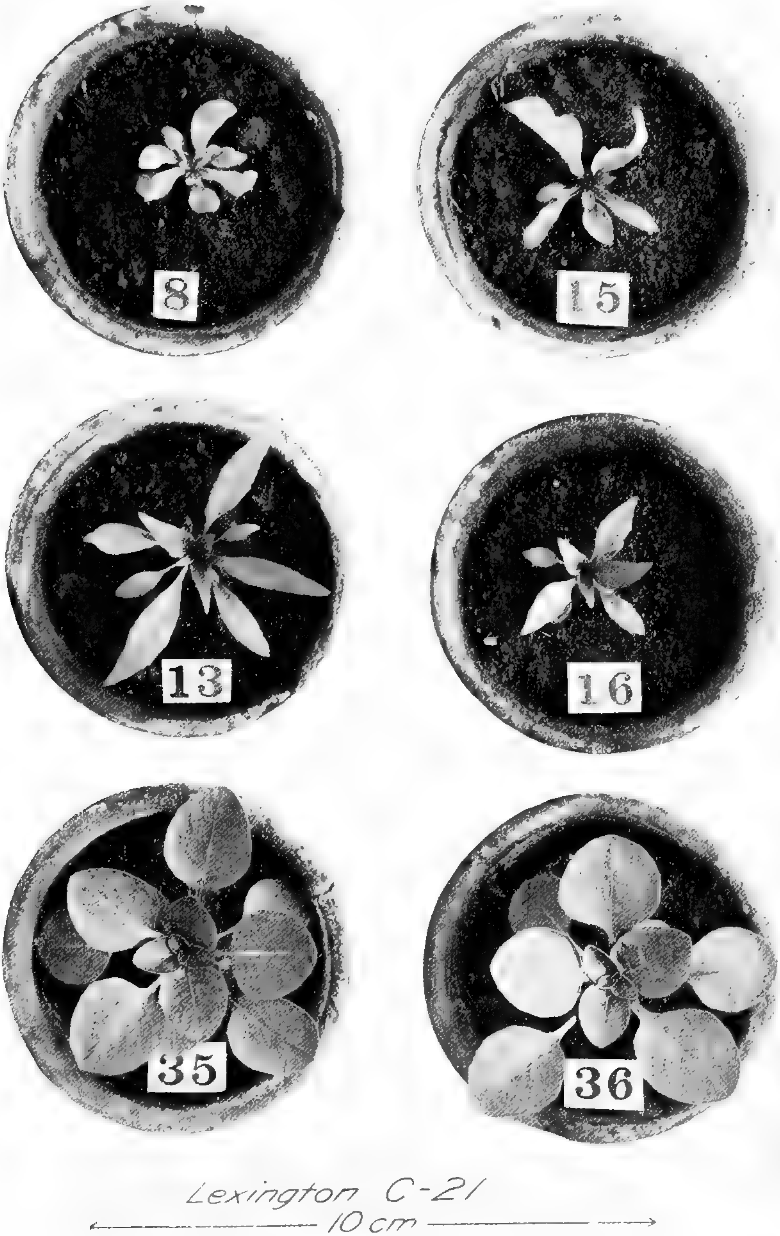

FIG. 10.—F_1 progeny of *Oenothera pratincola* mut. *nummularia*, Lexington C-21; the 2 upper plants, Lexington C-21–8 and C-21–15, are mut. *tortuosa;* the 2 in the middle row, C-21–13 and C-21–16, are mut. *rubricentra;* the 2 below are mut. *nummularia;* the plants shown in this cut are three weeks older than those shown in fig. 9.

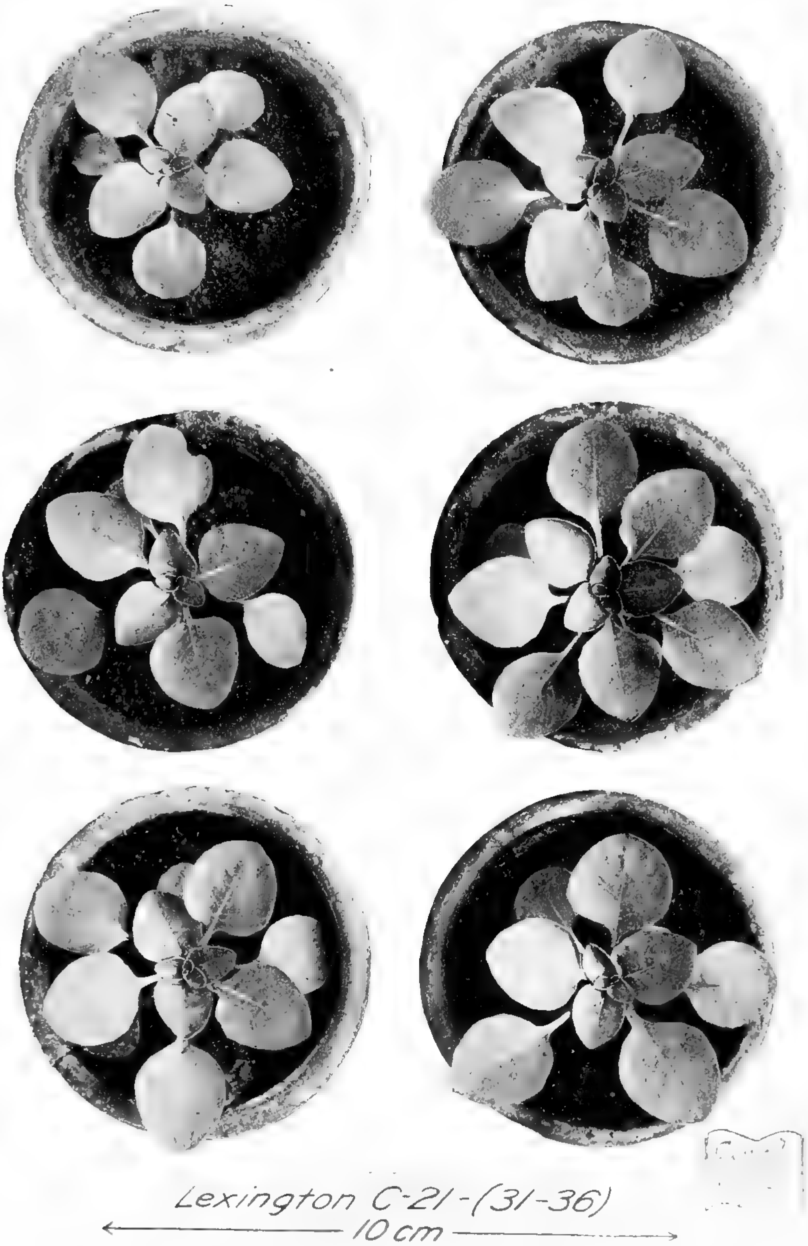

FIG. 11.—F_1 progeny of *Oenothera pratincola* mut. *nummularia;* typical examples of mut. *nummularia*, sister plants of those shown in fig. 10, of the same age.

Data in regard to the frequency of mut. *nummularia* in all the strains of *O. pratincola* except Lexington E are given in tables II–XI, and are summarized in table XII. Lexington E yielded striking mutations in both F_1 and F_2 generations, but they constituted an entirely different series of forms from those which were obtained from the other strains. In several respects the mutation phenomena presented by Lexington E were unique. It will be necessary, therefore, to defer an account of this strain until next year.

It will be noticed from the tables that a large number of seeds were planted capsule by capsule. The variation in number of seeds per capsule appears greater than it should, for in many cases the capsules had dehisced and lost part of their contents. In general, a capsule of *O. pratincola* contains 200–300 seeds.

TABLE II

ANALYSIS OF F_1 SEEDLING CULTURES OF "LEXINGTON C"

Culture	Seeds planted	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
2	1000	720	711	4 (nos. 10, 11, 17, and 21)	5
3	133*	101	93	0	8
4	130*	117	116	0	1
5	116*	111	106	0	5
6	88*	21	20	0	1
7	125*	20	20	0	0
8	162*	152	149	0	3
9	164*	143	140	0	3
10	237*	172	165	0	7
11	237*	223	211	1 (no. 123)	11
12	65*	35	35	0	0
13	217*	147	143	1 (no. 136)	3
14	200	156	153	0	3
15	200	154	152	0	2
16	147*	96	93	0	3
17	200	60	58	0	2
18	200	155	152	2 (nos. 150 and 151	1
19	200	98	95	0	3
20	200	130	124	2 (nos. 156 and 160)	4
21	200	112	109	1 (no. 162)	2
Total	4,221	2,923	2,845	11	67

* Indicates seeds from the same capsule.

TABLE III

ANALYSIS OF F_2 SEEDLING CULTURES OF "LEXINGTON C"

Parent	Culture	Number of seeds	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
Lex. C-5	1	244*	151	150	0	1
"	2	208*	155	154	0	1
"	3	190*	140	138	1 (no. 3)	1
Lex. C-5	Total	642	446	442	1	3
Lex. C-6	1	116*	41	39	0	2
"	2	106*	41	40	0	1
"	3	58*	31	27	0	4
"	4	41*	35	35	0	0
"	5	21*	10	10	0	0
"	6	14*	13	13	0	0
Lex. C-6	Total	356	171	164	0	7
Lex. C-15	1	196*	116	115	1 (no. 1)	0
"	2	233*	115	115	0	0
"	3	173*	106	106	0	0
"	4	134*	123	122	1 (no. 2)	0
"	5	28*	12	12	0	0
"	6	31*	12	12	0	0
"	7	48*	41	41	0	0
"	8	43*	32	31	1 (no. 11)	0
"	9	12*	9	9	0	0
"	10	17*	15	15	0	0
"	11	31*	15	15	0	0
Lex. C-15	Total	946	596	593	3	0
Lex. C-22	1	148*	122	119	0	3
"	2	203*	169	157	1 (no. 9)	11
"	3	172*	147	142	1 (no. 20)	4
"	4	225*	189	184	1 (no. 21)	4
"	5	250*	196	191	0	5
Lex. C-22	Total	998	823	793	3	27
Lex. C-36	1	182*	142	141	0	1
"	2	208*	150	147	0	3
"	3	210*	159	157	0	2
"	4	231	181	179	0	2
"	5	147*	99	96	0	3
Lex. C-36	Total	978	731	720	0	11
Lex. C-52	1	215*	148	146	1 (no. 1)	1
"	2	118*	100	100	0	0
"	2	189*	138	136	0	2
"	4	150*	75	73	1 (no. 28)	1
"	5	225*	173	173	0	0
Lex. C-52	Total	897	634	628	2	4

TABLE III—*Continued*

Parent	Culture	Number of seeds	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
Lex. C-72	1	192*	171	165	1 (no. 6)	5
"	2	223*	180	179	0	1
"	3	235*	187	186	0	1
"	4	279*	242	241	0	1
"	5	280*	230	225	0	5
Lex. C-72	Total	1,209	1,010	996	1	13
Lex. C-91	1	185*	146	144	2 (nos. 1 and 2)	0
"	2	284*	245	243	1 (no. 4)	1
"	3	245*	172	171	0	1
"	4	267*	125	121	0	4
"	5	316*	198	195	0	3
"	6	337*	300	293	5 (nos. 39, 40, 42, 43, 44)	2
"	7	242*	187	181	0	6
Lex. C-91	Total	1,876	1,373	1,348	8	17
Eight F_1 plants	Grand total	7,902	5,784	5,684	18	82

* Indicates seeds from the same capsule.

TABLE IV

Analysis of F_1 seedling cultures of "Lexington A"

Culture	Seeds planted	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
2	341*	66	59	0	7
3	405*	129	118	2 (nos. 44 and 45)	9
4	337*	60	53	2 (nos. 53 and 54)	5
Total	1,083	255	230	4	21

* Indicates seeds from the same capsule.

TABLE V

Analysis of F_2 seedling cultures of "Lexington A"

Parent	Culture	Number of seeds	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
Lex. A-5	1	119*	76	73	0	3
"	2	200	115	110	0	5
"	3	200	118	115	2 (nos. 9 and 11)	1
"	4	200	127	122	1 (no. 15)	4
Lex. A-5	Total	719	336	420	3	13

* Indicates seeds from the same capsule.

TABLE VI

ANALYSIS OF F_1 SEEDLING CULTURES OF "LEXINGTON B"

Culture	Seeds planted	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
2	149*	107	95	0	12
3	324*	188	175	0	13
4	247*	107	97	0	10
5	200*	106	101	0	5
Total	920	508	468	0	40†

* Indicates seeds from the same capsule.

† Of the 40 mutations and suspected mutations, 36 were merely smaller plants than the average, selected in the expectation that some might prove to be dwarfs.

TABLE VII

ANALYSIS OF F_2 SEEDLING CULTURES OF "LEXINGTON B"

Parent	Culture	Number of seeds	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
Lex. B-1	1	184*	157	157	0	0
"	2	269*	142	137	0	5
"	3	264	221	215	1 (no. 8)	5
"	4	195*	154	152	1 (no. 12)	1
Lex. B-1	Total	912	674	661	2	11
Lex. B-2	1	106*	72	68	0	4
"	2	250*	147	142	2 (nos. 26, 27)	3
"	3	284*	176	171	0	5
"	4	111*	82	80	0	2
"	5	113*	94	92	0	2
Lex. B-2	Total	864	571	553	2	16
Two F_1 plants	Grand total	1,776	1,245	1,214	4	27

* Indicates seeds from the same capsule.

TABLE VIII

ANALYSIS OF F_1 SEEDLING CULTURES OF "LEXINGTON F"

Culture	Seeds planted	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
1	92* (large, immature)	68	62	1 (no. 1)	5
2	139* (mature)	34	31	0	3
Total	231	102	93	1	8

* Indicates seeds from the same capsule.

TABLE IX

ANALYSIS OF F_1 SEEDLING CULTURES OF "LEXINGTON G"

Culture	Seeds planted	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
1	87* (very large, immature)	25	25	0	0
2	50* (large, immature)	17	17	0	0
3	285*	157	152	0	5
4	160	140	139	0	1
5	159*	136	133	2 (nos. 47, 49)	1
6	152*	95	93	0	2
7	187*	153	152	0	1
8	144*	86	80	0	6
9	120*	106	99	0	7
10	197*	157	154	1 (no. 54)	2
11	133*	98	97	0	1
12	147*	114	110	1 (no. 52)	3
Total	1,821	1,284	1,251	4	29

* Indicates seeds from the same capsule.

TABLE X

ANALYSIS OF F_1 SEEDLING CULTURES OF "LEXINGTON H"

Culture	Seeds planted	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
1	301*	152	145	2 (nos. 3 and 4)	5
2	157*	78	76	0	2
Total	458	230	221	2	7

* Indicates seeds from the same capsule.

TABLE XI

ANALYSIS OF F_1 SEEDLING CULTURES OF "LEXINGTON I"

Culture	Seeds planted	Total plants	Typical	Mut. *nummularia*	Other muts. and suspected muts.
1	125*	57	53	0	4
2	266*	147	145	1 (no. 13)	1
3	244* (immature)	64	61	2 (nos. 14 and 15)	1
Total ...	635	268	259	3	6

* Indicates seeds from the same capsule.

TABLE XII

SUMMARY OF TABLES II–XI, SHOWING THE FREQUENCY WITH WHICH *O. pratincola* GIVES RISE TO MUT. *nummularia*

Strain	Generation	Number of seeds	Number of plants	Germination per cent	Number of mut. *nummularia*	Ratio of mut. *nummularia* to seeds planted	Ratio of mut. *nummularia* to total plants
Lex. A ..	F_1	1083	255	23.5	4	1:271	1:64
" ..	F_2	719	436	60.6	3	1:240	1:145
Lex. A ..	F_1 & F_2	1,802	691	38.4	7	1:257	1:99
Lex. B ..	F_1	920	508	55.2	0		
" ..	F_2	1776	1245	70.1	4	1:444	1:311
Lex. B ..	F_1 & F_2	2,696	1,753	65.0	4	1:674	1:438
Lex. C ..	F_1	4221	2923	69.3	11	1:384	1:266
" ..	F_2	7902	5784	73.2	18	1:439	1:321
Lex. C ..	F_1 & F_2	12,123	8,707	71.8	29	1:418	1:300
Lex. F ..	F_1	231	102	44.2	1	1:231	1:102
Lex. G ..	F_1	1,821	1,284	70.5	4	1:455	1:321
Lex. H ..	F_1	458	230	50.2	2	1:226	1:115
Lex. I...	F_1	635	268	42.2	3	1:212	1:89
All......	F_1	9,369	5,570	59.5	25	1:375	1:223
"	F_2	10,397	7,465	71.8	25	1:416	1:299
All......	F_1 & F_2	19,766	13,035	66.0	50	1:395	1:261

In all, there were 19,766 seeds sown of the 7 strains which gave rise to mut. *nummularia*. They gave 13,035 seedlings, of which 5,570 belonged to F_1 and 7,465 to F_2 progenies. The average germination of the F_1 seeds was 59.5 per cent, or 58 per cent if the 1000 seeds of Lexington C sown in the winter of 1912–1913 are not figured in. Most of the F_1 seeds were over a year old when they were planted. The germination of the F_2 seeds, which were sown soon after they were harvested, was 71.8 per cent. Inspection of table XII shows the remarkable fact that the ratio of mut. *nummularia* to seeds planted was nearly identical for the F_1 and F_2 progenies, 1:375 in the one case, 1:416 in the other, but that the ratio of *nummularia* mutations to plants showed a variation roughly commensurate with the difference in germinability between the F_1 and F_2 seeds. In other words, the mortality among the year-old F_1 seeds appears to have been largely confined to seeds of typical *O. pratincola*. The ratio of *nummularia* mutations to seeds planted is seen from table XII to be reasonably constant for all 7 strains in both the F_1 and F_2 generations. The ratio of mutations to total plants, however, varies between wide limits, and in every case a low percentage of germination is associated with a high frequency of mutation. The F_1 progeny of Lexington A, for example, included 4 individuals of mut. *nummularia* among 255 plants, a ratio of 1:64. These 255 plants, however, were obtained by sowing 1,083 seeds, of which only a small proportion (23.5 per cent) germinated. There seems no escape from the conclusion that the percentage of germinable seeds of mut. *nummularia* had increased by virtue of the greater mortality among the seeds of typical *O. pratincola*.

The evolutionary significance of differential mortality is too obvious to require any lengthy discussion. Mut. *nummularia* has a distinctly greater survival value than its parent when subjected to conditions which delay germination. It has already been shown that mut. *nummularia* has an enormously greater chance to survive than typical *O. pratincola* when subjected to certain unfavorable soil conditions. These facts should be carefully weighed by critics of the mutation theory who persist in assuming, as a matter of course, that mutations would have no chance to survive in competition with the more numerous typical plants. De Vries[20] has already shown that the percentage of mutation in a culture of *O. Lamarckiana* from seeds 5 years old was 40 per cent instead of the usual 6 per cent. In his comment on this remarkable result he states that in general the seeds of the mutation remain germinable longer than those of typical *O. Lamarckiana*, and suggests that it might be possible to make use of differential mortality to increase the proportion of mutations in seeds, and thereby to facilitate the discovery of the mutations. The writer unconsciously put this suggestion to a test at the time mutations

[20] De Vries, H., Die Mutationstheorie 1:186. 1901.

were first found in *O. pratincola*. HUNGER[21] has recently recorded observations on selective mortality in the seeds of *O. Lamarckiana* which can only be interpreted as showing that the mutations of this species have decidedly a greater survival value than the parent form.

It is often remarked that the Onagras are not most usually found in undisturbed habitats with other native plants, but rather as weeds in fields and waste places, among the aliens of our flora. Wherever the soil is disturbed, as by plowing, road-making, excavating, they are frequently found in large numbers. They often dominate the flora on made land and on new railroad embankments, but are for the most part replaced by other weeds when the soil ceases to be disturbed at intervals. A fallow field which contains many Onagras for a season or two after cultivation is discontinued will thereafter contain fewer each year. If again plowed, it will apparently be restocked by the germination of seeds which have lain dormant, perhaps for years. Selective mortality among dormant seeds might result in such a field being restocked with plants among which mutations would be unexpectedly numerous.

The most interesting fact shown by table XII is that the frequency of mut. *nummularia* cannot correspond with any Mendelian ratio except that of a tetrahybrid splitting in the ratio 255:1. In the case of a number of progenies, to be sure, the ratio of mutations to plants more nearly approximates the trihybrid ratio 63:1, but it has already been shown that in each such instance the high mutation ratio is associated with a low percentage of germination. When the ratio of mutations to seeds is dealt with, there is no case of an approximation to the 63:1 ratio. The data of table XII, recalculated, are stated in table XIII in such form as to show that no single progeny was large enough to prove that the 255:1 ratio might not be the true one. On the contrary, the data afford no reason to believe that the mutation ratio is 255:1. It may be because of the smallness of the cultures that no single progeny shows a significant deviation from this ratio.

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[21] HUNGER, F. W. T., Recherches expérimentales sur la mutation chez *Oenothera Lamarckiana*, executées sous les tropiques. Ann. Jard. Buitenzorg 27:92–113. 1913.

Turning again to table XII, it is seen that the progenies might possibly be assembled in two groups, those with a mutation ratio of approximately 400:1 (group I of table XIII), and those with a ratio of about 250:1 (group II of table XIII). Testing separately the ratios from these groups (see table XIII), we find that the number of individuals in group II is too small to establish a significant deviation from the ratio for group I. (The difference is 0.18±0.13 per cent). It is therefore impossible to demonstrate either that the mutation ratio is or that it is not the same for all the progenies.

TABLE XIII

TEST OF THE FITNESS OF THE MUTATION RATIOS TO THE NEAREST MENDELIAN RATIO (235:1)

Culture	Group	Class 0 per cent not mut. *nummularia*	Class 1 per cent mut. *nummularia*	Number of seeds planted (n.)	Standard deviation ($\sigma=\sqrt{\%p_0 . \%p_1}$)	Mean error in per cent $\left(m=\frac{\sigma}{\sqrt{n}}\right)$	Expectation for each value of n if ratio is 255:1	Difference between observation and expectation
Lex. A-F_1	II	99.63	0.37	1,083	6.07	0.18	0.39±0.19	0.02±0.26
Lex. A-F_2	II	99.58	0.42	719	6.47	0.24	0.39±0.24	0.03±0.34
Lex. B-F_2	I	99.77	0.23	1,776	4.79	0.11	0.39±0.15	0.16±0.29
Lex. C-F_1	I	99.74	0.26	4,221	5.10	0.08	0.39±0.10	0.13±0.13
Lex. C-F_2	I	99.77	0.23	7,902	4.79	0.05	0.39±0.07	0.16±0.09
Lex. F-F_1	II	99.57	0.43	231	5.42	0.42	0.39±0.41	0.04±0.59
Lex. G-F_1	I	99.78	0.22	1,821	4.68	0.11	0.39±0.15	0.17±0.29
Lex. H-F_1	II	99.56	0.44	458	6.59	0.31	0.39±0.29	0.05±0.43
Lex. I-F_1	II	99.53	0.47	635	6.86	0.36	0.39±0.25	0.08±0.44
Group I		99.76	0.24	15,720	4.89	0.04	0.39±0.05	0.15±0.06
Group II		99.58	0.42	3,126	6.47	0.12	0.39±0.11	0.03±0.16
Groups I & II		99.75	0.25	18,846	5.00	0.04	0.39±0.05	0.14±0.06
Total		99.75	0.25	19,766	5.00	0.04	0.39±0.04	0.14±0.06

If we assume that it is justifiable to treat all of the progenies as one group, the numbers are then large enough to indicate, not however without considerable doubt, that the frequency of occurrence of mut. *nummularia* is not in accord with the tetrahybrid ratio 255:1, but with some ratio lying between 330:1 and 450:1. Of course we cannot assume that there is no mortality at all among the seeds which produce mut. *nummularia*. If in the 30 per cent of seeds *O. pratincola* which never germinate even when fresh the mortality among mutations and non-mutations were the same, then the mutation ratio would not significantly deviate from 255:1. It is obvious that a Mendelian explanation of the occurrence and frequency of mut. *nummularia* involves the assumption that each parent plant which gave rise to it was heterozygous with regard to at least four factors. Otherwise no segregate would occur with so low a frequency as 1:255. The following objections to a Mendelian explanation may be enumerated:

1. *O. pratincola* is probably almost invariably self-pollinated in a state of nature, for the anthers burst in contact with the receptive stigma the day before the flowers open. In a very few generations heterozygosis would be eliminated from a strain which had accidentally become crossed. Hybridization involving four factors, followed by several generations of self-pollination, would result in an F_2 with 6.25 per cent of homozygotes, an F_3 with 31.64 per cent, F_4 with 58.62 per cent, F_5 with 93.75 per cent, F_6 with 96.87 per cent, F_7 with 98.44 per cent, F_8 with 99.22 per cent, F_9 with 99.61 per cent, F_{10} with 99.80 per cent, etc. It would be utterly absurd to suggest that out of 8 wild mother plants growing far apart, selected at random, 7 were tetrahybrids.

2. An F_1 tetrahybrid would invariably show segregation in a 255:1 ratio. Out of its F_2 progeny, however, only one plant in 16 would be a tetrahybrid, and therefore only one F_2 plant in 16 could exhibit 255:1 segregation in the F_3. The other F_2 heterozygotes would be hybrids of a lower order. Some would segregate in the ratio 63:1, some in the ratio 15:1, and some in the ratio 3:1. It has already been pointed out (see tables III, V, and VII, summarized in tables XII and XIII) that every F_1 (that is, F_1 with regard to the wild mother plants from Lexington) plant of which seeds were planted either yielded a progeny containing no *nummularia* mutations, in which case the number was not large enough to be sure of getting this mutation, or else the only Mendelian ratio indicated as possible was 255:1. In all, 11 F_2 progenies were grown, of which only 2 failed to give the mutation. The only uncomplicated Mendelian explanation requires that in picking 11 mother plants at random from among 142 F_1 plants, 9 were selected from that one-sixteenth of the culture which was still heterozygous for four characters. It may be pointed out that among 142 plants, just 9 tetrahybrids might reasonably be expected. The chances

are infinitesimal that all 9 would be included among 11 plants chosen at random.

3. A tetrahybrid might give as many as 16 phaenotypes in the F_2. All of these would have a greater frequency than 1:255 except the pure recessive. We have seen that mut. *nummularia* cannot have a greater frequency than 1:255, and have also seen that it is not a pure recessive, for in the next generation after it originates it gives rise to several distinct types.

4. In the case of one F_2 progeny (Lexington C-91, see table III) from a single mother plant, 1,539 seeds from 6 capsules gave 3 specimens of mut. *nummularia*, whereas 337 seeds from one capsule gave 5. Such a result shows a frequency varying from 1:60 to 1:513 on capsules from the same spike. From a Mendelian standpoint it is practically impossible to explain such a result.

The mutation phenomenon in *O. pratincola* cannot be explained away by any reasonably plausible stretching of Mendelian theory. On the contrary, it seems obvious that mutation is quite a different process from hybrid segregation, although both processes may occur simultaneously.

Mut. *nummularia* is the only one of the mutations of *O. pratincola* the frequency of which has been determined. None of the others has been observed throughout the complete cycle from seed to seed and carried into a second generation. In tables II–XI all of the variants except mut. *nummularia* are thrown together as "other mutations or suspected mutations." In explanation of this mixed category, it is necessary to state that all unusually small or unusually large plants, regardless of whether or not they appeared otherwise different from the mass of the culture, were counted as "suspected mutations," in order to be sure that no such variation as a mut. *nanella* would be passed over. To judge from past experience, most of the "suspected mutations" will develop as quite normal plants. Consequently the mutability of *O. pratincola* is probably not as great as might be assumed from the tables.

Mut. Mummularia a discontinuous variation

Critics of DE VRIES' work on mutation in *Oenothera Lamarckiana* have not infrequently expressed skepticism as to whether or not the mutations were actually unconnected with the parent form by intermediates, which might have been overlooked in classifying the young seedlings. An endeavor has been made to forestall the same criticism of the writer's work on *O. pratincola* by the publication of a series of photographs showing some of the pans in which the mutations occurred. Each reader can judge for himself as to the discontinuity of the mutations from the rest of the plants. It is believed that no one has heretofore published so extensive a series of photographs representing random samples of cultures from which

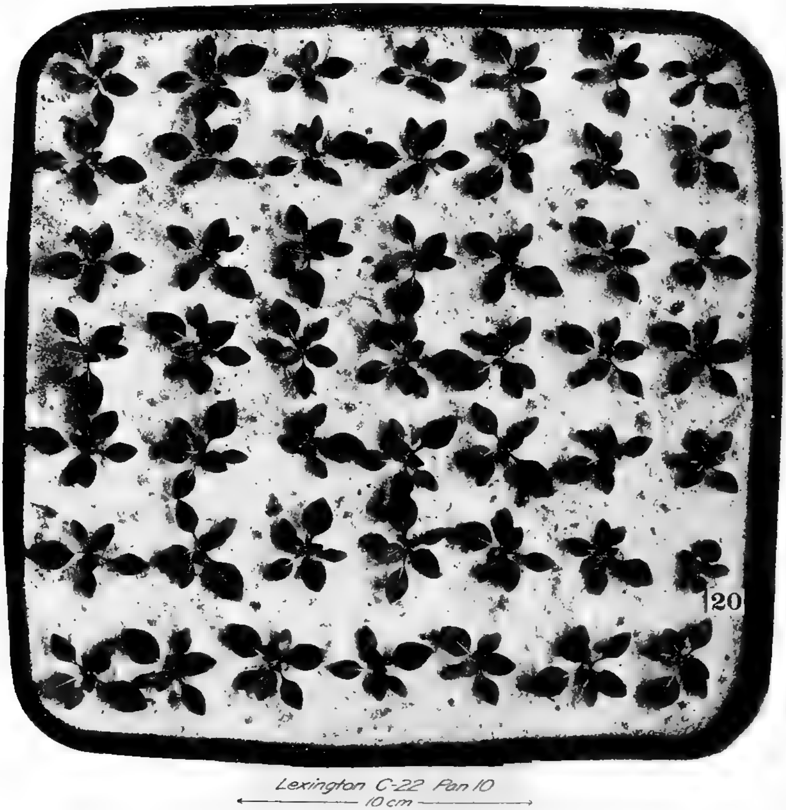

Fig. 12.—F_2 progeny of Lexington C, *Oenothera pratincola* (pan 10 of the progeny of C-22); the only mutation shown is C-22–20, mut. *nummularia;* the other plants are typical *O. pratincola.*

none of the seedlings had been discarded. It must be remembered that each pan is a fair sample of a whole culture, for the seedlings were pricked off when very small and were taken from the seed pan as they came, with no attempt at sorting.

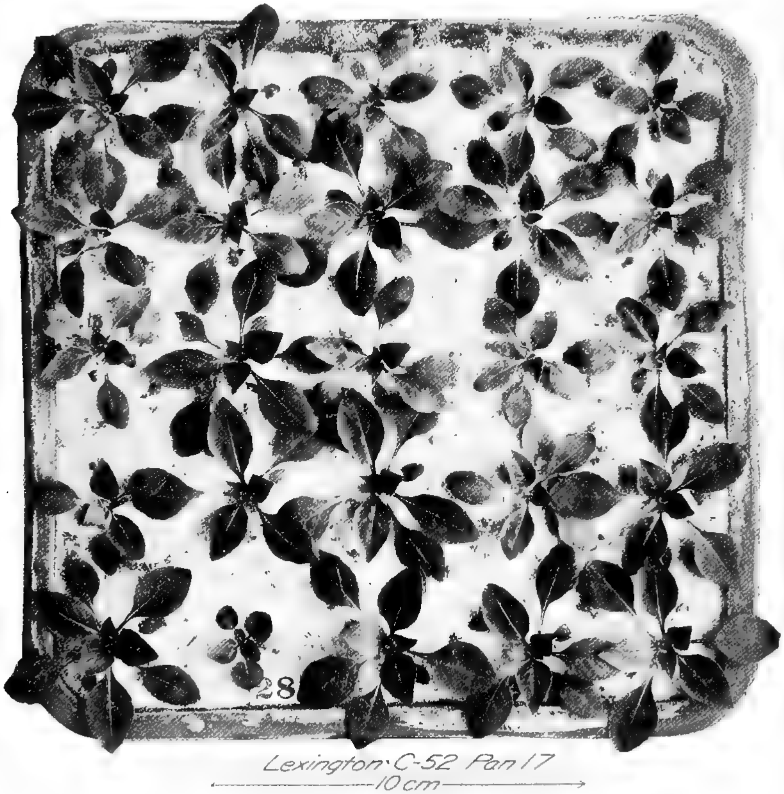

Fig. 13.—F_2 progeny of Lexington C, *Oenothera pratincola* (pan 17 of the progeny of C-52); one example of mut. *nummularia*, C-52-28, is shown; the remaining plants are typical.

Figs. 5, 6, 12, 13, 14, 15, and 17 show 7 of the 50 occurrences of mut. *nummularia* in cultures aggregating 13,035 plants. Three more of the original plants of this mutation are shown in figs. 3, 4, and 16. The figures showing entire pans should give a fairly clear idea of what the writer interpreted as fluctuating variation. It is believed that very few if any mutations escaped detection in the cultures of 1914. The two mutations of Lexington C (nos. 28 and 57) which passed muster as typical plants when the seedlings of 1913 were examined would probably not have been missed in the more searching scrutiny which the seedlings of 1914 underwent.[22] Although some of the mutations cannot be distinguished in the young seedling stage with ease, it is believed that the likelihood

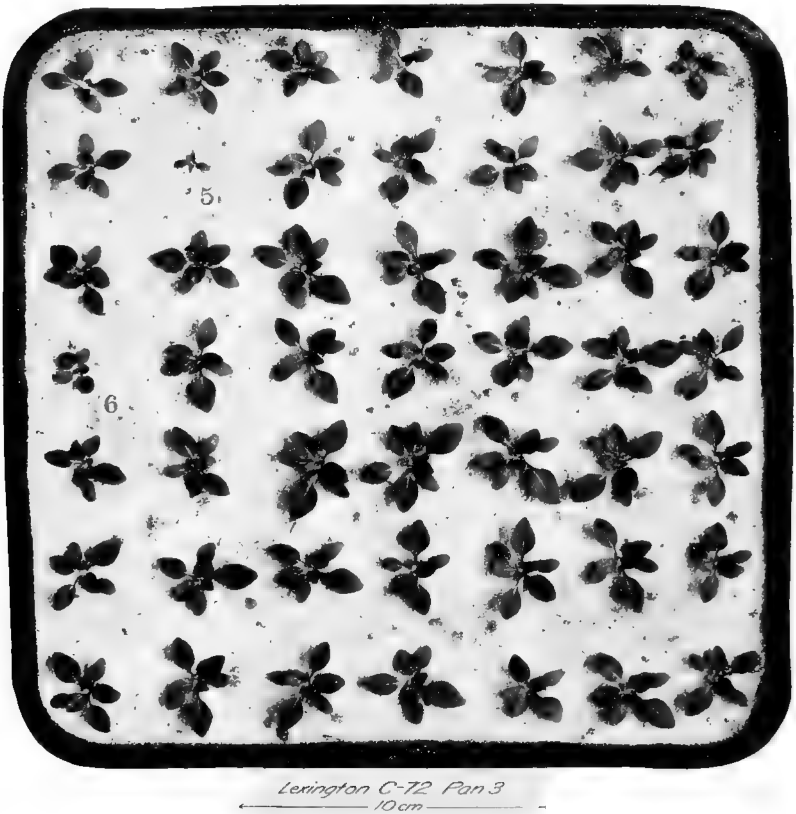

FIG. 14.—F_2 progeny of Lexington C, *Oenothera pratincola* (pan 3 of the progeny of C-72); two mutations are shown, mut. *subulata*, C-72-5, and mut. *nummularia*, C-72-6; the other plants are typical.

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[22] Mut. *nitida*, represented by Lexington C-57 in the cultures of 1913, occurred several times in 1914 and was detected in the young seedling stage in every case Nov. (1914).

of mistaking mut. *nummularia* for the parent type or for one of the other mutations is negligible. The orbicular seedling leaves are too striking a characteristic to be overlooked.

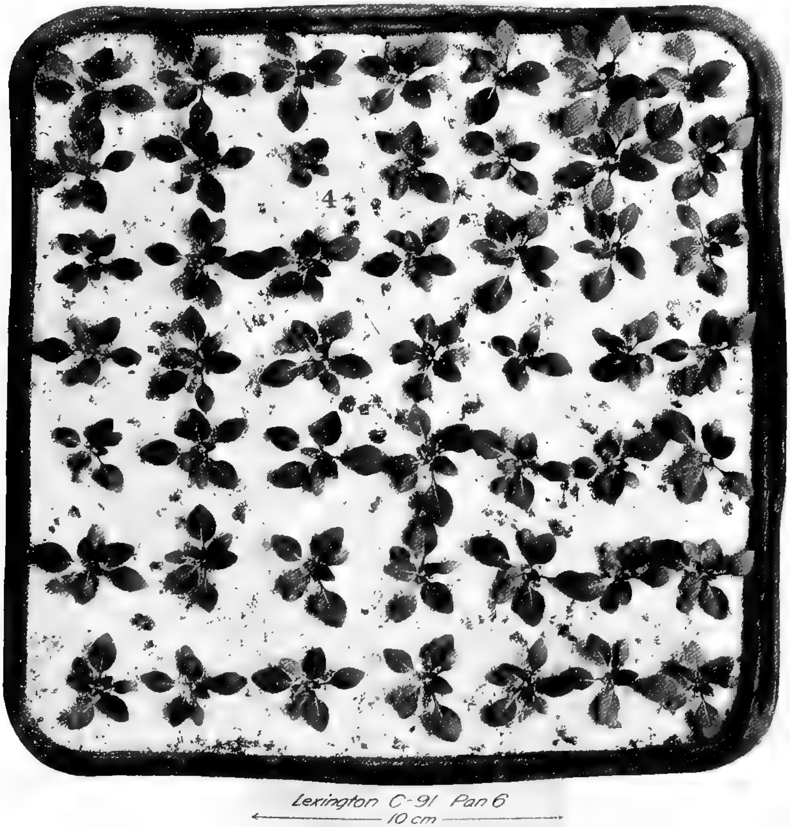

FIG. 15.—F_2 progeny of Lexington C, *Oenothera pratincola* (pan 6 of the progeny of C-91); one plant of mut. *nummularia* is shown, C-91-4; the other plants are typical.

The unlikeness of mut. nummularia and O. pratincola × O. numismatica

Before mut. *nummularia* had been found in F_2 progenies from guarded seed, it seemed possible that it might be an F_1 hybrid of *O. pratincola* with some other wild species, of which a few pollen

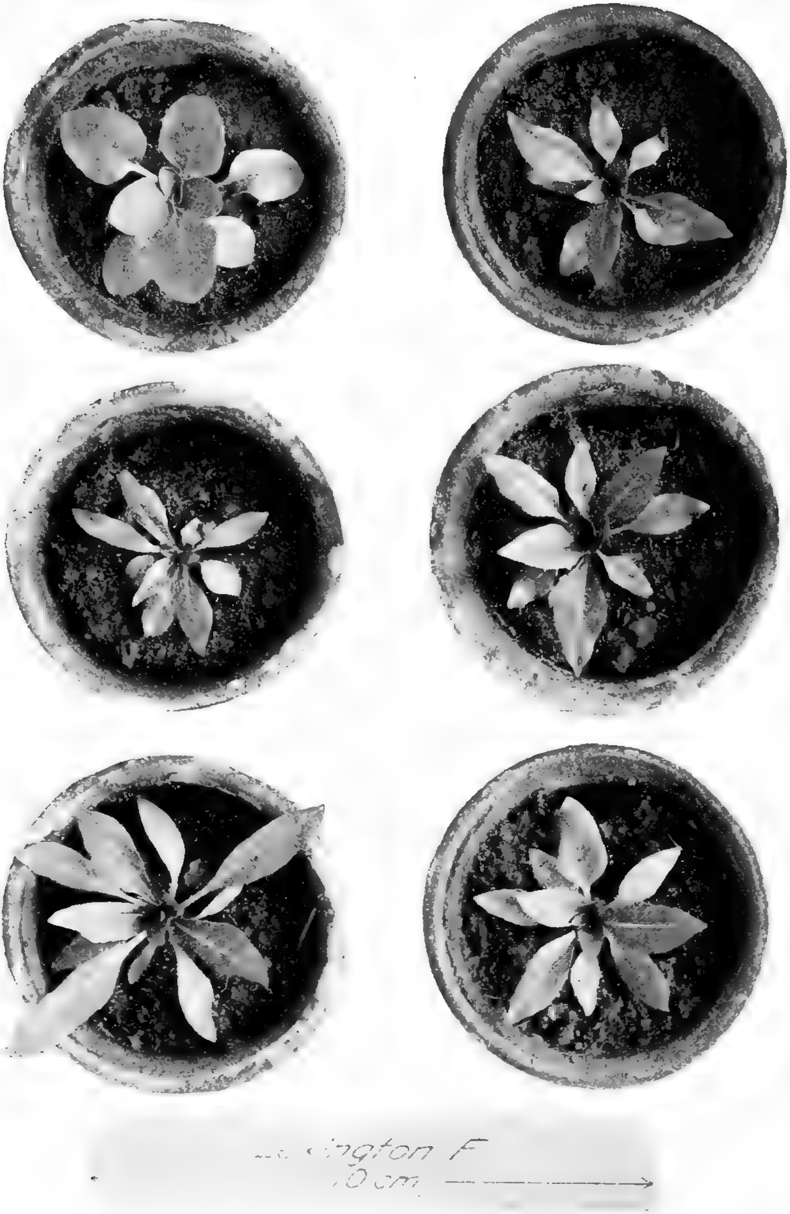

FIG. 16.—Mutations from the F_1 progeny of Lexington F, *Oenothera pratincola;* the plants are F-1, mut. *nummularia;* F-2, -4, -5, -6, mut. *rubricentra;* F-3, mut. *tortuosa* (?), taking the plants in order from the upper left-hand corner.

grains had accidentally reached the stigmas of the mother plants. This hypothesis was tested by crossing *O. pratincola* with *O. numismatica*. As already stated, these two species were the only Onagras which the writer found at Lexington. The latter, furthermore, is suspiciously similar in several characters to mut. *nummularia*, as may be seen by comparing the characters already recorded. The cross *O. pratincola* ♀ × *O. numismatica* ♂ was conspicuously fertile; 326 seeds from one capsule gave a culture of 222 plants, consisting

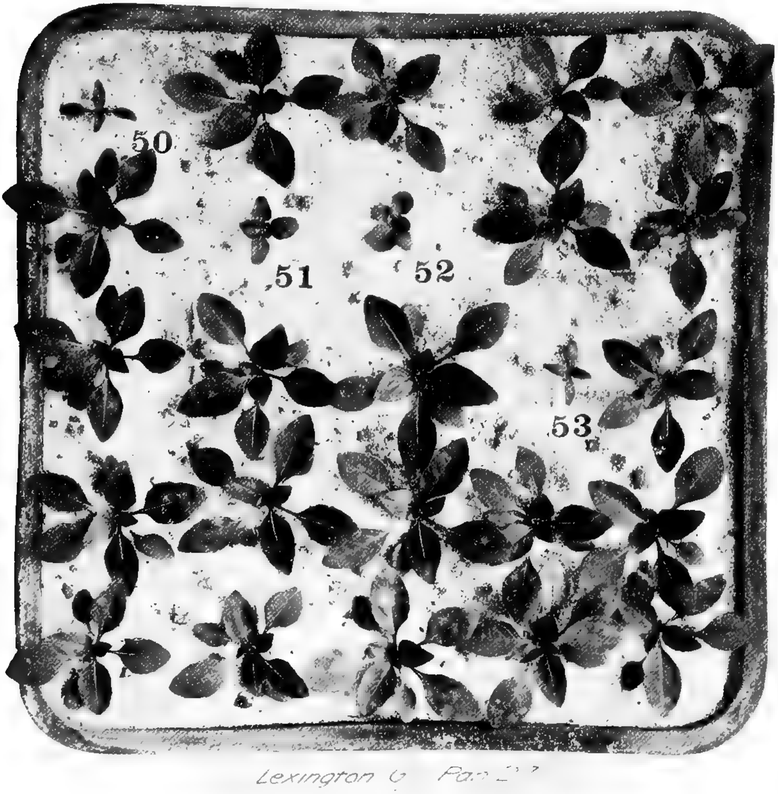

FIG. 17.—F_1 progeny of Lexington G, pan 27, *Oenothera pratincola;* four mutations are shown, G-50 and G-53, mut. *rubricentra;* G-51, mut. *nitida;* G-52, mut. *nummularia;* the other plants are typical *O. pratincola*.

of twin hybrids and one mutation. The solitary exception was broader leaved than the rest of the culture and is interpreted by the writer as the product of a cross between a mutated ♀ gamete, which if pollinated by *O. pratincola* would have yielded mut. *nummularia*, and a normal ♂ gamete of *O. numismatica*. This hypothesis will be tested later by appropriate crosses. It is clear that a cross between *O. pratincola* and *O numismatica* does not yield mut. *nummularia*, or anything resembling it, with greater frequency than does unhybridized *O. pratincola*. Perhaps *O. numismatica* is itself a mutation from *O. pratincola*, or a form which has segregated from the cross mut. *nummularia* × *O. pratincola*. One would expect the latter cross to occur rather often if, as seems to be the case, mut. *nummularia* itself is partially self-sterile. It seems not unlikely that in nature self-sterile or nearly self-sterile mutations may be perpetuated by effective cross-pollination, either as stable hybrids or as homozygous forms resulting from subsequent segregation. It is an interesting fact that although *O. pratincola* has a very high proportion of good pollen grains (90 per cent or more), mut. *nummularia* rarely has pollen which is 50 per cent perfect, and some anthers produce no good pollen at all.

Conclusions

1. *Oenothera pratincola*, a recently described small-flowered self-pollinating species from Kentucky, is in a mutating condition comparable with that of *O. Lamarckiana*.

2. The most striking of the mutations, *O. pratincola* mut. *nummularia*, occurred in strains derived from 7 wild mother plants out of 8 selected at random.

3. In two of these strains the mutation was found in both the F_1 and F_2 generations from the parent plant. In a third strain the mutation was found only in the F_2 generation, but a sufficient number of F_1 plants had not been grown to insure its detection in that generation.

4. Mut. *nummularia* appears to occur with a frequency of about one individual to each 300–400 seeds planted. The several progenies showed no significant variation in the mutation ratio.

5. The mutation ratio cannot be explained on Mendelian grounds.

6. Mut. *nummularia* is better adapted than the parent type to withstand influences unfavorable to germination. In every case where a progeny contained an unexpectedly large number of mutations, the germination was correspondingly poor.

7. Selective germination and differential mortality among dormant seeds may be important factors in natural selection.

8. Mutation is a distinct process from Mendelian segregation, and the phenomena exhibited by *Oenothera Lamarckiana*, *O. biennis*, and *O. pratincola* cannot be attributed to heterozygosis.

Bureau of Plant Industry
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THE TEST OF A PURE SPECIES OF ŒNOTHERA.

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By BRADLEY MOORE DAVIS.

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THE TEST OF A PURE SPECIES OF ŒNOTHERA.[1]

By BRADLEY MOORE DAVIS.

(*Read April 23, 1915.*)

There is probably no group of plants the genetic behavior of which has received so much study as the species of *Œnothera*. No group of plants is more prominently before the attention of experimental plant morphologists, and yet to many botanists it may appear that no group has yielded less of satisfaction. Among the workers with these forms there is the widest divergence of opinion, and of general conclusions there is little to show for the time that has passed since the appearance of "Die Mutationstheorie" in 1901 and the many years of study that De Vries devoted to the group previous to this date.

Can we find the point around which the difficulties cluster most thickly or from which the varied interpretations diverge most sharply? And, finding such a point can we formulate lines of experimentation that may clear the confusion of assumptions from which the various workers have proceeded to follow the lines of study that seemed to them to lead towards the light? To the writer the center of the difficulties lies in the fact that we have no accepted tests for the genetic purity of an *Œnothera* species.

By the genetic purity of a species we mean such a constitution of the germ plasm that a form is able to produce gametes of one type only for each sex. That is to say all male gametes of the form should have the same germinal constitution and thus be physiologically and morphologically equivalent, and all female gametes likewise should be of the same type. The male and female gametes may, however, differ in their respective effects upon the characters of a succeeding generation as shown by the marked differences exhibited by certain reciprocal crosses, for example, the reciprocals between *biennis* and *muricata,* or between *biennis* and *franciscana*

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[1] Genetical Studies on Œnothera—VI.

Reprinted from Proceedings American Philosophical Society, Vol. liv., 1915.

(De Vries '13, Davis '14). The zygotes of a pure species must be uniform since the gametes of each sex are respectively similar, and a pure species, to employ that convenient expression of Bateson's, is therefore homozygous.

It has generally been held that no further proof of the genetic purity of a species is necessary than the established fact that it will "breed true," and I venture to believe that at present most workers among the œnotheras regard this test as entirely sufficient to establish the character of any material with which they work. If any line of *Œnothera* breeds true in large cultures it is confidently regarded as homozygous. Should a line fail to breed true to any considerable degree it is stamped as a hybrid if the investigator inclines towards the methods of analysis characteristic of the Mendelian school. Those who believe in mutations are so fully content with this test that to them a form need breed only reasonably true to pass as a pure species and the departures from the type, called mutations, are interpreted as due to modifications of the germ plasm not, however, the result of hybridism.

If a line of *Œnothera* fails to breed true to a very considerable degree and thus becomes suspected of a hybrid constitution, few workers would think of using it as favorable material for experimental studies to test the mutation theory. It is the lines which breed reasonably true that chiefly form the subjects of *Œnothera* discussions with reference to the theory of mutation. Such a line is the *Lamarckiana* of De Vries's cultures which when grown in large numbers in selfed families appears uniform except for certain small proportions of individuals, "mutants," which stand out clearly from the mass with distinctive characters that are readily recognized and may be clearly described. It is important to note that these new types are not connected by intergrading forms with the parent *Lamarckiana* and that they appear in successive generations of *Lamarckiana* with certain degrees of regularity.

More impressive than this history of *Lamarckiana* which has flowers open-pollinated, and consequently likely in Nature to have been crossed by insects, is the behavior reported for certain lines of *Œnothera* with flowers close-pollinated in the bud, a condition that obviously gives their own pollen the first chance to function and thus greatly reduces the probabilities of cross-pollination. Such a plant is the *biennis* of Holland and other parts of Europe, a type of especial interest not only for its clear morphological characters but also because there is good reason for believing the line to be very old. This plant forms a large population in Holland with no near relatives and must have lived there for many years to have so thoroughly established itself. Indeed it seems probable that this *Œnothera,* the Dutch *biennis,* has come down to us essentially unchanged from the times of Linnæus who gave us its name. We know of no plant better representative of a species of *Œnothera* and we know of no *Œnothera* which better satisfies the generally accepted requirement that a species should "breed true."

Œnothera biennis L. in large cultures comes so true that hundreds of plants may be grown without finding a single departure from the type. Yet Stomps ('14) in large cultures of selfed lines from a single wild plant collected in 1905 discovered that this Dutch *biennis* throws occasional marked variants ("mutants") and he described a *biennis semi-gigas* with the triploid number of chromosomes (21), a dwarf type *biennis nanella,* and a color variety *biennis sulfurea* with pale yellow petals. De Vries ('15) at once took up the study of certain of the lines established by Stomps and grew cultures which totaled 8,500 plants. Among these were 4 plants of *biennis semi-gigas* about 0.05 per cent., 8 plants of *biennis nanella* about 0.1 per cent., and 27 plants of *biennis sulfurea* about 0.3 per cent. Since the percentages from *Lamarckiana* are for *semi-gigas* 0.3 per cent. and for nanella 1 to 2 per cent. it should be noted that with respect to these "mutants" *biennis* appears to be the more stable of the two species, although the color variety *biennis sulfurea* constitutes a new type of variant in experimental studies on œnotheras. A culture of over 1,000 plants from selfed seed of *biennis sulfurea,* all with pale yellow flowers, produced 2 dwarfs thus establishing a "double mutant" *O. biennis* mut. *sulfurea* mut. *nanella.*

As evidence for the mutation theory of De Vries this behavior of the Dutch *biennis* is to the writer much more trustworthy evidence than the behavior of *Lamarckiana* for the reason that the latter plant in his opinion does not have a clear record of long existence, and probably is a form of comparatively recent origin. De Vries ('15, p. 173) has asserted again most vigorously his belief that *Lamarckiana* may be identified with a specimen from the United States collected by Michaux and now in the collections of the Museum d'Histoire Naturelle in Paris (De Vries, '14). With this view I cannot accord for reasons recently published (Davis, '15*a*). The showing of "mutants" from *Œnothera biennis* can hardly be considered very encouraging for the mutation theory of organic evolution when it is remembered that *biennis semi-gigas* is self sterile, that *biennis nanella* is frequently weakly or diseased, and that *biennis sulfurea* is clearly a retrogressive type having lost the power of producing normal yellow flowers.

Although *O. biennis* of all the œnotheras brought into the experimental garden still seems to me the form most free from suspicion of gametic impurity, nevertheless the line of Stomps has not, so far as we know, been subjected to the tests of a pure species summarized at the conclusion of this paper. De Vries ('15, p. 173) is mistaken in quoting me as conceding for this species a pure origin. I regard it simply as the safest material yet known on which to conduct studies in mutation, and with which other forms may be crossed to determine by the constitution of the F_1 hybrid generation whether or not their gametes are uniform. If in such a breeding test the F_1 progeny fall into two or more classes the assumption is justified that the form crossed with *biennis* must produce different classes of gametes. If the F_1 hybrid generation is uniform then it is clear that the functioning gametes male and female are respectively uniform. The fact that *Lamarckiana* crossed with *biennis* produces the "twin hybrids" *laeta* and *velutina* is, as has frequently been pointed out, one of the most important facts favoring the hybrid nature of *Lamarckiana*. It seems to me not improbable that other species of *Œnothera* will eventually be isolated more stable than the Dutch *biennis*.

Some exceedingly interesting observations have recently been reported by Bartlett ('15 *a, b, c*) on the behavior of certain small-flowered, self-pollinated American œnotheras. When grown in selfed lines these forms exhibit a behavior similar to that of *Lamarckiana* and *biennis* in throwing off in successive generations certain new types. Thus from one of the species, *Œnothera stenomeres,* a mutant *gigas* appeared with the diploid number of chromosomes, and from another species, *O. Reynoldsii,* certain individuals throw from 60 per cent. to 80 per cent. of dwarfs. It is too early to discuss the remarkable peculiarities of these forms since the material of Bartlett has not yet been tested for its purity along the lines presently to be discussed. Bartlett regards the new types as "mutants" in the sense of De Vries. The important point for our consideration at present is the fact that these wild plants apparently continue to reproduce themselves from generation to generation even while giving rise to the new forms.

With respect to the taxonomic status of the plants which we have just considered the writer sees no alternative but their recognition as clear species. The *Lamarckiana* of De Vries, the *biennis* of Linnæus, and most of the types which Bartlett has segregated from the American wild œnotheras breed true as to the mass of their progeny. What further qualifications can taxonomy in reason demand? Species they are by virtue of their morphology and by the test of the experimental garden which shows their characters to be stable to an extent that renders it certain that each line self-pollinated will maintain itself unchanged, indefinitely as far as we can see, through successive generations.

The argument that will follow as to the genetic constitution of these species of *Œnothera* does not in the least affect the matter of their recognition in taxonomy as species. It may be prefaced by two questions stated as follows: Are the types pure species, homozygous because the plants develop male gametes of one type only and because their female gametes have a uniform germinal constitution? Or, are the types heterozygous developing different types of male gametes and different types of female; briefly expressed have they in some degree a hybrid constitution?

But it will at once be asked, how can a species be hybrid even to a small degree and yet breed as true as do these forms under consideration? Where in their behavior is evidence of a hybrid constitution such as might appear in the splitting off of numerous different forms varying from the parent type, some in small degrees and some in larger degrees? Where is evidence of an orderly segregation of characters such as has been demonstrated by the Mendelian research of recent years? To these questions it must frankly be answered that only here and there are glimpses of situations which may possibly be interpreted in terms of Mendelian analysis. For example the characters of the "mutants" are frequently clearly retrogressive which indicates that gametes are formed lacking certain factors and suggests phenomena characteristic of segregation from heterozygous stock and very common in Mendelian behavior. Again, the repetition of the same "mutants" in a series of generations suggests a mechanism of precision such as we have come to associate with Mendelian inheritance. It is not, however, my purpose to argue at present this phase of the discussion for the experimental data before us is not in such shape that it can be handled to the best advantage. We admit that the "mutants" themselves do not establish their parents as in their nature hybrids. If they did there would of course be no discussion.

Under two conditions and apparently two only can a heterozygous species be conceived as breeding true.

First, if of the varied possible types of gametes *only such unite and produce fertile zygotes as will perpetuate the same germinal constitution as the parent,* then from such zygotes a heterozygous line might continue indefinitely as an impure or hybrid species. Under such conditions gametes which might in varied combinations give a series of different forms (segregates) are either not matured or if matured fail to function. Some degree of pollen and ovule sterility must be expected as the result of such conditions.

Second, if of a varied assortment of zygotes formed by the union of different types of gametes, *only those develop which have the germinal constitution of the parent* then again a heterozygous line might continue indefinitely and constitute a species, although impure or hybrid in its nature. Since all of the zygotes which result from other combinations of gametes either die or fail to develop beyond some early stage in the life history this condition would result in some degree of seed sterility or in the production of weak plants that must soon perish.

Now the œnotheras as a group exhibit a very remarkable amount of pollen sterility and also a high degree of ovule abortion, and these plants frequently give extraordinarily low yields of fertile seeds although seed-like structures may be formed in abundance. These facts we are just beginning to appreciate as offering problems for study. They seem to the writer of vital importance to the discussion of *Œnothera* genetics, facts which the Mutationists cannot ignore and behind which the Mendelians can maintain at present a very strong defence for their interpretations of the peculiarities of *Œnothera* behavior.

With respect to pollen sterility it has for many years been known that *Lamarckiana* and other species of *Œnothera* present large proportions of abortive pollen grains. Bateson (1902) early seized on the point and suggested that the high degree of pollen abortion in *Lamarckiana* indicated a hybrid plant exhibiting partial sterility. Geerts ('09) in an excellent account of the cytology of *Lamarckina* showed that approximately one half of the pollen grains fail to mature and that one half of the ovules fail to develop embryo sacs. Geerts ('09, p. 89) also made an examination of more than one hundred species of the Onagraceæ, giving us the conditions of pollen and ovulue fertility represented in some fifteen genera. He found generally in species of *Œnothera* and allied genera a degree of sterility similar to that in *Œnothera Lamarckiana,* about 50 per cent. for both pollen and ovules. On the other hand certain species of *Jussieua, Zauschneria, Epilobium, Boisduvalia* and *Lopezia* are wholly or almost wholly fertile.

My own examination of conditions in the material of *Œnothera* with which in recent years I have worked has shown some remarkable differences in the amount of pollen and seed sterility. Such close pollinated types as the Dutch *biennis,* the Dutch *muricata,* American *muricata* (from Woods Hole), *Tracyi,* and a number of American small-flowered species (for example *biennis* A and *biennis* D of my cultures (Davis, '11, p. 197 and '12, p. 385)), have very large amounts of sterile pollen. In the case of the Dutch *muricata* much more than 50 per cent. of the pollen has been sterile. Yet these are types which by virtue of their long history of close pollination might be expected to be among the purest of the species. On the other hand the race *grandiflora* B (Davis, '11, p. 203), and the western species *franciscana* and *venusta,* all open pollinated species show hardly more than a trace of pollen abortion, and *Jamesii* from Texas only a small amount of sterile pollen. I have this winter tested the seed fertility of some of these species by germinating the seeds in Petri dishes after the method recently described (Davis, '15*b*). The Dutch *biennis* gave a germination of about 96 per cent., the Dutch *muricata* about 72 per cent., *grandiflora* B about 95 per cent., *franciscana* about 61 per cent., *venusta* about 87 per cent., and *Jamesii* about 91 per cent.

It is interesting to note in the above list that the Dutch *biennis* with its very high percentage of fertile seeds (96 per cent.) has extensive pollen abortion and the Dutch *muricata* with seed germination of about 72 per cent. has an even lower degree of pollen sterility. On the other hand there are species of *Œnothera* with both high seed and pollen fertility as illustrated by some races of *grandiflora, venusta* and *Jamesii.* I was especially interested in the conditions shown by my race *grandiflora* B with its almost perfect fertility both as to pollen and seeds. This race isolated from a collection of mixed seeds gathered by Tracy in 1907 at Dixie Landing, Alabama, has always seemed to me to present a type of unusual purity. The line was started in 1908 by a cross of two similar plants (Davis, '11, p. 203) representing the broader-leaved forms of *grandiflora* that were present at Dixie Landing and I have grown in small cultures several generations of the plant without noting departures from the type. I cannot accept the criticism of De Vries ('14, p. 348) that my race *grandiflora* B is impure because from the same collection of mixed seeds of Tracy's he obtained a diversified culture as I also reported (Davis, '11, p. 203) when the line was first isolated, and because De Vries and Bartlett found the Dixie Landing station "desolate" five years after the visit of Tracy. This type may prove to be nearer to the desired pure species than the Dutch *biennis.*

Jeffrey in recent papers ('14*a*, '14*b*, '15) has taken the position "that in good species the spores or pollen is invariably perfect morphologically" and from this standpoint refuses to consider *Lamarckiana* and other œnotheras as suitable material on which to base experimental studies on mutations. To him the mere presence of abortive pollen suffices to stamp a form as hybrid in character. This represents an extreme view which in consideration of our ignorance of possible physiological reasons for pollen sterility can at present scarcely be claimed as more than an hypothesis. For the œnotheras we are greatly in need of cytological and physiological studies on pollen sterility more detailed than the incidental observations that have so far been published.

With respect to the abortion of ovules among the œnotheras our information is practically confined to the observations of Geerts ('09), mentioned above. It appears that in *O. Lamarckiana* and a number of other species only about 50 per cent. of the ovules develop embryo sacs. Other species also show varying degrees of ovule abortion. The ovules that fail to mature are represented in the capsules by a fine light brown powder known to all who work with œnotheras. Such powder is very common in the capsules of various species and their hybrids, and it seems probable that ovule sterility is as widespread in this group of plants as is the degeneration of the pollen. As in the case of pollen sterility we do not know to what extent physiological conditions may also be responsible for the abortion of ovules.

Pollen and ovule sterility involve of course the elimination from the life history of immense numbers of gametes and raise the following questions. Can it be that this elimination throws out of the life cycle types of gametes with germinal constitutions different from the gametes that matured and that function? It is possible that some of the *Œnotheras* species, in hybrid condition, regularly mature for the most part particular classes of gametes which in conjugation will perpetuate the genetic line of the parent plant? Gametes even when normally developed may still not function as when pollen grains fail to germinate upon the stigma because its secretions are not suitable. It must also be borne in mind that there are yet other phases of the life history when gametes may become ineffective as through failure to conjugate or because of a high mortality among zygotes, embryos, or young plants; such forms of infertility are expressed in sterile seeds or in weak offspring which never mature. Possibly the so-called "mutants" arise when unusual gametes from hybrids, occasionally surviving the extensive process of degeneration, form zygotes also able to survive and to develop plants diverging from the parents.

The subject of seed sterility among the œnotheras has scarcely been touched by the students of the group and yet it seems likely to become a factor of prime importance in its bearings on the problems of *Œnothera* genetics. Any worker among these plants shortly becomes aware of the fact that very many of the seed-like structures which he sows fail to germinate even though seed pans are kept for many weeks. De Vries makes frequent reference to the facts of seed sterility and the writer has in recent years recorded the number of seeds sown in cultures and the number of seedlings that develop. The results are most surprising and must have significance although what that may be remains for the future to disclose. A line of research has opened before us that will demand a special technique, for it is not enough to know merely that certain proportions of the seeds germinate within the time practicable for keeping seed pans under observation.

Seed-like structures sown on the earth are obviously lost for further enquiry as to the facts of their viability; a proportion of seedlings appear but as for the residue, that cannot be examined. The residue may contain viable seeds the germination of which is delayed, or it may consist wholly of sterile structures. We must develop methods that will ensure the rapid and complete germination of seeds in convenient receptacles such that the residue of sterile structures may be left for study after the seedlings have been removed and set in the earth. By such methods cultures of *Œnothera* may be grown in which one may feel confident that all of the viable seeds have germinated since by an examination of the residue it may be determined whether or not the seed-like structures have embryos. It is probably safe to say that no culture of *Œnothera* has as yet been described in which we may feel certain that the progeny of the sowing is complete. During the past winter I have tested the percentage of seed fertility in some fifty species and hybrids of *Œnothera* germinating the seeds on pads of wet filter paper in Petri dishes. With this method may advantageously be combined the clever practical suggestion of De Vries ('15, p. 190) of forcing water into wet seeds by air pressure thereby greatly hastening their germination. A description of a method of seed germination which will, I think, prove to be satisfactory in genetical work on *Œnothera* may be found in the Proceedings of the National Academy of Sciences, Vol. I., p. 360, 1915.

The first investigator to make use of the facts of seed sterility in suggesting Mendelian interpretations of the behavior of *Lamarckiana* and certain *Œnothera* crosses has been Renner ('14) and his line of investigation has opened a field of research and speculation that must be reckoned with in the future. Renner has studied the seed structure in *Lamarckiana, biennis* and *muricata,* and in certain crosses among these forms. His conclusion on the genotype of *Lamarckiana* will illustrate the principles underlying the method of attack. Since *Lamarckiana* when crossed with *biennis* and certain other species gives in the F_1 hybrid generation the twin hybrids *læta* and *velutina* it may be assumed to develop two classes of gametes which function. These may be spoken of as the *læta* and *velutina* gametes and are produced in about equal numbers. When *Lamarckiana* is self-pollinated the *læta* and *velutina* gametes may combine in proportions to give 1 pure *læta*: 2 *læta-velutina*: 1 pure *velutina.* It is a fact that more than one half of the seeds of *Lamarckiana* fail to develop normal embryos and Renner concludes that these sterile seeds represent zygotes homozygous respectively for the *læta* and *velutina* factors. The fertile seeds develop from the heterozygotes with both *læta* and *velutina* factors combined and this combination gives the characters of *Lamarckiana.* *Œnothera Lamarckiana* may thus be an impure or heterozygous species breeding true because of the death of such zygotes as carry the factors for *læta* and *velutina* in homozygous conditions. This simple Mendelian explanation of the behavior of *Lamarckiana* points a line of interpretation and study certain to be fruitful in *Œnothera* research.

Among hybrids of *Œnothera* the seed sterility sometimes runs extraordinarily high. The most remarkable illustrations of this fact so far known appear in the second generations of crosses involving the Dutch *biennis* and the Dutch *muricata* which exhibit certain remarkable morphological peculiarities discovered and described by De Vries ('13). First generation hybrids of reciprocal crosses between these species grown by the writer in 1913 gave data on seed germination in the earth as presented in Table I.

TABLE I.

F_1 HYBRIDS OF RECIPROCAL CROSSES BETWEEN *O. biennis* AND *O. muricata.*

Culture.	Cross.	Seeds Sown.	Sown in	Seedlings.	Germination.	Duration of Experiment.
13.33	F^1 *biennis* × *muricata*	673	Earth	139	20%	6 weeks
13.34	F^1 *muricata* × *biennis*	153	Earth	97	63%	7 weeks

It is probable from my experience with other species crosses that the viability of the seeds of these F_1 hybrids is really high and that the relatively low percentages recorded above are due to delayed germinations. But the figures for germination in the earth of F_2 hybrids and of double reciprocals, sesquireciprocals, and iter-

TABLE II.

F_2 HYBRIDS OF RECIPROCAL CROSSES BETWEEN *O. biennis* AND *O. muricata,* INCLUDING CERTAIN DOUBLE RECIPROCALS, SESQUIRECIPROCALS, AND ITERATIVE HYBRIDS.

Culture.	Cross.	Seeds Sown.	Sown in	Seedlings.	Germination.	Duration of Experiment.
14.41 (13.33a)	F_2, *biennis* × *muricata*	466	Earth	8	1.7%	9 weeks.
14.42 (13.34c)	F_2, *muricata* × *biennis*	205	Earth	35	12%	9 weeks.
14.43 (13.33a × 13.34)	double reciprocal (*b* × *m*) × (*m* × *b*)	73	Earth	8	11%	9 weeks.
15.31 (14.33 × 14.16)	sesquireciprocal (*b* × *m*) × *b*	267	Earth	25	9%	9 weeks.
*15.31 (14.33 × 14.16)	sesquireciprocal (*b* × *m*) × *b*	282	Petri dish	132	46%	6 weeks.
15.32 (14.16 × 14.33)	iterative *b* × (*b* × *m*)	22	Earth	1	4%	9 weeks.
15.33 (14.33 × 14.20)	iterative (*b* × *m*) × *m*	212	Earth	2	0.9%	9 weeks.
*15.33 (14.33 × 14.20)	iterative (*b* × *m*) × *m*	292	Petri dish	42	14%	7 weeks.
15.34 (14.34 × 14.16)	iterative (*m* × *b*) × *b*	217	Earth	47	21%	9 weeks.
*15.34 (14.34 × 14.16)	iterative (*m* × *b*) × *b*	373	Petri dish	73	19%	4 weeks.
15.35 (14.34 × 14.20)	sesquireciprocal (*m* × *b*) × *m*	246	Earth	43	17%	9 weeks.
*15.35 (14.34 × 14.20)	sesquireciprocal (*m* × *b*) × *m*	498	Petri dish	198	39%	7 weeks.
15.36 (14.20 × 14.34)	iterative *m* × (*m* × *b*)	198	Earth	51	25%	9 weeks.

ative hybrids are most surprising in the degree of sterility or delayed germination shown. They are given in Table II., where are also presented the records of four cultures sown in Petri dishes in which the germination was complete as proved by an examination of the residue.

A comparison in Table II. of the record for culture 15.31 with *15.31, 15.33 with *15.33, and 15.35 with *15.35 will illustrate the gain in germination that may come through sowing seeds in Petri dishes. The percentages of germination presented above for the hybrids of *biennis* and *muricata* must not be regarded as expressing exactly the degree of seed fertility under the conditions of the experiments since with the harvests of seed are frequently found very many structures too large to be abortive ovules and too small to be counted as "seeds" in the sense of falling within the limits of seed size. These structures are probably undeveloped seeds but only a microscopical examination can determine this point; if so, their presence of course always lowers the percentage of zygotes capable of giving progeny.

Bearing in mind the fact that pollen sterility in *biennis* and *muricata* is 50 per cent.. or more and that pollen abortion in the F_1 hybrids is very much higher (in fact very little good pollen is produced) the total amount of sterility both gametic and zygotic is simply amazing. Under such conditions how can the behavior of these hybrids be looked upon as indicative of anything but a most unusual situation, in itself very interesting, but far beyond the expectations of normal hybrid behavior. This remarkable degree of sterility among the hybrids of *biennis* and *muricata* is perhaps extreme for the œnotheras, but it serves to illustrate conditions extensively present in the writer's experience and doubtless also in the experience of others.

De Vries has described the hybrids between *biennis* and *muricata* as breeding approximately true which in the main has also been my observation. Apparently largely upon this behavior and that of certain other crosses he has reached the conclusion that hybrids between species of *Œnothera* are stable. In this opinion of De Vries I cannot agree for my crosses between *grandiflora* and certain small-flowered American species (Davis, '12 and '13), and between *biennis* and *franciscana* have in the F_2 generations given abundant evidence of that extensive variation interpreted as segregation. I believe that the apparent stability of the very small progenies produced by hybrids of *biennis* and *muricata* simply means that the remarkably high mortality among gametes and zygotes of these hybrids, or the delayed germination of their seeds, has prevented the appearance in our cultures of the diverse types which theoretically would be expected. Any general conclusions on genetic behavior in the œnotheras which fails to take into account the phenomena of sterility rests upon insecure foundations.

It is true that we do not know to what extent physiological factors may affect seed sterility as well as pollen and ovule abortion. Nevertheless a main fact is clear, namely that seed sterility eliminates in certain *Œnothera* species and hybrids immense numbers of zygotes which fail to develop seeds. And, furthermore, we know for œnotheras that large classes of weak offspring are sometimes produced that are unable to reach maturity. Seedlings with white or yellow cotyledons, which quickly die, are not uncommon in my experience with *Œnothera* cultures; in certain cases they have appeared in very large numbers (Davis, '11, p. 222) and probably have important genetical significance. This situation in *Œnothera* finds a close parallel in the behavior recorded for a number of animals and plants. Thus Baur's " golden " variety of *Antirrhinum* is an impure or heterozygous form which besides reproducing itself throws a class of normal green plants and a class represented by weak yellow seedlings that shortly die. The yellow mice studied by Castle and Little although interbred always remain impure giving progeny heterozygous for yellow because of the death of zygotes with a double dose of the factor for yellow. A dwarf wheat isolated by Vilmorin cannot be fixed since it always remains heterozygous throwing talls but never producing homozygous dwarfs. The white female form of the clover butterfly, *Colias,* was found by Gerould always to give yellow offspring either because of the failure of the gametes carrying white to conjugate or because zygotes homozygous for white fail to develop. A form of *Drosophila* characterized by confluent wings has been found by Metz only in the heterozygous condition, always throwing normals and never breeding true; flies homozygous for confluent wings are apparently not viable. Is it not possible that parallel or related phenomena are extensively present among the œnotheras? The mortality as shown by sterile seeds may indicate the elimination of large groups of forms divergent from the parent types, and some of the curious dwarfs and aberrant plants which again and again have been reported in *Œnothera* lines may be from zygotes barely able to survive the death-producing conditions that eliminate so many of their companions.

So far we have considered evidence chiefly of a negative character for the contention that many of the species of *Œnothera* are impure or hybrid species. We have tried to show that pollen, ovule, and seed sterility must all be reckoned with as conditions which may eliminate Mendelian classes of gametes and hold a line to a history of relatively true breeding even though the stream of germ plasm remain heterozygous or impure in character. The natural corollary of such behavior, if proven, might be the interpretation of so-called "mutants" as segregates from a hybrid stock that were able to survive the destruction meted out by conditions that produce sterility. To what extent the causes of sterility may lie in the history of gametogenesis or may be due to unfortunate combinations of gametes, or to what extent sterility is the result of physiological factors, these are problems that lie before us.

Let us now examine some positive evidence that certain species of *Œnothera* do form distinct classes of gametes and in consequence seem likely to be heterozygous in their constitution. That which first demands attention is the situation discovered by De Vries in certain first generation hybrids and by him named "twin hybrids." We have already referred to this phenomenon first described by De Vries ('07) for the behavior of *Lamarckiana* which as a pollen parent in crosses with other species of *Œnothera* gives not uniform F_1 generations but the two types *læta* and *velutina* (twin hybrids), produced in about equal numbers. Certain "mutants" of *Lamarckiana* also give twin hybrids under the same conditions as those produced by *Lamarckiana*. The behavior is so exact that the simplest hypothesis must suppose that *Lamarckiana* and these "mutants" form two classes of gametes which are fertile in these particular crosses. De Vries ('09) has also described "triple hybrids" when the "mutants" *scintillans* and *lata* are pollinated by such species as produce the twin hybrids from *Lamarckiana*. In such cases two of the forms have the characters of *læta* and *velutina* combined with those of the other parent, and the third form resembles the mother, either *scintillans* or *lata*. The phenomena of twin and triple hybrids is treated in detail by De Vries ('13) in "Gruppenweise Artbildung."

From a Mendelian standpoint the production of twin and triple hybrids is strong evidence that *Lamarckiana* and such of its "mutants" as behave in this manner are impure or hybrid since the male or female gametes are not uniform, a point which has been emphasized by several critics of the mutation theory. De Vries assumes that *Lamarckiana* forms its different classes of gametes as a result of its mutating instability but the precision of the process falls completley in line with what we know of Mendelian behavior. The remarkable studies of Shull show that crosses between *Lamarckiana* and *cruciata* give in the first generation polymorphic progenies of much greater complexity than the twin hybrids of De Vries. Shull's results have not been published in full but, as I understand them, they indicate the interaction of several classes of gametes, a condition very far from what would be expected if genetically pure species had been crossed.

Very interesting are the observations of Atkinson ('14) on first generation crosses between *Œnothera nutans* and *O. pycnocarpa*. These two forms are American species recently segregated by Atkinson and Bartlett from the *biennis* alliance. They have bred true in garden cultures. When *pycnocarpa* is pollinated by *nutans* twin hybrids appear in the first generation. In the reciprocal cross *nutans* × *pycnocarpa* the same twin forms are produced and in addition a third type, making this generation a compound of three distinct forms, triple hybrids. Atkinson, apparently confident of the genetic purity of *nutans* and *pycnocarpa* assumes that the determination of the twin and triple hybrids takes place through a differential division in the zygote by which factors representing certain characters are side tracked in the suspensor cell and only those responsible for the twins and triplets pass on to the embryo. There is no cytological evidence that the first mitosis in the zygote of a higher plant is ever a differential division. To the writer the situation indicates that one or both of the two species is heterozygous and that for this reason classes of gametes are formed, appropriate combinations of which give the twins and triplets. No data has been published respecting the sterility of these two species, either of pollen or ovules, and nothing of seed abortion. An understanding of the genetic constitution of the species is likely to be a difficult matter, but it does not seem probable that both are pure.

What shall be said of the probable purity of the plants of *Œnothera* and *Raimannia* with which MacDougal worked in his experiments designed to create new species by the injection of certain fluids into the ovaries. The parent material was reported to breed true, but the cultures were small and not long continued and there is no reason to suppose that a complete germination of the seeds was obtained. No information is given on the fertility of the species either with respect to the abortion of gametes or the proportion of good seeds. The material was not tested by cross breeding with other forms (the purest known) to determine whether the F_1 hybrids were uniform, a most necessary test in the establishment of a stock as homozygous. Thus from our present viewpoint we cannot accept MacDougal's conclusion since the probabilities are very great that the new types which appeared in his cultures were produced not as the result of the injections but because of the genetic impurity of the plants themselves.

In the above discussion the writer has taken definitely a Mendelian attitude in sympathy with the criticisms of Bateson and the studies of Heribert-Nilsson ('12) and of Renner ('14). There are constant suggestions of order in the phenomena of inheritance among the œnotheras which while they may not fall into simple schemes of Mendelian notation nevertheless do indicate system even though masked by complexities. That the complications at least in great part are due to the genetic impurity of the *Œnothera* material which has been so far the subject of study is the writer's belief. The difficulties that surround the analysis of *Œnothera* inheritance are probably in very large measure due to the extraordinary amount of sterility, gametic or zygotic, or both, that is present in the group.

Upon students of this genus rests the responsibility of obtaining data on this sterility and, if possible, of discovering its causes. The assumption that a line represents a pure species because it breeds true is not a safe foundation upon which to conduct experimentation in the œnotheras. This is the assumption upon which have been based many of the conclusions of the Mutationists, and from it we must dissent. We cannot depart from the principles underlying Mendelian methods of research which have so brilliantly opened the present century of biological investigation.

Finally what are the tests that must be applied to an *Œnothera* species to determine whether or not it is pure.

First.—There is the breeding test and that must be applied with such experimental methods of seed germination (Davis, '15) as will insure a complete progeny from the sowing, a progeny wholly representative of all types of viable seeds. Even then the breeding test is negative rather than affirmative in its conclusions. Should the form throw off numerous variants it naturally becomes a subject of suspicion, but should it breed true or relatively true that does not in this group of plants prove it to be homozygous in its germinal constitution.

Second.—Information must be obtained on the character and degree of sterility present, both gametic and zygotic. Sterility, unless shown to be strictly physiological in its character, suggests genetic impurity.

Third.—Cross-breeding tests must be planned and followed in which the form under observation is mated with material of known genetic purity. If the hybrid plants of the first generation are essentially uniform and the result of a normal germination of the seeds the indications are strong that the form is truly pure provided that the gametes are likewise normally fertile. If the hybrids of the first generation fall sharply into classes the material must develop gametes of different germinal constitutions and is consequently heterozygous. One favorable cross with a pure species may not be sufficient to establish the purity of a form; a number of favorable tests with pure types will carry increasing conviction.

It is thus not an easy matter to determine the fact whether or not a species of *Œnothera* is pure, and yet this is fundamental to experimental studies in the group. On the assumption of specific purity the Mutationists rest their conclusions. This condition with respect to the characters studied is also basic to Mendelian experimentation. It need scarcely be emphasized that no species of *Œnothera* has as yet passed the tests for genetic purity outlined above and that consequently we have at present no standard material with which forms may confidently be mated in the test of cross-breeding. It should become the concern of *Œnothera* geneticists to find and isolate pure material as the starting point of further studies in experimental morphology. Whether such pure forms will be found among the wild species or as products of the garden time will determine.

University of Pennsylvania,
May, 1915.

LITERATURE CITED.

Atkinson, G. F.

1914. Segregation of Unit Characters in the Zygote of *Œnothera* with Twin and Triplet Hybrids in the First Generation. *Science,* XXXIX., 834, 1914.

Bartlett, H. H.

1915a. Additional Evidence of Mutation in *Œnothera. Bot. Gaz.,* LIX., 81, 1915.

1915b. The Mutations of *Œnothera stenomeres. Amer. Jour. Bot.,* II., 100, 1915.

1915c. Mutation *en masse. Amer. Nat.,* XLIX., 129, 1915.

Davis, B. M.

1911. Some Hybrids of *Œnothera biennis* and *O. grandiflora* that Resemble *O. Lamarckiana. Amer. Nat.,* XLV., 193, 1911.

1912. Further Hybrids of *Œnothera biennis* and *O. grandiflora* that Resemble *O. Lamarckiana. Amer. Nat.,* XLVI., 377, 1912.

1913. The Behavior of Hybrids between *Œnothera biennis* and *O. grandiflora* in the Second and Third Generations. *Amer. Nat.,* XLVII., 447, 1913.

1914. Some Reciprocal Crosses of *Œnothera. Zeits. ind. Abstam. u. Vererb.,* XII., 169, 1914.

1915a. Professor De Vries on the Probable Origin of *Œnothera Lamarckiana. Amer. Nat.,* XLIX., 59, 1915.

1915b. A Method of Obtaining Complete Germination of Seeds in *Œnothera* and of Recording the Residue of Sterile Seed-like Structures. *Proc. Nat. Acad. Sci.,* I., 360, 1915.

De Vries, Hugo.

1907. On Twin Hybrids. *Bot. Gaz.,* XLIV., 401, 1907.

1909. On Triple Hybrids. *Bot. Gaz.,* XLVII., 1, 1909.

1913. Gruppenweise Artbildung. Berlin, 1913.

1914. The Probable Origin of *Œnothera Lamarckiana. Bot. Gaz.,* LVII., 345, 1914.

1915. The Coefficient of Mutation in *Œnothera biennis* L. *Bot. Gaz.,* LIX., 169, 1915.

Geerts, F. M.

1909. Beiträge zur Kenntniss der Cytologie und der partiellen Sterilität von *Œnothera Lamarckiana. Rec. Trav. Bot. Neerland.,* V., 93, 1909.

Heribert-Nilsson, N.

1912. Die Variabilität der *Œnothera Lamarckiana* und das Problem der Mutation. *Zeits. ind. Abstam. u. Vererb.,* VIII., 89, 1912.

Jeffrey, E. C.

1914a. The Mutation Myth. *Science,* XXXIX., 488, 1914.

1914b. Spore Conditions in Hybrids and the Mutation Hypothesis of De Vries. *Bot. Gaz.,* LVIII., 322, 1914.

1915. Some Fundamental Morphological Objections to the Mutation Theory of De Vries. *Amer. Nat.,* XLIX., 5, 1915.

Renner, O.

1914. Befruchtung und Embryobildung bei *Œnothera Lamarckiana* und einigen verwandten Arten. *Flora,* CVII., 115, 1914.

Stomps, T. J.

1914. Parallele Mutationen bei *Œnothera biennis* L. *Ber. deut. bot. Gesell.,* XXXII., 179, 1914.

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STUDIES OF INHERITANCE IN THE EVENING PRIMROSE.*

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It might appear at first sight that the botanist could not contribute directly to the solution of the problems of heredity in man. But I think you will realize that since all organisms have many fundamental features in common, and since the processes of heredity show a wonderful uniformity, both in mechanism and results, throughout the plant and animal kingdoms, data derived from the study of variability and inheritance in plants may be applied, with the necessary minor corrections, to problems concerning man himself. While the special problems of Eugenics resulting from man's civilization and social development are foreign to the plant breeder, yet inasmuch as man is an organism, studies based on plants can contribute to an understanding of the phenomena of heredity in man equally with those based on animals. It is a well-known fact that students of animal and plant breeding are wont to apply their results to the solution of problems in each other's fields, and while this practice may be carried too far, yet in general the results have amply justified such a procedure.

With these preliminary remarks I wish to bring to your attention some remarkable facts of variation among certain of the Evening Primroses.

Professor Hugo De Vries, of Amsterdam, Holland, was the first to make a prolonged study of the Evening Primrose. He found it growing wild near Amsterdam, where it had escaped from gardens, having been introduced into Europe from America in a previous century as a garden flower. The species concerned is called *Oenothera Lamarckiana,* and it showed a remarkable range of variability. Pro-

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fessor De Vries removed certain plants of this species to his experimental garden and found that they continued to exhibit this wide range of variation, a number of new types arising from the parent form and most of them breeding fairly true to their particular type. When the seeds of *O. Lamarckiana* were sown in quantity about 1 to 5 per cent of the plants developing from them belonged to one of the new types, the remainder being like the parent form.

This process of the sudden origin of a series of new types from one parental form De Vries called "mutation," and chiefly on his observations of phenomena of this sort in the Evening Primroses, extending over many years, he founded his mutation theory of evolution. This theory may be very briefly stated as follows: This is the general method of species origin in nature, new forms originating suddenly and breeding true from the start, these jumps or saltations replacing the slow and gradual Darwinian process of natural selection. Each of the new types presents a series of new unit characters which were not present in the parent species. Some mutants are said to be retrogressive, in which there is a loss of characters through their becoming latent. Others are considered to be progressive mutants in which additional units have appeared which the parent form did not contain.

In order to explain the sudden origin of new unit characters in the case of progressive mutants, De Vries made an assumption which to many of us seems unjustified, namely, that at some time in the previous history of the mutating species, representatives of these new units had made their appearance in some mysterious manner in the germ plasm. The fact that this is purely an assumption without any basis in observation needs to be emphasized.

My own studies of these plants have led me to the opinion that this assumption is wholly unnecessary and that the phenomena concerned may be more reasonably explained in another manner. I have gradually come to view this process of mutation as one of *analysis* in which each of the new types or mutants is lacking in some character or set of characters which the parent form possessed. This view places quite a different evolutionary value on these phenomena, but it would take far too long to discuss these facts in all their bearings on present day views of evolutionary processes at this time.

According to this view all the mutants, with one exception, to be explained later, are considered as originating through the *loss* of characters and hence would all come under De Vries' category of retrogressive mutants. Even in the case of *O. rubrinervis,* which De Vries cites as a progressive mutant, while there is no apparent loss of characters, experimental studies which I can not undertake to explain here have also shown that there is no reason for assuming that anything new or additional has been acquired which was not present in *O. Lamarckiana.*

In the case of *O. gigas,* another "progressive mutant" of De Vries, it is also believed to be a false conception to say that additional characters have suddenly appeared in its germ plasm, for this mutant differs from all the others I have studied in that it has double the number of chromosomes present in the parent form, *O. Lamarckiana.* This means that when *O. gigas* originated there was a sudden doubling in its number of chromosomes, but this does not necessarily imply anything more than a duplication of the set of chromosomes already present in the parent. It will be seen, however that on account of this change in the number of chromosomes, *O. gigas* comes in a different category from all the rest. It has lost no characters, but seems to have merely had a duplication of the chromosome set present in *O. Lamarckiana.* The assumption that new unit characters suddenly appeared in one of the germ cells giving rise to the O. *gigas* mutant is just as uncalled for as in the case of the other mutants.

Several series of facts which I can not take up here support my view that the mutants, with the exception of *O. gigas,* have arisen through a process of analysis, different sets of characters being lost from the germ cells giving rise to each mutant. The peculiar phenomena of hybridization among these forms are simply explained on this basis. In general, when two mutants are crossed, the parent form, *O. Lamarckiana,* appears in the first generation of hybrid offspring, in addition to both the mutants. Other complexities may enter in some cases, but these are the only facts that it is necessary to consider here. These two results, first that the mutants themselves breed true when self-pollinated and never revert; second that when crossed they produce the parental type, *O. Lamarckiana,* at once, but never any type showing new synthetic characters, are both easily explained if we suppose that each of the mutants was lacking in a different set of characters which the parent possessed. This principle will also explain some of the well-known cases of reversion on crossing cited by Darwin and others.

The Mendelian type of inheritance described by Professor Castle appears also to be due to a process of analysis, and in many cases, as in mice and rabbits, coats of various colors seem to have arisen by the loss of different factors which were present in the ancestral form. This analytical process, however, appears to be simpler and more easily understood than in the case of mutations.

It is probable that certain cases in man, such as a predisposition to particular diseases, can best be explained as due to the loss of certain factors in the inheritance.

Having thus very briefly and hastily presented before you a few of the facts of mutation in the Evening Primroses, and a glimpse of the general viewpoint growing out of these results, I should like for a moment to direct your attention to an entirely different line of work, which, however, led me toward the same conclusion I have already stated to you, and in fact furnishes a further basis for it. This is a study of the structure of the germ cells of these forms, to find out if there was any microscopic or cytological basis in their nuclei, for the sudden origin of these new types. I have been engaged in this work for several years and a discussion of the interesting results might well have occupied all my time this evening. Their technical character, however, renders them difficult to present in a short time, and I will merely say that these studies have shown that there is a possible basis for the sudden origin of the new types in the behavior of the chromosomes in the germ cells at the time the latter are formed. Owing to this peculiar behavior[1] occasional irregularities occur in the distribution of the chromosomes at the time the germ cells are produced. Ordinarily the germ cells contain a single set of chromosomes, but cases will occur, owing to these irregular distributions, in which a germ cell will contain two chromosomes of one pair and lack both representatives of another pair. The *number* of chromosomes therefore will remain constant, but certain germ cells will nevertheless be entirely deficient in a particular kind of chromosome. Modern cytology has produced many lines of evi-

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[1] Anyone wishing to read an account of this matter may refer to the Botanical Gazette 46:1-34.

dence, which are too involved to discuss here, tending to show that the chromosomes are not all alike in their relation to heredity, but that they are, as we say, qualitatively different. Therefore a germ cell lacking both members of a given type of chromosome (one derived from each parent) would be lacking in the ability to produce the corresponding set of characters. You thus see that in these occasional irregular distributions of chromosomes in the germ cells in the Evening Primrose we have a possible basis for the sudden appearance of apparently new sets of characters which are, however, believed to be due to the *loss* and not to the addition of anything.

It should be borne in mind that this view of mutation as a process of analysis is equally valid whether it be based upon the chromosome distributions or considered entirely apart from these phenomena.

It seems probable that much species-formation may have taken place in the manner I have suggested, by an analytical process in which certain factors are lost from the germ plasm of the parent species, thus giving rise to a series of different types. But this evidently can not be the only evolutionary factor, for quite a different set of forces is necessary to account for the origin of new organs and for the steady progression in complexity which has taken place so many times in the evolution of the plant and animal kingdoms.

In conclusion I should like to outline to you a study I am making in quantitative inheritance, because it may have a direct bearing on the complex problem of the inheritance of purely quantitative variations in man. This study concerns the amount of red pigment present in the sepals of the flower buds of *Oenothera rubrinervis,* a mutant which is characterized in part by having red streaks on its sepals. The extent of this color pattern shows a wide range of variability on either side of the commonest or modal condition. And I have already found that in some cases, at least, the offspring of an individual show the same amount or extent of pigment as their parent form, *i. e.,* they breed true to this purely quantitative difference. This shows that some initial difference in the germ cells determines their capacity for producing a certain amount or extent of pigment in the adult individual developed from them under given conditions.

Some recent work seems to indicate that the different coat colors of mammals, such as Professor Castle has described, are due to different stages of oxidation of a single melanin pigment. If this is the case, then Mendelian inheritance would appear to resolve itself into the inheritance of purely *quantitative* differences. Some quantitative factor or condition of the germ cell determines that the oxidation of this pigment shall stop in the adult individual at different points in different cases, giving for instance, a black mouse in one case and a yellow one in another.

A knowledge of the inheritance of purely quantitative differences would therefore seem to be more important than ever before, because many apparently qualitative differences may in the last analysis prove to be purely quantitative. The study of the inheritance of the capacity for producing different quantities of pigment, which I have briefly outlined to you, is only begun, but I hope later to get many more data of quantitative inheritance from this source. Needless to say, a knowledge of the inheritance of quantitative differences in man would be valuable from the standpoint of Eugenics.

Abnormalities in Oenothera

By R. R. GATES

(From the Twenty-first Annual Report of the Missouri Botanical Garden)

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ABNORMALITIES IN OENOTHERA.

BY R. R. GATES.

In connection with my *Oenothera* cultures, particularly among plants grown during the past two seasons at the Missouri Botanical Garden, I have had occasion to observe several interesting "abnormalities" of structure. These include virescence or frondescence and polymery of the flowers, tricotyly and variegation of leaves. I have thought it worth while to devote a short paper to a description of some of these cases which have an evident bearing on problems of variation and inheritance.

VIRESCENCE.—In my experimental garden of 1909 four plants exhibited virescence of the flowers. These were all descendants in the second generation from plants which were derived from the English coast near Liverpool, the first generation having been grown at Woods Hole, except in the case of one (No. 47), which was grown in the tropical greenhouse at the University of Chicago. These four plants were therefore all from cultures of closely related forms, and in some of their characters were intermediates between *O. grandiflora* and *O. Lamarckiana.* The summer temperature at St. Louis in 1909 ranged exceptionally high, reading 100° F. in the shade in one instance. The change in climate which the plants experienced was therefore very considerable, and one of the cultures had been subjected to such high temperatures for two successive seasons. This may perhaps have had something to do with the appearance of these cases of virescence, the alteration in the conditions acting as a stimulus to the production of the abnormality. That the tendency to produce virescent individuals is inherited, is shown by the reappearance of virescent plants in one race in successive generations, and their failure to appear in many other races, *e. g., O. Lamarckiana* and its mutants.

Two of the cases of virescence in 1909 occurred in a race which I have called *O. multiflora,* the description of which will be published at another time. This race is descended from a single individual grown at Woods Hole in 1908. A total of 376 first-generation offspring of this individual have been grown in the two following years, and also (in 1910) 50 plants of the second generation from the self-pollination of one individual of the first generation. The plants of the F_1 included a total of 15 virescent individuals, or very nearly 4%. The 50 plants of the F_2 contained one showing virescence. In a culture of 36 plants from seeds received from the Botanical Garden at Karlsruhe under the name *O. chilensis,* which proved to contain two very distinct types, one plant was virescent. This abnormality has not appeared in any others of the many races of which I have grown cultures.

All the plants showing virescence were affected in exactly the same way, although in some the early flowers were normal and produced fruits, only the later flowers showing the peculiarity. I have not compared the offspring from such capsules with those of normal plants, though if this were done it might be found that the virescent tendency was inherited more strongly in the former case. In one plant a side shoot produced flowers which were quite normal while the main stem produced only flowers of the virescent type.

One plant of *O. multiflora,* in which all the flowers but the earliest were virescent, is illustrated in plate 29. The peculiarities of structure exhibited by these flowers may now be described. Plate 30, f. 1, shows a group of the flowers, natural size. The sepals are green inside and outside, large and bag-like and more or less crinkled or curled. They are tapering at the end, terminating in long, slender sepal tips. Perhaps frondescence or phyllody would be a more suitable term than virescence to apply to this condition, for the sepals have become quite leaf-like. Plate 30, f. 2, shows several flowers opened and photographed to show the other organs of the flower. The petals retain a greenish yellow color, but are in all cases very small (usually about half an inch in length, though sometimes larger) and blunt at the tip. The anthers are small, with very short filaments, empty and sterile. The style is frequently markedly pubescent almost to the top. It tapers strongly and gradually to the top which is very slender, and the stigma lobes are reduced to four delicate prongs.

A remarkable peculiarity of all these flowers is the complete, or almost complete, suppression of the hypanthium. I have remarked elsewhere (Gates, 1910, footnote, p. 208) that the attacks of a certain insect also lead to suppression of this organ. Its wide variability, which Shull (1907) has proved statistically, and its suppression under various abnormal conditions, as I have shown, are probably significant facts, related to its recent phylogenetic development as suggested by MacDougal. A marked feature of this type of virescence is that the flowers do not drop off but remain permanently attached to the stem. In many cases an elongation occurs below the ovary. This is more slender than the ovary and is hard and woody, tough, and strongly attached to the stem. In the meantime (see plate 30, f. 2, flowers to the left) leaves grow out from the interior of the flower and in this way the flower becomes transformed into a short side branch. The ovary in the meantime almost completely disappears, possibly becoming transformed into a portion of the woody branch by an alteration in its structure. This stem is always more slender than was the original ovary. A whole group of young leaves of abnormal shape (long and narrow) may grow out of the flower in this manner. The elongation to form a side branch is sometimes partly above and partly below the ovary, as may be seen from plate 29. It may also be seen from this figure, though not clearly, that the lower flowers on the main stem were normal and have dropped off leaving the growing ovaries behind. Some of these afterward developed into large capsules.

The plant in 1909 which produced only virescent flowers, wilted and died about August 10th for no assignable cause, while the other plants continued to bloom long afterwards. It seemed as though the production of virescent flowers was equivalent to seed production in the physiology of the plant, and was therefore followed by drying up and death such as occurs with normal plants later in the season. The plant in the offspring of No. 47, showing virescence, was not observed to have virescent flowers until September 29, when the blooming season was nearly past. On this plant the ends of all the branches bore only virescent flowers, while farther down the branches normal seed capsules had been produced. Virescence therefore developd in all the flowers simultaneously but only appeared at the end of the season. The virescent flowers on this plant became fairly stout branches, in some cases even possessing internodes.

In the virescent flowers there was no departure from the normal number of parts, but when leaves developed within these they exhibited no regularity in number or arrangement, though always growing out from just within the cycle of the petals.

DeVries refers to what appears to be a similar case in *Oenothera subovata* (1909, p. 423), but does not describe it. He has also described a different type of virescence which is pathological in nature, due to the attacks of certain parasites. Masters (1869) gives a list of cases of virescence (p. 338) in which he includes Oenothera, with the suggestion that it might perhaps better be called frondescence or phyllody. On p. 252 of the work referred to, cases of frondescence or virescence of petals in *Oenothera striata* are cited.

POLYMERY OF THE FLOWERS.—A number of cases of flowers with an increased number of parts were observed in the cultures of 1909 and 1910. No special effort was made to find them all, but they were recorded as they happened to be observed by myself or my assistant. Masters, on p. 44 of the work above cited, refers to species of Oenothera as exhibiting synanthy. Many of the cases of polyphylly in flowers of Oenothera, to be described shortly, are due to synanthy, as I shall show. Certain other cases will require a different explanation.

DeVries (1909, pp. 472, 482) has recorded a number of cases of polymery from his cultures and in the field at

Hilversum. I will add some observations which extend the range of variation in number of parts, and shall then suggest what appears to me a probable explanation of the phenomenon as it occurs in most of the races of Oenothera. All the cases in 1909, with the exception of two, occurred in hybrid *O. Lamarckiana* from various sources, and these two were *O. brevistylis* plants from a cross with *O. Lamarckiana.* Whether this is of significance as indicating greater variability in plants derived from a cross, I cannot say, but it seems not improbable that this is the case. Using signs for the flower parts I shall now give the formulæ for the flowers recorded in 1909, in which K=sepal, C=petal, S=stamen, N=stigma lobe.

1.	$K_7C_?S_{15}N_{13}$	6.	$K_5C_5S_{10}N$
2.	$K_6C_6S_{12}N_{11}$	7.	$K_6C_6S_{12}N_9$
3.	$K_7C_7S_{16}N_{13}$	8.	$K_7C_7S_{14}N_9$
4.	$K_{5+}C_7S_{14}N_{12}$	9.	$K_7C_7S_{16}N$[1]$_{7+5}$
5.	$K_3C_3S_6N$	10.	$K_3C_3S_6N$
11.	$K_3C_3S_6N$		

This list of flowers, while shorter than that of DeVries, extends in both directions the range of variations observed by him. The highest number of stamens recorded by DeVries in a flower is 14, while I observed one remarkable flower with 16 stamens and two styles which were separate at the top, in contact below, but terete and easily pulled apart. The hypanthium was also considerably flattened and much thicker than usual and even had a longitudinal groove down its center. This flower gave me the clue to the explanation of these cases of polymery.

DeVries states (1909, p. 483) in regard to his cultures of *O. Lamarckiana* forms, that "trimerous flowers are certainly not present," but he has observed them, though very rarely, in *O. biennis* and in hybrid cultures. In the season of 1909 I observed three such cases, in *O. Lamarckiana* of various descent. The flowers were normal in every way except that the parts were in threes, which made the flowers smaller, though the individual organs were not reduced in size.

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[1] This flower had two independent stigmas, and styles which were merely in contact in the calyx tube.

Regarding the explanation of these cases, I soon found that every polymerous flower had two bracts at its base instead of being in the axil of a single bract. These bracts may be entirely independent or they may be more or less coalesced at the base, but they project in opposite directions. (See photograph by DeVries, 1909, p. 472.) In all these cases the ovary and hypanthium are more or less flattened. An examination of the stems which bore these polymerous flowers, disclosed the fact that they exhibited irregularity in the placing of the flowers on the stem, or in other words, variations in phyllotaxy. The flowers and their bracts were not uniformly distributed on the stem, but certain flowers were very close together and others long distances apart. It seems clear that this is the explanation of the phenomenon, which is therefore one of synanthy rather than of polymery. The Anlagen of the flowers are of course laid down and their position determined when the terminal rosette of the stem is very small. Anlagen of successive flowers therefore arise very close together, and if anything leads to variation in their position they will sometimes occur partly in contact or overlapping, giving a flower in which the parts are more or less completely doubled in number. The flower having two independent styles, and the fact that two bracts are always found at the base of polymerous flowers, shows that it must be due to a partial coalescence of primordia, such as I have mentioned. It is interesting to note that flower No. 5, having its parts in threes, was immediately below No. 4, which is heptamerous, and on the same side of the stem. Similarly, the plant bearing flower No. 9 also bore at the same time (Aug. 20) the two trimerous flowers, Nos. 10 and 11. It may also be noticed that in all the polymerous flowers the number of stigma lobes is less than the number of stamens. The same is true of DeVries' records. These polymerous flowers are much larger than the normal owing to the larger number of parts, the parts themselves retaining their usual size, except that the hypanthium and style are stouter, as might be expected, and the filaments are sometimes thicker.

In the season of 1910 a number of additional observations were made on this subject. The records of these were kept by my assistant, Mr. V. Follenius, during my absence, but I had the opportunity of examining the most interesting cases before the end of the season. Cases of polyphylly or synanthy were found in a much wider range of Oenothera forms than in the previous year. The following is the list:

FORMULA	RACE	REMARKS
1..$K_7C_7S_{14}N_{11}$	*O. multiflora*	Two bracts at base of flower.
2..$K_6C_6S_{12}N_8$	*O. multiflora*	Two bracts partly coalesced.
3..$K_6C_6S_{12}N_8$	*O. multiflora*	Two bracts at base.
4..$K_4C_4S_8N_4$ $K_4C_4S_8N_5$	Race No. 25, from near Liverpool, England	Two perfect tetramerous flowers, with their hypanthia in contact throughout their length and partly fused. Ovaries in contact and partly fused. Two bracts.
5..$K_3C_3S_6N_6$	*O. biennis* × *Lamarckiana*	One bract.
6..$K_3C_3S_6N_4$	" "	One bract.
7..$K_3C_3S_8N_5$	" " (same plant as No. 6)	One bract.
8..$K_6C_6S_{12}N_8$	*O. grandiflora* from Alabama	Hypanthium and ovary flattened. *One* bract.
9..$K_5C_5S_?N_?$	Race 54 × 40	*One* bract.
10..$K_5C_5S_8N_8$	*O. biennis*, Chelsea Physic Garden	Only *one* bract at base of each flower in this race. In one case the bract had two tips, as though resulting from the incomplete coalescence of two bracts.
11..$K_5C_5S_8N_8$	" "	
12..$K_5C_5S_8N_8$	" "	
13..$K_5C_5S_8N_7$	" "	
14..$K_5C_5S_8N_5$	" "	
15..$K_5C_5S_8N_5$	" "	
16..$K_5C_5S_8N_5$	" "	
17..$K_5C_5S_8N_5$	" "	
18..$K_5C_5S_8N_5$	" "	
19..K_5[1]$C_4S_9N_4$	" "	[1] Two sepals of normal width, 3 narrower, occupying about the width of the other two.

The case of No. 4, in which two tetramerous flowers were found, each with its bract, and only partly fused by their ovaries and hypanthia, is particularly instructive and confirmatory of my explanation. One hexamerous (No. 8) and one pentamerous (No. 9) flower, however, had each but *one* bract at its base, as well as the three trimerous flowers in the race *O. biennis* × *O. Lamarckiana*. It is therefore probable that the latter are real cases of polyphylly and not of synanthy, in which, instead of the partial coalescence of two primordia or their failure to separate, there is a variation in the division of the Anlagen of the various cycles of organs in the flower, resulting in a flower having a larger or smaller number of parts than normal. When, as in flowers 10–18, the androecium is normal while the calyx and corolla show an increase of parts, this may be considered to be due to polyphylly rather than synanthy.

The ten pentamerous flowers in *O. biennis* from the Chelsea Physic Garden were found in a culture of 33 plants, and careful search would doubtless have revealed further cases. Evidently the phenomenon is relatively common in this race.[1] The characters of the race are very constant and are remarkably different from those of any other race of *O. biennis* I have seen. They will be described elsewhere. These pentamerous flowers had invariably but one bract at their base, which would indicate that the phenomenon of pentamery is here due to polyphylly rather than to synanthy, although the fact that one of these basal bracts had a double tip might be considered to favor the interpretation of this also as due to synanthy.

It would seem therefore that while most of these are cases of synanthy, or coalescence of two primordia, the trimerous flowers and also evidently some at least of the other cases with only one bract at base, are real instances of polyphylly, due to variations in the divisions which the primordia of a flower normally undergo.

My conception of the process of synanthy is that, owing to variations in phyllotaxy, two independent flower primordia become so closely approximated that they partly coalesce, and develop harmoniously into a single flower in a somewhat similar fashion to the growth of a plant chimera (sectorial chimera) as described by Baur and by Winkler.

TRICOTYLY.—A number of cases of tricotyly and other abnormalities of the cotyledons have been observed in my

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[1] Penzig (1890) states that in *O. biennis* pentamerous flowers are common, the number of "carpels" often running up to 9.

germinating pots each year. They are particularly common in *O. gigas,* but no record of them has been kept.

VARIEGATION OF LEAVES.—Yellowish areas not infrequently appear on the rosette leaves, particularly in the English Oenotheras. One striking case of what was evidently a sectorial chimera according to Baur's (1909) terminology, occurred in a culture of 55 plants very closely resembling *O. Lamarckiana,* but having larger rosettes with rather broader leaves. They constituted the second pure generation from seeds of a plant near Liverpool, England. The green areas on the leaves in this plant are contrasted with areas which are yellowish white, showing a complete absence of chloroplasts. It will be seen that in several leaves the line between white and green tissue passes down the midrib, while one or two leaves exhibit patches of white adjoining the midrib. Plate 31, from a photograph taken June 30, 1909, shows the partly developed rosette. The leaves arising from one side of the stem are wholly white, those on the opposite side are mostly pure green, while several others are green on one-half and white on the other. A few areas of pale green, owing to partial absence of chlorophyll, were also observed. The white areas were of course unable to nourish themselves, and continually died away. The plant never formed a shoot, but died before the end of summer, notwithstanding the most careful treatment. The plants of the previous generation gave no indication of such a condition, which therefore appeared suddenly in this individual, and appeared, moreover, from a seed of a plant which was normal green throughout. Presumably one side of the young growing point was without chloroplasts, but just how this condition came about is at present a matter of conjecture.

LITERATURE CITED.

1869. Masters, Maxwell, T. Vegetable Teratology. London.

1890. Penzig, O. Pflanzen-Teratologie. Genua.

1907. Shull, Geo. H. In Mutations, variations and relationships of the Oenotheras, by MacDougal, Vail and Shull. Carnegie Institution Pub. No. 81. Washington.

1909. Baur, E. Das Wesen und die Erblichkeitsverhältnisse der "Varietates Albomarginatæ Hort." von Pelargonium zonale. Zeitschr. f. ind. Abst.- u. Vererbungslehre 1:330–351.

1909. DeVries, Hugo. The Mutation Theory. Translated by J. B. Farmer and A. D. Darbishire. Vol. I. Chicago.

1910. Gates, R. R. The material basis of Mendelian phenomena. Amer. Naturalist 44:203–213.

EXPLANATION OF PLATES.

Plate 29.—Plant belonging to a race known as *Oenothera multiflora*, originally derived from the English coast near Liverpool. All but the earliest flowers are virescent or frondescent.

Plate 30.—1, Virescent buds photographed natural size, showing the peculiar baggy appearance of the calyx. 2, Virescent buds natural size, opened to show the small petals, tapering pubescent style and (buds on the left) leaves growing out from the interior.

Plate 31.—Sectorial chimera, in which the leaves on one side of the rosette are lacking in chloroplasts. In certain cases half the leaf is white and half green.

VIRESCENCE OF OENOTHERA.

VIRESCENCE of OENOTHERA.

CHIMERA OF OENOTHERA.

18

RECENT PAPERS ON *ŒNOTHERA* MUTATIONS.

By R. Ruggles Gates, M.A., Ph.D.

[*Reprinted from* The New Phytologist, *Vol. XII, No. 8,*

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SINCE the publication of De Vries's mutation theory the investigations with *Œnothera* have become manifold, and have included almost every phase of the subject which bears in any way on genetic research. The Œnotheras have been and are still being closely examined from every point of view which may throw light upon their peculiar and complex behaviour. As a result of these extensive investigations of the phenomena of heredity and variation, as well as of the cytology, distribution, systematics and various other features, the mutating Œnotheras are perhaps better known than any other group of plants of corresponding size.

The accumulated data of the last decade have added much to the complexity of the facts, without, in many cases, an equivalent amount of explanatory simplification. Many of the hybridization results are now, however, becoming more clarified,—at least in the sense that they are seen to be consistent with each other,—while the cytological work has been most serviceable in furnishing an explanatory basis for the mutation phenomena themselves, removing some of these problems from the region of speculation to that of fact.

The papers on *Œnothera* have become so numerous in recent years that a complete bibliography of the subject is already a somewhat extensive undertaking, so I shall mention only certain of the more recent papers to indicate the later results and the present position of investigation in this subject. The contributions for the most part group themselves as dealing with (i.) the heredity and variation, (ii.) the cytology and (iii.) the systematics of the group. We may therefore conveniently consider them in that order in part, though the close relationship between the cytological and breeding results in this genus makes it quite impossible to deal with these two phases independently of each other. Indeed, the Œnotheras furnish the best example we have in plants, of the manner in which hybridization and microscopic study should go hand in hand in attempting an explanation of hereditary phenomena.

The breeding experiments with *Œnothera* have been greatly extended in scope since the publication of *Die Mutationstheorie* by De Vries, and I shall only mention a few of the papers on this subject. Extensive crossing experiments have been carried on, not only with *Œnothera Lamarckiana* and its mutants, but with various races of *O. biennis*, *O. grandiflora*, *O. muricata*, *O. Hookeri* and other species.

The earlier crosses made by De Vries among the mutating forms showed a variety of types of behaviour, the peculiarities of which have since been explained in part by the cytological results. When such mutants as *rubrinervis*, *nanella* and *lata* are crossed with *Lamarckiana* the F_1 contains both parent types in varying proportions, and in the first case both these types breed true. On the other hand, when *Lamarckiana* is crossed with its putative derivative *brevistylis* the latter behaves as a simple Mendelian recessive; and the new characters in the mutant *rubricalyx* behave as a simple Mendelian dominant in relation to its parent *rubrinervis*. Again, *gigas* × *Lamarckiana* according to De Vries yields an intermediate race which remains constant, though in some cases the behaviour is more variable, depending apparently on chromosome mechanisms. These three types of hereditary behaviour are doubtless indicative of different types of germinal change involved in the origin of certain mutants, a view which is fully corroborated by the cytological evidence.

As regards interspecific crosses in *Œnothera*, the most important paper which has yet appeared is that of De Vries (11) on double reciprocal hybrids between certain races of the Linnæan species *O. biennis* and *O. muricata*. In general, it was found that both reciprocal crosses yielded uniform but strongly patroclinous hybrid races which remained true in later generations. These reciprocal crosses, which were therefore unlike, were in 1908 reciprocally crossed with each other, i.e. (*biennis* × *muricata*) × (*muricata* × *biennis* and (*muricata* × *biennis*) × (*biennis* × *muricata*). In both cases the offspring were a uniform race corresponding with the "outside grand-parents." Thus (B × M) × (M × B) gave B or *biennis*, while (M × B) × (B × M) gave *muricata* which remained constant. The double reciprocal crosses therefore gave complete reversion to one of the grandparents, while the characters of the grandfather could not be transmitted through the mother and those of the grandmother could not be transmitted through the father. Similar results were obtained in crosses between races of *O. biennis* from Holland and Illinois, also with *biennis* and *cruciata*, *biennis* and *strigosa*, *biennis* and *Hookeri*, and *biennis* and *Lamarckiana*. In the *biennis-muricata* series of hybrids, what are called sesquireciprocal crosses were made, thus (*muricata* × *biennis*) × *muricata* [=(M) B × M] and (*biennis* × *muricata*) × *biennis* [=(B) M × B]. The former of these crosses is again identical with *muricata*, and the latter with *biennis*. Iterative hybrids were also produced in the following manner: (M) B × B and B × (B) M, etc. The iterative hybrids were like their hybrid parent. Thus (M) B × B=(M) B and B × (B) M=(B) M.

An ingenious explanation of these curious results has since been offered by Goldschmidt (23) whose interpretation is based on cytological study of these hybrids. Goldschmidt believes that a condition of merogony exists, the male nucleus developing in the cytoplasm of the egg, the nucleus of the latter degenerating. The cross *biennis* × *muricata* would therefore contain in its cells a *muricata* nucleus and *biennis* cytoplasm, while the cells of *muricata* × *biennis* would be derived from a *biennis* nucleus embedded in *muricata* cytoplasm. It is of course well known that the so-called "male cell" in Angiosperms is really a male nucleus which has lost its cytoplasm.

If the explanation of Goldschmidt proves to be correct, then these hybrids will furnish conclusive proof of the predominating influence of the nucleus in inheritance, for in each case the hybrid strongly resembles the parent from which its nucleus was derived.

Although the evidence for Goldschmidt's view is by no means complete and final, yet it establishes a certain presumption in its favour. Among the points figured are (i.) the degeneration of one of the nuclei (presumably the female) in the fertilized egg; (ii.) the apparent presence of only 7, the *x* number of chromosomes, in the cell-divisions of the embryo; (iii.) the smaller size of the embryo and its cells and nuclei in *biennis* × *muricata* than in *biennis*, which would be anticipated according to Boveri's law. Nevertheless, there are various difficulties, and the results of a fuller study of the subject will be awaited with interest. A number of other questions remain to be solved. If the hybrid embryo begins its divisions with only 7 chromosomes it is not probable that this number persists throughout the sporophyte, and Goldschmidt believes he has found evidence that the 2*x* number is restored in the later mitoses of older embryos. This introduces difficulties, however, for it is scarcely probable that all the cells would double their chromosome-number simultaneously, and if both types of cells continued we should anticipate as a result various distortions or changes in the shape of organs, for we should have different chromosome-numbers in different parts of the individual. The manner of chromosome pairing in meiosis would also be of interest, though we might anticipate the formation of seven pairs by analogy with the chromosome behaviour in the tetraploid mutant *gigas*. If more critical study sustains Goldschmidt's foreshadowing, we shall be able to add one more to the number of cases in *Œnothera* where cytological research has furnished the key to certain otherwise obscure or inexplicable hereditary phenomena.

It is worthy of mention that these reversions to one of the grandparents in double reciprocal crosses were predicted by Giglio-Tos (22) on generalized highly theoretical grounds concerning the structure and arrangement of protoplasmic elements, but it is highly improbable that this type of hereditary behaviour will be found to be common even in the genus *Œnothera* itself.

If Goldschmidt has correctly ascribed these results to merogony,[1] then a similar explanation may be applied (as that author has already done) to the various cases of "false hybrids," such as the well known results of Millardet with strawberries. In this case the hybrids were found to be all purely paternal in character and to breed true. The converse condition known in various Orchids, in which the hybrids are purely maternal in type, may conceivably result from the degeneration of the male nucleus after entering the egg or, as has often been suggested, from stimulation of the egg to parthenogenetic development by the presence of the pollen-tubes.

Another series of interspecific crosses has been made by Davis (7, 8, 9). He chose races of *O. biennis* from Massachusetts and of *O. grandiflora* from Alabama for the parents of his crosses, in the hope of producing *O. Lamarckiana*. But it must be said that from this point of view the results have not been successful. Hybrid forms were obtained, some of which showed a certain amount of crinkling of the leaves, but that is only one of many features of *O.*

[1] Since the above was written, Renner ("Über die angebliche Merogonie der Œnotherabastarde," Ber. d. deutsch. bot. Ges,, Bd. 31, pp. 334-335, 1913) has re-investigated the subject in *O. muricata* × *O. biennis*, *O. biennis* × *O. Lamarckiana* and *O. Lamarckiana* × *O. biennis*. He finds the usual double fertilization in all cases, with 2*x* chromosomes in embryo and endosperm. Re-examination of Goldschmidt's preparations leads to the same result, so it must be concluded that there is no evidence for the theory of merogony in these hybrids as expressed by Goldschmidt.

Lamarckiana and one which is furthermore present in varying degrees in various *Œnothera* races. The flowers of the *Lamarckiana* of De Vries are distinctly larger than those of the *grandiflora* forms from Alabama. The F_1 hybrids of Davis were, however, (as would be anticipated) intermediate in flower-size between *grandiflora* and the small flowers of *biennis*, the intermediacy also extending to all the other characters, though forms with larger flowers have been obtained in later generations. The reciprocal crosses were made, *biennis* × *grandiflora* yielding eight plants, seven of which resembled *grandiflora* and were therefore patroclinous while one exhibited a certain amount of crinkling of the foliage. *O. grandiflora* × *biennis*, from the same parent individuals, produced twenty plants which were in two groups (twin hybrids), nine being *grandiflora*-like in foliage and habit while eleven resembled *biennis*.

Larger cultures of these F_1 and F_2 hybrids from fresh crosses were made in 1910 and 1911. The chief defect of these papers as descriptions of the hybrids is that the search for *Lamarckiana*-like plants among the offspring was allowed to overshadow the really more important general results of the crosses, since it was not to be expected in any case that *Lamarckiana* could have resulted from a single simple cross. In his last paper on these hybrids Davis virtually admits the correctness of this position.

In 1907 De Vries first described twin hybrids (*læta* and *velutina*) in the F_1 when *Lamarckiana* is used to pollinate *biennis*, *Hookeri* and other species. Notes on the anatomical features of these hybrids have been published by Andrews (1). The hybrid types both breed fairly true when self-pollinated. This hybrid behaviour has been confirmed by Gates (21) in the case of *biennis* × *Lamarckiana*, with full illustrations of the broad-leaved and narrow-leaved forms. Corresponding results were also obtained with *biennis* × *lævifolia*. It therefore appears that in *Lamarckiana* and its mutant derivatives, including *lævifolia*, the pollen grains are of two types, leading to a constant dimorphism in the F_1 of the hybrids when these forms are used as male parent. In the reciprocal crosses, however, De Vries obtained a single constant race, indicating an absence of this type of dimorphism in the egg-cells of *Lamarckiana*, though these results have not been fully corroborated by the later investigations.

This short review of the more recent hybridization results is necessarily very incomplete, but even a general summary of the data involved would be much too lengthy for the present purpose. The results show clearly, however, that several types of hereditary behaviour exist, and that these types depend upon the manner of origin and hence the relationship to each other of the various races and species concerned. Certain crosses give blended inheritance, others give alternation or segregation, others twin types unlike either parent, etc. A knowledge of the cytological conditions is necessary for an explanation of the hereditary behaviour of such mutants as *gigas* and *lata*, and also apparently of the results of certain double reciprocal crosses. In conjunction, these two classes of data furnish a consistent and rational view of very complex and sometimes apparently conflicting phenomena.

In connection with the twin hybrids produced by *Lamarckiana*, Honing (25) has made an interesting comparison of *Lamarckiana* and *rubrinervis*, treating them both anatomically and chemically. He points out that the differences between *Lamarckiana* and *rubrinervis*, are analogous to those between the twin types *læta* and *velutina* produced in such a cross as *biennis* × *Lamarckiana*; and he believes that *Lamarckiana* and *rubrinervis* are each under certain circumstances capable of giving rise to the other. This view is borne out by certain results of the reviewer. It is also of interest that several collections of wild seeds of *O. muricata* from widely sundered parts of Canada show a corresponding dimorphism (21), indicating that such a condition may be widespread in this section of the genus.

Three cytological papers have been published by Davis (4, 5, 6) which are in large part a confirmation of the earlier results of Gates (13a, etc.) It was found, however, that in *O. grandiflora* the pairing of the chromosomes in synapsis was closer than in either *biennis* or *Lamarckiana*, closed rings being formed by the chromosome pairs in diakinesis, while in the latter two species and their derivatives the homologous chromosomes are very loosely paired or not paired at all at that time. Hence it appears that the attraction which causes pairing is greater in *O. grandiflora* than in the other species. As I have pointed out, the loosely paired condition gives greater opportunity for irregularities, such as actually occur, in the distribution of chromosome pairs during meiosis. It is now certain that this process is concerned in the appearance of some of the mutations (*lata* and *semilata*).

In a detailed account of somatic mitoses in *Œnothera*, Gates (17) found the number of chromosomes in an individual to be constant, the rare exceptions in metaphase groups being explicable in entire accord with the belief in the genetic continuity of chromosomes from cell to cell. Certain peculiar cases were found in the cells of the nucellus in *O. lata*, in which the chromosomes were closely paired in metaphase as though about to undergo a reduction-division, though the chromosomes retained their somatic shape.

Several recent papers have dealt with the question of the origin *O. gigas*. There have been two chief views on this subject. Gates, in 1909, in showing the increased size of the cells and nuclei in *gigas* as compared with *Lamarckiana*, indicated the probability that the chromosome-doubling to give twenty-eight occurred in the fertilized egg or the young embryo, through a suspended mitosis. It was further pointed out that in various wild species the 4*x* number of chromosomes had probably originated in the same way. Strasburger (30) entirely concurred in these views and extended them to cover many new cases of 4*x* or tetraploid species. In a subsequent paper, Gates (20) has brought together a list of over thirty cases of tetraploidy, natural or experimental, in plants and animals. Tetraploidy is therefore a well recognized evolutionary condition, and many new cases will doubtless be found when the chromosome numbers of more plants are known. The gigantic character of the cells in *O. gigas* accounts for most, though probably not all, the peculiarities of this mutant.

The manner of origin of the tetraploid condition becomes, therefore, a matter of much interest. In addition to the view expressed by Gates and afterwards by Strasburger, Stomps (28) and Miss Lutz (27) have suggested another method, namely that tetraploidy in O. *gigas* originates from the chance union of two unreduced or diploid germ cells. In support of this view these investigators announced independently the discovery of triploid or $3x$ mutants having twenty-one chromosomes. Stomps found one such mutant from *Lamarckiana*, which he calls *semigigas*; and eleven Hero or $3x$ mutants from *Lamarckiana* and its mutants *rubrinervis* and *lata* pollinated by *cruciata*, *muricata*, *biennis* or *Millersi*. The frequency of triploid forms in these crosses (they were easily recognizable by their larger size and deep green colour) was about three per thousand. But it seems probable that these triploid mutants have all originated from the fertilization of a $2x$ (diploid) egg by a normal or haploid pollen-grain, especially as in the reciprocal crosses triploid forms do not appear to have been found. These crosses do not therefore, as Stomps has supposed, furnish evidence of the occurrence of diploid pollen-grains. The same is true of the eight triploid mutants obtained by Miss Lutz. They may all have come from $2x$ eggs fertilized by pollen-grains having x chromosomes.

There is, furthermore, no observational evidence of the existence of diploid pollen-grains, though the megaspores which have been much less studied have furnished a case (Geerts) of a megaspore mother-cell of *Lamarckiana* having twenty-eight chromosomes. I pointed out (16) the probability that such a cell would develop an embryo after omitting both reduction and fertilization, and that *gigas* mutants may therefore originate in this manner. It has also been pointed out (20) that the occasional rare pollen-grains of *Lamarckiana* which, like *gigas*, have four lobes instead of three, may be diploid in chromosome-content. But there is at present no evidence that such pollen-grains are functional. The exact manner of origin of *gigas* hence remains uncertain, though it is possible that both methods of origin may occur. The discovery of triploid mutants, however, indicates the sporadic occurrence of diploid eggs in *Lamarckiana* and its derivatives, though there are of course other conceivable ways in which triploidy might have originated, such as the formation of the embryo from a triple fusion endosperm nucleus. This method is improbable, however, for the *Œnothera* embryo-sac only contains four nuclei (two synergids, the egg and a polar nucleus) and there is very little endosperm-formation.

It is highly probable that the exceptional degree of variation in *gigas* is concerned, at least in part, with changes in the chromosome-number of different individuals. A number of these types have been figured (21, 24).

Series of mutations which are parallel to those of *Lamarckiana* have been obtained by Stomps (29) and by Gates (18) in different races of O. *biennis*. Stomps obtained two mutants from the F_2 of *biennis* × *biennis cruciata*. The cruciate variety differs from the normal (from which it has probably originated by a mutation) only in the cruciate character of the flowers. This character behaves as a Mendelian recessive, splitting out in F_2. In the F_2 appeared one O. mut. *biennis nanella* (dwarf), and one O. *biennis semigigas* which was larger and possessed twenty-one chromosomes, having also long styles unlike *biennis* races.

In a race of O. *biennis* from the Madrid Botanical Garden, which had evidently undergone crossing (18), many of the plants belonged to types corresponding to *Lamarckiana*, *rubrinervis* and *lævifolia*, while one resembled *gigas* somewhat in foliage, and one was *biennis lata*, having *lata* foliage and no pollen, but with small *biennis* flowers.

Gates (21) has also obtained a dwarf mutant as well as other variations from wild *O. grandiflora* from Alabama. He has also (20) cultivated a race of *O. gigas* identical with that of De Vries, which originated (evidently as a mutation) in the Botanical Garden of Palermo, Italy. This also has twenty-eight chromosomes in typical individuals. Another extensive series of parallel mutations, some of which agree with the De Vriesian forms while others differ widely, has been studied by Heribert-Nilsson (24) in a Swedish race of *O. Lamarckiana* which differs somewhat from the race of De Vries. The giant race in particular is markedly different from the Amsterdam form, though it gives in its progeny one type closely resembling the latter. Of the nine mutant types obtained, only one (*lata*) agreed entirely with the mutants of De Vries.

It is evident, therefore, that the mutation behaviour is by no means confined to *O. Lamarckiana*, but is found in other species as well, races even of *O. grandiflora* showing a certain amount of it when taken immediately from their native wild conditions. Davis (7) has shown that wild *O. grandiflora* contains a number of biotypes. This is, of course, not surprising, for it is clear that many wild species consist of numerous freely intercrossing biotypes. And it has come to be recognized that numerous open-pollinated species are hybrid in the sense that various biotypes have contributed to their ancestry.

The activity in the cytological and experimental study of the Œnotheras has led naturally to a much more critical systematic study of the group, with the result that scores of distinct forms are now being recognized which were formerly classed with such species as *O. biennis* L. or *O. muricata* L. Many of these at least are not merely elementary species in the narrow sense, but forms which stand apart from the described species to a surprising degree.

Among such new species recently described are *O. ornata* and *O. MacBrideæ* of Nelson from Wyoming. These both have larger flowers and longer styles than *O. biennis*, thus forming a transition to the large-flowered species. Bartlett has described *O. Tracyi* from Alabama. This is virtually a small-flowered *O. grandiflora*. Steele has described a new segregate from the *O. biennis* series from Illinois under the name *O. canovirens*. Quite recently a very distinct small-flowered form was described by Gates (19) from Ithaca, New York under the name *O. angustissima*, and Bartlett and Atkinson (3) have characterized two other new forms from the *O. biennis* series of the same locality, under the names *O. nutans* and *O. pycnocarpa*. In another paper (2) Bartlett concludes that the species now commonly naturalized on the dunes of Holland should represent the type of *O. biennis*, and he identifies a paler-flowered race which is now common in Holland and which was formerly known under several pre-Linnæan polynomials, as *O. biennis* var. *sulphurea* De Vries.

The third part of Léveillé's monograph (26) has appeared, but its treatment is not critical and it can be of little benefit in the present intensive study of the genus.

Professor De Vries (13) with Mr. Bartlett made a visit to the type-locality for *O. grandiflora*, in Alabama, last year—the locality where Bartram discovered this species in 1778. They found both *O. grandiflora* and *O. Tracyi*, and a number of races or variations of each. These forms freely intercrossed, at least in the case of *grandiflora*, so that no forms were free from the suspicion of hybridization. This confirms a fact which had already been emphasized by Gates (15), namely, that in open-pollinated plants the intercrossing of many closely-related races which make up the population is continually taking place in every generation. The fact that *O. Lamarckiana* has undergone crossing does not therefore render its condition essentially different from that of any other allogamous species.

Much attention has been devoted to the history not only of *O. Lamarckiana*, but of all the related species in Europe. Many of the early records, from 1614 to the present time, have been brought together by Gates (14), and in this and subsequent papers many of the plants referred to or figured under pre-Linnæan polynomials have been identified with reasonable certainty. The writer's first conclusion, that the original form brought to Europe most resembled *O. Lamarckiana*, has since been modified, but it seems certain that forms agreeing with *O. Lamarckiana* were growing wild in Europe at the time this species was recognized and described from garden material in Paris about 1797.

In drawing any conclusions concerning the origin and history of *O. Lamarckiana*, whether through crossing or otherwise, the following crucial facts must be kept in mind: (i.) That a large-flowered *Œnothera* from "Virginia" was recognized by Ray as early as 1686. This must have belonged to a race either of *O. grandiflora* Solander or *O. Lamarckiana* Ser., and the possibility that it may have been the latter is certainly not excluded. (ii.) Three forms, including (a) *O. biennis* in the general sense, (b) *O. muricata*, and (c) a large-flowered form belonging to *O. grandiflora* or *O. Lamarckiana*, were clearly recognized and figured by Barrelier in 1714; (c.) was probably the same as the large-flowered form of Ray. (iii.) The early synonomy gives clear evidence that this large-flowered form was cultivated in many Botanical Gardens in pre-Linnæan times. (iv.) An *Œnothera* which belongs to *O. Lamarckiana* in the rather narrow sense is now the commonest form in English gardens, where it seeds itself from year to year. (v.) A very similar form has been found by Heribert-Nilsson (24) in the gardens of Southern Sweden. (vi.) A form which is practically identical with that of De Vries has been flourishing in abundance in a naturalized condition on the Lancashire coast since at least 1805.

These facts equally permit two explanations. (a) That *O. Lamarckiana* as it now exists in England, naturalized and in gardens, is essentially the same plant described by Ray and by Barrelier and is descended directly from seeds brought from "Virginia." We now know it to be probable that such seeds would not produce a uniform race to begin with. (b) The other possibility is that the race above-mentioned from Virginia belonged to *O. grandiflora* rather than to *O. Lamarckiana*, the latter originating through crossing afterwards. One weakness of this theory is the fact that *O. biennis* races also occupy this area of Virginia which was first colonized, and that any such crosses would therefore have been repeatedly made there long before the interference of man. Another weakness of this view is that there is no particular reason for supposing that *O. Lamarckiana* characters can be duplicated by single crosses between *biennis* and *grandiflora*, any more than *biennis* could be produced by crosses between *muricata* and *grandiflora*.

It has been suggested by Davis (10) that *O. Lamarckiana* Seringe is only a form of *O. grandiflora* Solander. The suggestion is based chiefly on a comparison of photographs of the type specimens in the Muséum d' Histoire Naturelle in Paris.

The new introduction of *O. grandiflora* from Alabama in 1778 was, no doubt, at least slightly different from the "Virginian *grandiflora*" of Ray and Barrelier, and it appears probable that Seringe meant to express this difference in recognizing *Lamarckiana* as well as *grandiflora*. In any case it is obvious that the question cannot be settled merely by determining the source of De Vries's race of *Lamarckiana* in 1860, for the origin of the much older race of *Lamarckiana* in England must also be considered, and this may easily go back to the time of Ray.

Since it is now clear that numerous races both of *grandiflora* and *Lamarckiana* exist, it seems possible that the original seeds of the large-flowered form brought from "Virginia" contained a mixture of interbreeding races, some of which would now be classed with either species. Certain of the Œnotheras now grown in English gardens might very well represent such intermediate races. Considering the great number of local geographic races of *O. biennis* now being described, it is probably safe to assume that the *grandiflora* of Virginia was different from that of Alabama.

Finally, three of the recent papers have dealt with various general aspects of the mutation problem. These papers are by De Vries (12), Heribert-Nilsson (24) and Gates (21). De Vries reviews the progress which has been made in the study of mutations, particularly in *Œnothera*, and reaffirms his earlier views, such as the premutation theory. He points out that natural selection, mutation and orthogenesis are not mutually exclusive as evolutionary factors, but that all have probably played their part. Heribert-Nilsson contributes a mass of breeding data on a Swedish race of *O. Lamarckiana*, and attempts to explain the mutation phenomena in terms merely of Mendelian splitting. In doing so he disregards the cytological facts and frequently runs counter to them. He elaborates a purely hypothetical theory involving the gradual accumulation of unit-factors or genes in particular germ-cells, but his theory falls to pieces in the light of the cytological facts. As the writer has pointed out, the Mendelian theory of mutation has been disproved and the premutation theory of De Vries rendered unnecessary by the study of the nuclei. The time has come for a new theory of mutation, based on our present cytological and experimental data, and the main achievement of the last three years has been to show that mutation is an independent process requiring a special explanation.

LITERATURE REFERRED TO.

1. Andrews, F. M. "Twin hybrids (*læta* and *velutina*) and their anatomical distinctions." Bot. Gaz., Vol. 50, 1910, pp. 193-201.

2. Bartlett, H. H. "Systematic studies on *Œnothera*. II. The delimitation of *Œnothera biennis* L." Rhodora, Vol. 15, 1913, pp. 48-53, 2 plates.

3. ,, "Systematic studies on *Œnothera*. III. New species from Ithaca, New York." Rhodora, Vol. 15, 1913, pp. 81-85.

4. Davis, B. M. "Cytological studies on *Œnothera*. I. Pollen development of *O. grandiflora*." Ann. Bot., Vol. 23, 1909, pp. 551-571, plates 41-42.

5. ,, "Cytological studies on *Œnothera*. II. The reduction divisions of *O. biennis*." Ibid., Vol. 24, 1910, pp. 631-651, plates 52-53.

6. ,, "Cytological studies on *Œnothera*. III. A comparison of the reduction divisions of *O. Lamarckiana* and *O. gigas*." Ibid., Vol. 25, 1911, pp. 941-974, plates 71-73.

7. ,, "Genetical studies on *Œnothera*. I. Notes on the behaviour of certain hybrids of *Œnothera* in the first generation." Amer. Naturalist, Vol. 44, 1910, pp. 108-115.

8. ,, "Genetical studies on *Œnothera*. II. Some hybrids of *O. biennis* and *O. grandiflora* that resemble *O. Lamarckiana*." Ibid., Vol. 45, 1911, pp. 193-233, 18 figs.

9. ,, "Genetical studies on *Œnothera*. III. Further hybrids of *O. biennis* and *O. grandiflora* that resemble *O. Lamarckiana*." Ibid., Vol. 46, 1912, pp. 377-427, 15 figs.

10. ,, "Was Lamarck's evening primrose (*Œnothera Lamarckiana* Seringe) a form of *Œnothera grandiflora* Solander?" Bull. Torrey Bot. Club, Vol. 39, 1912, pp. 519-533, 3 plates.

10a. ,, "The problem of the origin of *Œnothera Lamarckiana* De Vries." New Phytologist, Vol. 12, 1913, pp. 233-241. 1 Fig.

11. De Vries, H. "Ueber doppeltreziproke Bastarde von *Œenothera biennis* L. und *O. muricata* L." Biol. Centralbl., Bd. 31, 1911, pp. 97-104.

12. ,, "Die Mutationen in der Erblichkeitslehre." Berlin, 1912, 42 pp.

13. ,, and Bartlett, H. H. "The evening primroses of Dixie Landing, Alabama." Science, N.S., Vol. 36, 1912, pp. 599-621.

13a. Gates, R. R. "A study of reduction in *Œnothera rubrinervis*." Bot. Gazette, Vol. 46, 1908, pp. 1-34, pls. 1-3.

14. ,, "Early historico-botanical records of the Œnotheras." Proc. Iowa, Acad. Sci., 1910 (published 1911), pp. 85-124, 6 plates.

15. ,, "Mutation in *Œnothera*." Amer. Naturalist, Vol. 45, 1911, pp. 577-606.

16. ,, "Pollen formation in *Œnothera gigas*." Ann. Bot., Vol. 25, 1911, pp. 909-940, 4 plates.

17. ,, "Somatic mitoses in *Œnothera*." Ann. Bot., Vol. 26, 1912, pp. 993-1010, pl. 1.

18. ,, "Parallel mutations in *Œnothera biennis*." Nature, Vol. 89, 1912, pp. 659-660.

19. ,, "A new *Œnothera*." Rhodora, Vol. 15, 1913, pp. 45-48, 2 plates.

20. ,, "Tetraploid mutants and chromosome mechanisms." Biol. Centralbl., Bd. 33, 1913, pp. 92-99, 113-150, 7 figs.

21. ,, "A contribution to a knowledge of the mutating Œnotheras." Trans. Linn. Soc. Lond., Ser. 2, Vol. 8, Pt. 1, 1913, pp. 1-67, 6 plates.

22. Giglio-Tos, E. "Les dernières expériences du Prof. De Vries et l'éclatante confirmation de mes lois rationelles de l'hybridisme." Biol. Centralbl., Bd. 31, 1911, pp. 417-425.
23. Goldschmidt, R. "Die Merogonie der *Œnothera*-Bastarde und die doppeltreziproken Bastarde von De Vries." Arch. f. Zellforsch., Bd. 9, 1912, pp. 331-344, 6 figs.
24. Heribert-Nilsson. N. "Die variabilität der *Œnothera Lamarckiana* und das Problem der Mutation." Zeitschr. f. Abst.—u. Vererbungslehre, Bd. 8, 1912, pp. 89-231, 3 plates, 36 figs.
25. Honing, J. A. "Die Doppelnatur der *Œnothera Lamarckiana*." Zeitschr. f. Abst.-u. Vererbungslehre, Bd. 4, 1911, pp. 227-278, 10 figs.
26. Léveillé, H. "Monographie du genre *Onothera*. III." Le Mans, 1913.
27. Lutz, Anne M. "Triploid mutants in *Œnothera*." Biol. Centralbl., Bd. 32, 1912, pp. 385-435, 7 figs.
28. Stomps, T. J. "Die Entstehung von *Œnothera gigas* De Vries." Ber. d. deutsch. bot. Ges., Bd. 30, 1912, pp. 406-416.
29. ,, "Mutation bei *Œnothera biennis* L." Biol. Centralbl., Bd. 32, 1912, pp. 521-535, pl. 1, fig. 1.
30. Strasburger, E. "Chromosomenzahl." Flora, Bd. 100, 1910, pp. 398-446, pl. 6.

POSTSCRIPT.

Since this very condensed review was written, an important work by De Vries[1] has appeared, dealing chiefly with *Œnothera* experiments and considering the whole mass of results in relation to the mutation theory. An impression of its comprehensive treatment of the subject of heredity and mutation in *Œnothera* may be obtained from the headings into which the work is divided. These are (i.) the origin of species through mutation, (ii.) reciprocal and double reciprocal hybrids, (iii.) twin hybrids, (iv.) the pangenetic investigation of new species, (v.) the causes of mutations. Many of the results here presented *in extenso* have been published in summary form during the last few years.

The great value of the present book lies not only in the huge accumulation of experimental data which it contains—and this is far more extensive than has ever been brought together for any other similar group of forms—but in the remarkable manner in which the hereditary behaviour and the mutation behaviour are shown to be correlated. The analysis of various wild species, such as *O. biennis* L., *O. muricata* L., *O. Hookeri* Torr. and Gray, *O. cruciata* Nutt., *O. strigosa* Rydb., and several undescribed species, is carried out by means of extensive series of crosses. These are the reciprocal and double reciprocal hybrids. For the most part the reciprocal hybrids are unlike, being usually patroclinous. In this way it is shown that the pollen and egg-cells of various species are carrying different qualities, those of the pollen being usually nearly the same as the external characters of the plant, while those carried by the eggs are quite different and can only be brought to light by crossing with certain species whose pollen and egg-cells carry the same characters.

[1] De Vries, Hugo. "Gruppenweise Artbildung, unter specieller Berücksichtigung der Gattung *Œnothera*." Gebrüder Borntraeger, Berlin, 1913; pp. 365, with 22 coloured plates and 121 text-figures.

Species which bear the same qualities in both the male and female sex-cells, and whose reciprocal hybrids are therefore alike, are designated *isogamous;* while species whose functional male and female cells are unlike in their latent capacities are called *heterogamous.* Thus *O. Hookeri, O. Cockerelli* and *O. strigosa* are found to be isogamous as is also *O. Lamarckiana;* while *O. biennis, O. biennis Chicago, O. cruciata* and *O. muricata* are heterogamous.

In all these cases there is nothing resembling the Mendelian recombination of many independent characters, but the various hybrids remain constant and uniform in later generations, except in an occasional character such as flower-size. The hybrid types agree in their main essentials for various crosses, and are therefore given names:—*rubiennis, conica, gracilis, rigida,* etc. Thus *O. muricata* × *O. Hookeri, O. muricata* × *O. Cockerelli, O. Hookeri* × *O. Cockerelli* and *O. Cockerelli* × *O. Hookeri,* etc., all give the *rigida* type, differing from each other only in minor features. By such parallel series of crosses the character of the "Pollenbild" and "Eizellenbild" of each species is determined, and De Vries calls the process *gamolysis.*

Among other cases in which a similar behaviour occurs may be mentioned *O. Hookeri* × *O. biennis,* which gives an F_1 of the *rubiennis* type, the latter splitting in later generations into *rubiennis* and "*Hookeri.*" *O. biennis Chicago* × *O. Hookeri* and *O. cruciata* × *O. Hookeri* give the same result. This is explained by the isogamous condition of *O. Hookeri* and the heterogamy of the other three species. In *O. Hookeri* × *O. biennis,* e.g., the *rubiennis* hybrid bears in its egg cells only the characters of *Hookeri* while the pollen bears the segregated characters of both parents. Hence the type of splitting observed.

Further, not only these crosses but also the twin hybrids (*læta* and *velutina*) and the equally extensive series of mutation crosses (with the mutants), involving yet a third type of hereditary behaviour, are all finally explained and harmonized in connection with the theory of mutation.

De Vries explains not only all this hereditary behaviour but also the mutation phenomena in terms of his hypothesis of intracellular pangenesis. Each pangen represents a special character, and a pangen may be in (i.) the active, (ii.) the inactive, or (iii.) the labile condition, pangens in the labile condition giving rise to mutations. A mutation also consists in the passage of a pangen from one condition to another, or sometimes in the addition of a new pangen. Thus in *O.* mut. *nanella* the pangen for stature has passed from the active to the inactive condition, in *O.* mut. *rubrinervis* this pangen is active, while in *O. Lamarckiana* it is in a labile condition. Hence *Lamarckiana* × *nanella* gives some dwarfs in F_1 while *rubrinervis* × *nanella* yields only talls in F_1 but a varying proportion of dwarfs in F_2.

I have only touched upon a few of the items in this remarkable book, which boldly attempts to explain all the intricate breeding behaviour in *Œnothera.* Though one cannot agree with all its statements, yet the lucid explanations given make the work of great value to all students of heredity and evolution.

One other point to which reference may be made is found in the recent work of Gates and Miss Nesta Thomas. They have not only corroborated the independent results of Miss Lutz and Gates regarding the constancy of the fifteen chromosomes in *O.* mut. *lata*, but have found the same number constantly in *semilata* and also in two cases in which *lata* foliage, occurring as a mutation, is combined with other characters inherited from the parents.[1]

Thus *O. biennis* mut. *lata* appeared in a race of normal *O. biennis* , having *lata* foliage and *biennis* flowers (15 chromosomes). Again. *O.* mut. *lata rubricalyx* occurred in the F_2 of *O. rubricalyx* × *O. grandiflora.* The great bulk of these plants were blends and combinations of the characters of the parents, but *lata rubricalyx* had *lata* foliage and habit together with the red pigmentation of *rubricalyx.* The possession of fifteen chromosomes by this plant also shows that whenever a meiotic irregularity leads to the formation of an individual having an extra chromosome, such a plant will have the leaves and habit of *lata* or *semilata.*[2] It further shows the sharp contrast which must be drawn between sporadic mutations and the regular processes of inheritance either in pure races or in hybrids.

We may conclude that the work of De Vries and other students of *Œnothera* has resulted in showing that really new characters may and do arise by a germinal change, and are not merely recombinations of the characters of hybrids. The importance of this conclusion is very great at a time when we have been asked to suppose that all evolution has been accomplished by the shuffling and successive loss of fixed Mendelian unit-characters.

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[1] Evidence which shows that Mutation and Mendelian splitting are different processes. Section K, British Association, Birmingham.

[2] It is possible that one of two other mutants also have an extra chromosome.

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Some Oenotheras from Cheshire and Lancashire

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ŒNOTHERAS FROM CHESHIRE AND LANCASHIRE[1]

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OBSERVATIONS

Œnotheras are known to have been naturalized on the Lancashire coast since 1805, and probably existed there much earlier. They are now found on the sand dunes in many places, from Liverpool and the vicinity of Birkenhead northwards along the coast to Southport and Blackpool. They are notably abundant at St. Anne's-on-Sea, where they have been described by Bailey ('07), and in certain localities near Birkenhead (MacDougal '07). I have grown, chiefly at the Missouri Botanical Garden, extensive cultures of plants from the latter region, from seeds obtained through Dr. D. T. MacDougal in 1907, and have visited the Lancashire coast in 1910 and again in July, 1914, when I travelled along the coast from Liverpool to Southport and from Blackpool to St. Anne's. The œnotheras everywhere appear to be spreading, although children gather the flowering shoots in armfuls. The profusion of individuals is greatest at St. Anne's, where acres of waste land in the town are dotted over with them. Smaller colonies occur in various other places, notably at Bidston Junction, near Hightown and at Formby. Small groups of half a dozen plants are sometimes found in isolated places on the dunes.

I will first refer to some of these colonies as I saw them during my last visit, and will then describe a few of the many forms observed in cultures.

The Bidston Junction colony, referred to in MacDougal ('07), is a compact and almost uniform one occurring on a triangular piece of ground between railway tracks, about five minutes' walk down the foot path from Bidston Junction towards Wallersy, on the right-hand side. Some years ago, quantities of sand were dumped here from the coast between Wallersy and New Brighton. Soil from neighboring gardens has also been

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[1] Issued January 30, 1915.

deposited here, and the advent of the œnotheras is doubtless from one or other of these two sources.

The plants closely resemble the "Isle of Wight" race of *Œ. Lamarckiana* (to be described in a book now in process of publication) and the species as it generally appears in English gardens. The rosettes in this colony differ in having green midribs (both dorsally and ventrally), or pink midribs (both dorsally and ventrally), but the depth of red varies. The same applies to the stem-leaves. This is curiously different from other races, such as *Œ.* mut. *rubrinervis,* in which the midribs are red dorsally and green ventrally. The rosette leaves are usually nearly or quite smooth, but some may be crinkled. The plants were short, their average height being about twenty-two inches, though some reached a height of over three feet. The stems bear many red papillæ. The smaller plants were unbranched, the lower stem-leaves being closely crinkled and curled while the upper leaves and bracts are often quite smooth. A peculiarity of the race was the irregular disposition on the stem of much-crinkled and nearly smooth leaves, without gradual transitions between them such as usually occur in de Vries's race of *Œ. Lamarckiana.* Not infrequently crinkled and smooth leaves alternate. The buds have fewer long hairs than in the above mentioned race, and the sepals have uniformly the red color pattern 5–7 of *Œ.* mut. *rubrinervis,* though they vary somewhat in depth of shade. The dimensions of the flowers were as follows: bud cone 50 mm., hypanthium 43 mm., ovary 11 mm., diameter of cone at base 11 mm., length of petals 50 mm., width 60 mm. One plant was identical with the race of de Vries, except in its larger flowers, reddish sepals and fewer long hairs. In most plants there is also a strong distinction between the smooth and crinkled leaves.

This colony differs, therefore, in minor peculiarities from any race of *Œ. Lamarckiana* previously observed, and it exhibits a relatively narrow range of variation.

Along the electric railway tracks north of Liverpool, between Crosby and Hightown, an equally extensive and uniform colony of *Œ. biennis* was found. Thousands of plants, in flower and rosettes, were growing on uncultivated land with a nearly pure sandy soil, behind the coast range of sand hills in a long narrow area near a clump of small poplar trees. Near the upper end of this area the plants differed in having smaller flowers (petals 21 mm.) and narrow leaves (20 mm. broad). The remainder of the plants had somewhat larger flowers (petals usually 25–27 mm. long), and broader leaves (extreme width 50 mm.).[1] This was almost the only variation observed, and the race comes very close to the type of *Œ. biennis* L. The dimensions of the buds were as follows: bud cone 20 mm., hypanthium 25 mm., ovary 11 mm., anthers surrounding the stigma. The rosette-leaves and stem-leaves *all* have red midribs both dorsally and ventrally. On the same stem some leaves are smooth and some more or less crinkled. The buds are green, devoid of red, with some long hairs, and there are no red papillæ on any part of the plant. Some of the larger plants are well-branched and with very stout stems, a huge pith and a very narrow ring of wood.

This colony is even more uniform than the previous one, and must have originated from one or a very few plants.

Small colonies of *Œ. biennis* were seen at Formby, near the station and in other places. A race of *Œ. Lamarckiana* also grows here on the dunes, although I did not succeed in finding the spot, but local gardens cultivate it. The species is depicted, however, in a rose window erected in St. Luke's Church, Formby, in 1898, containing representative plants of the local flora. The central portion of the window is divided hexagonally and in the six sections the evening primrose alternates with the sea holly. The foliage and large flowers of the former are distinctly shown. Around the margin of the window are *Pyrola rotundifolia* and irises.

At Blundell Sands, near Crosby, a small colony of *Œ. Lamarckiana* was seen on waste ground, and again on the extensive sand dunes between Birkdale and Ainsdale, near Southport. In the latter case there were only three plants, and these possessed red sepals, color pattern 7, green midribs, crinkled leaves, and about $\frac{n}{4}$ long hairs.

By far the greatest abundance of plants was found at St.

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[1] These apparently correspond to *Lysimachia virginiana altera, foliis latioribus, floribus luteis majoribus*, Cat. Altdorff. See Gates, R. R. The mutation factor in evolution [pp. 61, 65, 70]. Macmillan. London.

Anne's. In addition to those in the town, which are in great profusion, numerous smaller colonies are scattered along the adjacent sand dunes. The great majority of the plants is the same as at Bidston Junction except in the crinkling of the leaves, having foliage closely resembling that of de Vries's *Œ. Lamarckiana,* midribs red both above and below, the red absent in some individuals. The flower measurements were, length of petals 50 mm., hypanthium 45 mm., ovary 10 mm. Several aberrant individuals were also observed. One dwarf mutant was found growing in the shade of a large plant. It resembled *Œ.* mut. *nanella* but had red midribs. One large rosette, having leaves very obtuse and pale pink midribs, probably belonged to *Œ.* mut. *brevistylis.* A number of plants represented a shorter spindling type with very narrow rosette-leaves (18 mm. wide x 14 cm. long). Another plant belonged to a new type, large and branching with thicker, narrower leaves (33 mm. x 13 cm.), stiffer and narrowly pointed, midribs white, and later in beginning to flower (buds only half developed, July 16).

In addition to these probable mutants, there were found in one field a few plants of a small-flowered *Œ. biennis* race growing with the *Œ. Lamarckiana.* They differed from the latter only in the small flowers (petals 22 mm., style short), and hence were unlike the *Œ. biennis* race previously described. Near by were also found plants, evidently hybrids of these two races, with petals about 30 mm. in length.

Cultures

Some of my cultures of œnotheras from near Birkenhead have already been described in a general way (Gates, '13). Here I wish to describe a few of these forms in detail, and also to refer to my experiments with plants from St. Anne's. I have not seen the colony from which the Birkenhead seeds were obtained, but it evidently contains a great profusion of forms belonging to both *Œ. Lamarckiana* and *Œ. grandiflora,* while all the colonies I have observed have a much more uniform population.

Œ. MULTIFLORA

One of the distinct races in these cultures I have already (Gates, '10) referred to as *Œ. multiflora.* It is descended entirely from one individual from a sowing of Birkenhead seeds at Woods Hole in 1908. From this individual an F_1 of 376 plants was grown in the two following years. About 4 per cent of these plants showed virescence, as described in the above paper. In 1910 a total of 297 plants were grown, most of which belonged to the F_2. An F_3 numbering 193 plants in nine families was grown in 1911, and an F_4 of 356 plants in eight families in 1912. The plants were by no means uniform, and they varied considerably from year to year. The description given is therefore a generalized one, and the condition of variability is no doubt similar to that of many wild "species." By isolating the offspring of a larger number of individuals, no doubt this variation could have been further analyzed, but more pressing problems have prevented this being done.

Plate 20 fig. 1 shows a typical rosette of my 1909 culture, pl. 20 fig. 3 the full-grown plant, and pl. 20 fig. 6 a flowering shoot on a larger scale. Specimens of this species are preserved in the herbarium of the Missouri Botanical Garden from my cultures of 1909, and in the British Museum (Natural History) from the 1912 families.

Description: Rosette of few leaves, broad and obtuse-pointed, somewhat crinkled. Full-grown plant pyramidal in outline, with lateral branches and persisting rosette leaves. Average height about 88 cm. Stems slender, stem-leaves smooth, lanceolate, bracts broadly cuneate at base with a very short petiole, tip long-pointed, more or less curled, margin irregularly repand-denticulate. Inflorescence compact, flowers numerous; buds squarish, slender with very long and slender sepal tips, sepals thin, bud cone 35 mm. long, hypanthium 37 mm., sepal tips 7 mm., ovary 10 mm., petals 43 mm., very broad and overlapping when flower is open, long hairs fairly numerous. Few red papillæ on main stem, many on side branches. In 1909 culture the buds were all green, but in 1911 they had the red color pattern of *Œ.* mut. *rubrinervis* and the stems were also reddish.

As regards variations, virescence appeared in the first two generations but not in the last two. On the other hand, a var. *elliptica* was first observed in F_2 and further studied in F_3 and F_4. This variety differs essentially in being smaller and having narrower leaves and narrow, more or less elliptical petals. Plate

20 fig. 2 shows a rosette of this variety in F_3 (1911). One family of 50 plants in 1910 contained 5 of this variety. Usually these plants show partial variability, some flowers having broad petals and others narrow and elliptical ones. Even the different petals of the same flower may show these differences. Flowers with elliptical petals are invariably smaller and are frequently found on the side branches when those of the central stem have normal petals. Hence this variation may be a matter of strength in the plant. The variation, from petals which are broad and truncate or emarginate to those which are narrow and elliptical, or even almost cruciate, is continuous. Thus on one plant in 1911, the dimensions of the petals in two flowers were as follows:

Flower 1. Petal (1) 31 mm. x 21 mm.
Petal (2) 25 mm. x 17 mm.
Petal (3) 20 mm. x 12 mm.
Petal (4) 22 mm. x 13 mm.

In this flower the petals are very small and very unequal in size but all elliptical.

Flower 2. Petal (1) 38 mm. x 39 mm.
Petal (2) 37 mm. x 37 mm.
Petal (3) 34 mm. x 36 mm.
Petal (4) 35 mm. x 36 mm.

In this flower the petals were nearly full size, nearly equal, and scarcely elliptical.

The inheritance of this condition is on a sliding scale, plants with only broad petals giving some offspring with elliptical petals, and plants with elliptical petals giving some offspring having only broad petals, though in the latter case the plants bearing elliptical petals are more numerous than in the former case. Thus the F_3 family from a normal plant contained 14 specimens having broad petals only and 15 having some elliptical petals; while another F_3 family of 44 plants derived from a plant having elliptical petals contained only 5 plants having exclusively broad petals. These peculiarities of the petals are probably to a large extent under the control of environmental features such as temperature and water supply.

The difference between broad and narrow leaves is much sharper. Thus in my F_4 cultures in 1912 certain families contain both the broad or normal type (pl. 20 fig. 5) and the *elliptica* variety (pl. 20 fig. 4). The latter had a number of flowers with elliptical petals and it also had a different method of branching. Plate 21 fig. 12 is representative of a uniform F_4 culture of 49 plants of the variety *elliptica.* This photograph is taken on a larger scale, and the nodding of the stem is merely due to wilting. This differs from *typica* (pl. 20 fig. 5) constantly in having narrower leaves and short branches, as well as in the occasional elliptical flowers which appear to be largely under environmental control.

The variability of this race is therefore as interesting as are the features, such as the general bud and leaf characters, in which it is constant. The fact should also be mentioned that a *lata*-like mutant, doubtless having 15 chromosomes, appeared in the F_4 generation, and also a mutant resembling *Œ.* mut. *albida.*

Œ. RUBRINERVOIDES

This race resembles *Œ.* mut. *rubrinervis* in many features, and yet differs from it constantly throughout. I have previously referred to this Birkenhead race as No. 25 (Gates, '11, p. 350) and studied the variation of the red stripes on the buds. In all, 1968 plants of this race have been grown in the years 1909–1912, so that four generations of offspring from a single individual have been cultivated. An illustration of that individual has already been published (Gates, '12, pl. 3). One family of offspring was grown in 1909, two in 1910, eight in 1911 and nine in 1912. Usually the variability of families progressively decreased, since each family was derived from the selfing of one individual of the previous generation. The discussion of the precise ancestry of this race is of course out of the question, but its characters bear nearly though not quite the same relation to the *Œ. Lamarckiana* from this region that the *Lamarckiana* and *rubrinervis* of de Vries's cultures bear to each other.

The 1909 family, or F_1, numbered 111 plants. Plate 21 fig. 8 shows one of these as a rosette. The leaves are narrower and more pointed than in mut. *rubrinervis,* and nearly smooth. About 20 of the plants in this culture omitted the rosette stage altogether and shot up a stem directly from the seedling stage (pl. 20 fig. 7). A normal mature plant of this family is shown in pl. 21 fig. 11. It will be seen that there is no indication of a rosette, and the branching is quite different from that of *Œ.* mut. *rubrinervis*. In many cases, however, a rosette is formed. When the rosette is omitted the branching is changed. Plate 21 fig. 10 shows on a larger scale another individual in flower. The stem-leaves differ from those of *Œ.* mut. *rubrinervis* in being narrower, more pointed and smoother.

In this race the red papillæ on the stem were very numerous, and the buds likewise were slightly more red than in *Œ.* mut. *rubrinervis*. The modal color pattern of the whole population was *5* as in *Œ.* mut. *rubrinervis*, but plants with their mode at *7* were much more numerous than in the latter (see Gates, '11, p. 351). The race as a whole inherited the capacity for producing a slightly greater amount of pigment. The ovary usually bore many long hairs arising from red papillæ; on the hypanthium were few long hairs from slight green mounds; and on the bud cone scattered long hairs from conspicuous red papillæ. In occasional buds, when the color pattern was only *3*, the green papillæ were more numerous. In addition to the color pattern of the sepals there was usually weak red on the hypanthium.[1]

The same conditions as regards pigmentation have been maintained in later generations. The plants were, however, by no means uniform in all respects, and this was not to be expected since they were derived from one individual of a freely intercrossing population. Plate 21 fig. 9 represents a rosette of one of the F_2 plants. The latter differs obviously from the one represented in pl. 21 fig. 8, but the race retained in this and subsequent generations the long, narrow, smoothish leaves as well as the pigmentation. The various F_3 and F_4 families, each derived from a selfed individual, produced sub-races differing more of less from each other and varying within narrower limits. It does not appear that the Mendelian theory of the sorting out of factors, or "genes," affords an adequate explanation of all these phenomena.

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[1] Since this condition of bud-pigmentation resembles that obtained in certain F_2 and F_3 hybrids of *Œ.* mut. *rubricalyx* and *Œ. grandiflora* (see Gates '14), it is possible that it may have arisen in a similar way, i. e., by the appearance of a red-budded mutation which subsequently crossed with other species, in which crosses some blending of pigmentation occurred giving rise to the present condition.

Œ. TARDIFLORA

This name I have used for another race having many peculiarities and showing more resemblance to *Œ. grandiflora* in its flowers and foliage. It is race No. 52 from the same source as the above. A single individual produced in 1909 nineteen plants which were fairly uniform. The rosettes contained only a few leaves, but large plants were formed, one of which is shown in pl. 22 fig. 17. Although this photograph was taken on August 21, the plants with one exception had not begun to flower. The leaves resembled those of *Œ. grandiflora.* They were large with long and acute tips, tapering to the bases, often bearing reddish blotches, sometimes much curled, somewhat crinkled along the midrib. The margin was conspicuously serrately toothed (see pl. 22 fig. 17). At the end of the season (September) these plants came into bloom, and pl. 22 fig. 20 shows a plant photographed on October 2. The buds resembled those of *Œ. grandiflora* but were small. The bud cones were pointed, smooth and rounded, the petals slightly larger than in *Œ. biennis,* or in a few cases much larger. The petals were also deeply emarginate, strongly cuneate and narrow; and the bracts were very small, narrowly lanceolate and yellowish, giving a peculiar appearance to the flowering shoot. The margins of the bracts were nearly entire or in some cases distantly denticulate.

The offspring of the plant in pl. 22 fig. 20 were grown and showed the same peculiarities. The race has not been cultivated further. It was doubtless of hybrid origin and was more nearly allied to *Œ. grandiflora* than to the *Lamarckiana* complex.

Œ. RUBRITINCTA

Reference may be made to one further race which was known as "type M." It originated from one plant in a sowing of the Birkenhead seeds in 1909. It will be understood that scarcely two plants from this sowing were alike, but some were much more distinct than others. The plant in question was a handsome one with very narrow leaves and bright red midribs. Its offspring, grown in 1911, were lost with the exception of one plant which was the same as the parent. It is shown in pl. 22 fig. 16. The basal leaves were very long with long petioles, the stem leaves very narrow, smooth, with margin closely repand-denticulate, blade narrowing gradually to a very short petiole, midribs and petioles bright red dorsally and ventrally; lowermost bracts 17 mm. in width by 9 cm. in length, upper bracts 11 mm. wide by 58 mm. in length. The buds most resemble those of *Œ. grandiflora,* being nearly devoid of long hairs, slender and somewhat rounded, with setaceous sepal tips and some red on the sepals; length of petals 32 mm., hypanthium 43 mm., sepal tips 9 mm., ovary 10 mm.

In 1912 three families of F_2 offspring, numbering in all 236 plants, were grown from the plant just described. All three families agreed in containing several types exhibiting a remarkable degree of variability.

An attempt was made to place the plants in five classes, but the categories overlapped and made classification for the most part impossible. The majority of the plants resembled the parent individual in their main features but they varied enormously in width of leaf from broad (21 mm.) to very narrow (8–6.5 mm.). These conditions were connected by intermediates, and, moreover, there were considerable variations within the individual, one branch with very narrow leaves being found on a plant with broad leaves. In addition to these variants, the three families contained 35 dwarfs, or 14.8 per cent, and the latter varied in leaf-width in the same remarkable manner. The dwarfs agreed only in having short internodes. Two of them are shown in pl. 21 figs. 13, 14, the former having narrow leaves and extremely short internodes, the leaves of the latter being quite linear. The plant would never be taken for an œnothera.

The advent of a large percentage of dwarfs in this family is similar to their occurrence in other *Œ. grandiflora* races from that locality (see Gates, '14, p. 246). The precise manner in which this capacity for producing dwarfs is inherited, is a difficult question which need not be considered here, particularly as it has been discussed elsewhere (Gates, '14).

Plate 22 fig. 15 represents one of the *Lamarckiana*-like rosettes from this source, grown in 1909. Others approached de Vries's race more closely, to the point of identity. Plate 22 figs. 18, 19 represent selected rosette-leaves taken from this culture to show the range of types exhibited. Such leaves as the two on the right in pl. 22 fig. 18 were greatly overgrown and were far larger than ever appear even in *Œ.* mut. *gigas.* These forms have not been sufficiently studied since to give an adequate account of them.

It will be obvious that the forms described here under the names *multiflora*, *multiflora elliptica*, *rubrinervoides*, *tardiflora* and *rubritincta* are not pure species or even true-breeding races. They are undoubtedly as diverse from each other as average species, however, and many systematic species if bred experimentally would probably not breed true within narrower limits than these races have done. One feature of interest attaching to these races is the fact that the main type persists essentially unchanged, though various mutants and heterozygous forms are thrown off. The behavior is not, in the main, like the Mendelian process of recombination. Repeated selfing of each race usually decreases its variability by eliminating various hybrid elements. But this process does not extend to the basal differences between the races, which, as we have seen, remain as unlike as they were before. In this aspect the hereditary behavior of these races resembles that of *Œ. Lamarckiana.* But there are a number of differences which I need not fully consider. Thus *Œ. multiflora* gives rise to its variety *elliptica* much as though it were split off from a heterozygous condition, and the variability of *rubritincta* in leaf-width, as well as its production of numerous dwarfs, is unlike anything in the behavior of *Œ. Lamarckiana.*

Many other equally distinct types were derived from this locality (see, e. g., pl. 22 figs. 18, 19), but they have not been cultivated in subsequent generations.

Œ. LAMARCKIANA FROM ST. ANNE'S

In 1910 I obtained seeds from a colony of *Œ. Lamarckiana* growing by the Manchester Children's Hospital Convalescent Home, at St. Anne's-on-Sea. Many of these were found in later cultures to agree exactly with the *Lamarckiana* of de Vries except in the red color pattern of the sepals. I was formerly inclined to lay little stress on this difference but there is no doubt that it is inherited. The fact therefore remains that a precise duplicate for de Vries's race of *Œ. Lamarckiana* is relatively infrequent on the Lancashire coast, although many forms approach it very closely and differ only in this one feature. As will be seen below, certain other plants agreed with de Vries's *Lamarckiana* except in the shape of the buds.

In 1911 a sowing of the seeds yielded 22 plants. The rosettes were for the most part uniform and very similar to *Œ. Lamarckiana*, two, however, having red midribs and lighter green leaves (*rubrinervis* type). One plant was aberrant, resembling *Œ.* mut. *semilata* in its buds, which were, however, small as in *Œ. biennis*. The bud cone was also somewhat rounded and barrel-shaped, length of ovary 11 mm., hypanthium 37 mm., cone 19 mm., petals 22 mm., style short so that anthers surround base of stigma. The features of this plant make it scarcely likely that it arose as a hybrid. It produced plenty of pollen and seeds.

Another sowing of these seeds in 1912 yielded 140 plants, which included one mut. *lata* with bad pollen (doubtless having 15 chromosomes) and one variegated *Lamarckiana* plant. The variegation was noticed when the plant was a young seedling. It reached maturity and proved to be a periclinal chimæra. Nearly all the leaves were variegated green and yellow. Many leaves were green bordered with yellow, showing the absence of chloroplasts from the epidermal and probably also the hypodermal layer. Occasional leaves were almost entirely yellow, and some were yellow on one side of the midrib and green on the other. There were also broad white bands on the margin of the sepals. The pollen was abundant and plenty of seeds were set.

Two sowings of seeds from this plant were made in 1912. The seeds numbered respectively 121 and 145. Only two seeds in one pan were observed to germinate, and the seedlings quickly died, probably from lack of chlorophyll. Regarding the origin of this periclinal mutation, it would appear to have originated in the embryo after fertilization through the loss of chloroplasts from the outer layers of the growing point.

The foliage in the rest of the culture agreed with the type of *Œ. Lamarckiana*. One plant differed in having stem-leaves more or less pointed at the base, not crinkled, midribs pink, and smaller flowers (petals 29 mm. long x 38 mm. broad, style short, buds squarish). Two other plants agreed exactly with *Œ. Lamarckiana* except in the buds. The petals were 35 mm. long x 48 mm. broad, emarginate, anthers reaching nearly to top of stigma lobes, sepals green and with the same pubescence as in *Œ. Lamarckiana,* from which these two plants therefore differed only in the somewhat smaller flowers and shorter style. One mut. *nanella* also occurred in this culture, and several other slightly aberrant individuals, including a plant with broadly elliptical foliage. The "*Lamarckiana* foliage" was also more variable than in cultures from de Vries, this no doubt being due to the continued inbreeding in the latter case.

It will be understood that the new forms described here are scarcely to be looked upon as "new species" according to the usual interpretation at the present time. They merely represent a partial analysis of a complex interbreeding colony of forms, and their variability is one of their most interesting features. Nearly all if not all the differences observed are inherited, however, and the mutations can in many instances be separated from the characters arising through hybridization. The forms are, moreover, as distinct from each other as many species of *Œnothera.*

In conclusion, I am indebted to the Missouri Botanical Garden and the John Innes Horticultural Institution for the facilities provided for growing the plants, and to Mr. E. J. Allard for several of the photographs. A portion of the expenses of my second visit to Lancashire was defrayed by a grant from the Royal Society.

LITERATURE CITED

Bailey, C. ('07). De Lamarck's evening primrose (*Œnothera Lamarckiana*) on the sandhills of St. Anne's-on-the-Sea, North Lancashire. (Address, Annual Meeting Manchester Field Club.) 1–28. *pl. 1–6.* 1907.

Gates, R. R. ('10). Abnormalities in Œnothera. Rept. Mo. Bot. Gard. **21**: 175–84. *pl. 29–31.* 1910.

———, ('11). Studies on the variability and heritability of pigmentation in Œnothera. Zeitschr. f. induct. Abst.- u. Vererbungsl. **4**: 337–72. *pl. 6. f. 1–5.* 1911.

———, ('12). An onagraceous stem without internodes. New Phytologist **11**: 50–53. *pl. 2–3.* 1912.

———, ('13). A contribution to a knowledge of the mutating œnotheras. Trans. Linn. Soc. Bot. **8**: 1–67. *pl. 1–6.* 1913.

Gates, R. R. ('14). Breeding experiments which show that hybridization and mutation are independent phenomena. Zeitschr. f. induct. Abst.- u. Vererbungsl. **11**: 209–79. *f. 1–25.* 1914.

MacDougal, D. T., Vail, A. M., and Shull, G. H. ('07). Mutations, variations, and relationships of the œnotheras. Carnegie Inst. of Washington Publ. 81: 1–92. *pl. 1–22. f. 1–73.* 1907.

Explanation of Plate

PLATE 20

Fig. 1. *Œ. multiflora*, rosette, 1909.
Fig. 2. *Œ. multiflora elliptica*, rosette, 1911.
Fig. 3. *Œ. multiflora*, full-grown plant, 1909.
Fig. 4. *Œ. multiflora elliptica*, 1912.
Fig. 5. *Œ. multiflora*, 1912.
Fig. 6. *Œ. multiflora*, flowering shoot, 1909.
Fig. 7. *Œ. rubrinervoides*, young plantlet showing absence of rosette, 1909.


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GATES—OENOTHERAS

Explanation of Plate

PLATE 21

Fig. 8. *Œ. rubrinervoides*, rosette, 1909.
Fig. 9. *Œ. rubrinervoides*, rosette, 1910.
Fig. 10. *Œ. rubrinervoides*, showing nearly smooth, pointed leaves, 1909.
Fig. 11. *Œ. rubrinervoides*, no rosette, 1909.
Fig. 12. *Œ. multiflora elliptica*, 1912. (Tip of plant drooped from wilting.)
Fig. 13. Linear-leaved dwarf in offspring of *Œ. rubritincta*, 1912.
Fig. 14. Dwarf offspring of *Œ. rubritincta*, 1912.


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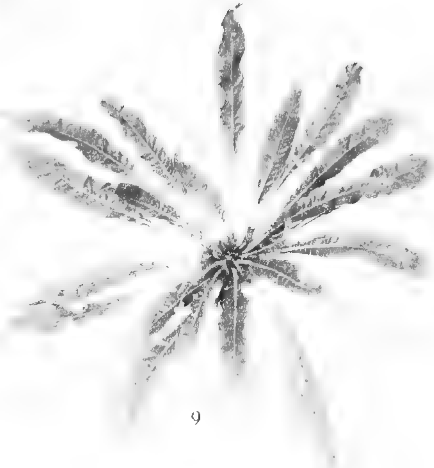
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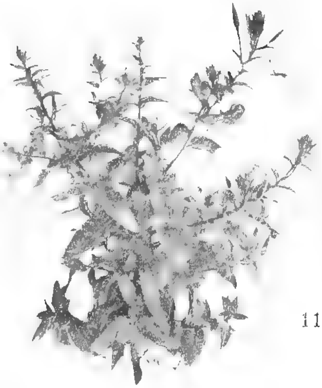
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GATES—OENOTHERAS

Explanation of Plate

PLATE 22

Fig. 15. *Œ. Lamarckiana*-like rosette, 1909.

Fig. 16. *Œ. rubritincta*, 1911.

Fig. 17. *Œ. tardiflora*, showing serrated leaves and absence of flowers, August 21, 1909.

Fig. 18. Selected leaves from various rosettes, 1909.

Fig. 19. Selected leaves from various rosettes, 1909.

Fig. 20. *Œ. tardiflora*, showing late appearance of buds, October 2, 1909.


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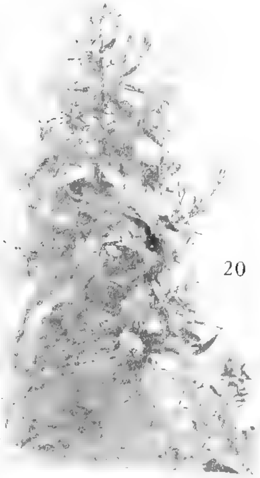
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GATES—OENOTHERAS

ON SUCCESSIVE DUPLICATE MUTATIONS.

R. RUGGLES GATES

[Reprinted from BIOLOGICAL BULLETIN, Vol. XXIX., No. 3, September, 1915]

ON SUCCESSIVE DUPLICATE MUTATIONS.

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ON SUCCESSIVE DUPLICATE MUTATIONS.[1]

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Nilsson-Ehle[2] was the first to formulate the hypothesis of duplicate factors or representatives for the same character. He brought forward evidence from crosses of red and white varieties in certain Swedish strains of wheat, tending to show that in different F_2 families plants with red and white grains occurred in the ratios respectively 3:1, 15:1 and 63:1; from which he concluded that three independent units for red were present, each of which could produce the color alone. Although his conclusions were criticized by Kajanus,[3] yet there remains a strong presumption in their favor, and several other cases of supposed duplicate factors have been described, though these have for the most part rested upon more insecure data than the original instances of Nilsson-Ehle.

Certain suggestions have been made concerning the origin of this duplicate or triplicate condition. Emerson and East[4] pointed out in general terms that if a factor should become located in a different chromosome or should be affected in any way so as not to be always allelomorphic to itself, then a duplication of determiners would result. Shull[5] has listed the supposed cases of duplicate determiners and remarks that such a condition of duplication might also result from "repeated progressive mutations." In the same paper, Shull endeavors to account for the origin simultaneously of a duplicate "gene"

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[1] Presented before the American Genetic Association, San Francisco meeting, August 3, 1915.

[2] Nilsson-Ehle, H., 1909, "Kreuzungsuntersuchungen an Hafer und Weizen," I., *Lunds Univ. Årsskrift.*, N.F., Afd. 2, Bd. 5, Nr. 2, pp. 122.

[3] Kajanus, B., 1914, "Zur Kritik des Mendelismus," *Zeitschr. f. Abst. u. Vererb.*, 12: 206–224.

[4] Emerson, R. A., and East, E. M., 1913, "The Inheritance of Quantitative Characters in Maize," Agric. Exp. Sta. Nebraska, Research Bull. 2, pp. 120.

[5] Shull, Geo. H., 1914, "Duplicate Genes for Capsule-form in *Bursa bursa-pastoris*," *Zeitschr. f. Abst. u. Vererb.*, 12; 97–149, Figs. 7.

for capsule form in *Bursa bursa-pastoris* and, at the same time, of the mutant *B. Heegeri.* That hypothesis will not, however, apply to the probably more frequent cases in which duplicate factors for a particular character are found without any other mutation having taken place. An explanation will therefore have to be found for the duplicate or triplicate condition in wheat or in any other organisms in which it occurs.

It is the purpose of the present paper to discuss more precisely the manner in which such monohybrid characters originate and particularly the way in which they may afterward become duplicate or triplicate. *Œnothera rubricalyx* affords a typical case of a mutant originating as a monohybrid, probably through a transformation in one chromosome or one pair of chromosomes.[1] I have pointed out elsewhere[2] that when the duplicate or triplicate condition occurs it might be reasonably supposed to have arisen through the same general change having taken place independently in two or three different chromosomes of the x series.

In an original mutation of this kind the new character of course forms a pair by contrast with the old unaltered character. If a single chromosome has undergone this change and the new condition is dominant, then a heterozygous mutant Aa will be produced having the new character but splitting in its offspring in a 3:1 ratio. This is the way in which *Œnothera rubricalyx* originated from *Œ. rubrinervis*, as I have shown elsewhere.[1]

If now in the mutant race one or both members of a second pair, $a'a'$, of chromosomes undergoes a corresponding change, to $A'a'$, or $A'A'$ then we shall have duplicate factors AA' for the same character, and in the offspring of such individuals the new type and the original type would appear in the ratio of 15:1. A similar mutation in a third pair would give the triplicate condition with a ratio of 63:1.

It may be pointed out that this assumption of similar changes in different members of the x series of chromosomes is by no

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[1] See Gates, R. Ruggles, 1915, "On the Origin and Behaviour of *Oenothera rubricalyx*," *Journ. of Genetics*, 4: 353–360.

[2] Gates, "The Mutation Factor in Evolution," p. 317, Macmillan, London, 1915.

means an improbable one. It does not assume that the chromosomes which underwent the change were alike, but merely that they were more nearly alike than the others of the series. That the chromosomes of the x series are actually differentiated there are many lines of evidence to show. One of the most recent is the fact, ascertained by Doncaster and Gray,[1] that in certain echinodern crosses particular chromosomes swell up and form vesicles in the strange cytoplasm of the egg or of another species while other chromosomes exhibit no such effect. On the other hand, the materials of the chromosomes obviously possess many similarities which probably outweigh their chemical differences.

It may further be pointed out that if both members instead of one member of a pair of chromosomes underwent a change, say in a pollen mother cell, the only difference would be that four instead of two mutated germ cells would result, each of which might function in producing a mutant. It is almost impossible to determine whether one or both members of a pair of chromosomes underwent the change in any particular instance, but in either case the original mutant would be heterozygous, though continued inbreeding would produce ultimately a homozygous race, as in the case of *Œ. rubricalyx*. This is probably the history of Nilsson-Ehle's wheats which are duplicate or triplicate for the red color factor in their grains.

From the evidence obtained in F_2 and F_3 in crosses of various Swedish wheats having red kernels, with white-grained varieties, Nilsson-Ehle concludes[2] that while the varieties known as Sammet and Grenadier have 3 independent units for red, Extra-Squarehead has only one, since it gave (p. 67) only ratios approximating 3:1. In a later paper[3] continuing this work the same author finds (p. 22) that Swedish Binkel wheat contains two factors for red. From one F_2 family he grew 94 F_3 families, with results which may be tabulated as follows:

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[1] Doncaster, L., and Gray, J., 1913, "Cytological Observations on the Early Stages of Segmentation of *Echinus* Hybrids," *Quart. Journ. Micr. Sci.*, 58: 483–510, pls. 28–29.

[2] Nilsson-Ehle, H., 1909, Kreuzungsunterschungen an Hafer und Weizen. I. *Lunds Univ. Årsskrist.*, N.F., Afd. 2, Bd. 5, Nr. 2, pp. 122.

[3] Nilsson-Ehle, H., 1911, "Kreuzungsuntersuchungen an Hafer und Weizen," II., *Lunds Univ. Årsskrift.*, N.F., Afd. 2, Bd. 7, Nr. 6, pp. 82.

TABLE I.

Expected Ratio of Families.		Totals.	Expectation.
7	40 families were constant red		
4	23 families split in the ratio 3 : 1	483 : 142	468.75 : 156.25
4	25 families split in the ratio 15 : 1	789 : 47	783.75 : 52.25
1	6 families were constant white		

It will be seen that the frequency of families is very close to expectation. The totals of the families containing a 15:1 ratio are also very close to expectation, but for the 3:1 families the agreement is not so good. The evidence seems sufficient, however, to justify the conclusion that two factors and two only are here concerned.

In the same way evidence is obtained (p. 25) to show that a certain pure line (0406) has in one case a single factor for red and in another case two factors. To use the terminology of Lang, the race is monomerous in one case and dimerous in another. In crosses between the 0406 race and 0234, which was also red,[1] ratios of 15:1 and 3:1 were obtained showing that two factors were present, one of which must have been derived from each parent. Hence the 0406 race must in this case have been monomerous. In crosses between 0406 and a white race, 15:1 ratios were again obtained, showing that the 0406 race is now dimerous. The genetic relationships of the strains used in these two crosses is not stated, but a simple explanation is that in the meantime the strain had undergone a second (invisible) mutation.

No explanation of the origin of this condition was offered. But there are at least two ways in which the dimerous condition may have been derived from the monomerous: (1) Through a mutation on the part of a second pair of chromosomes, (2) through a re-mating of the chromosome pairs. Later we shall compare the consequence of each of these methods of deriving the duplicate condition. In the first case the duplicate mutation is produced by a change very similar to that which produced the original mutant. In the second case the secondary change is a mechanical one, very different from the primary change which was probably chemical in nature.

[1] The results are given in *Ber. deut. bot. Gesells.*, 29: 65–69, 1911.

Another pure line of wheat (0290) was also found to be dimerous for the red factor in one case and monomerous in another. A race called 0501 was found to be probably trimerous like Swedish Sammet. Nilsson-Ehle considers it scarcely probable that in these two wheats the same three factors for red are present, and thinks that perhaps many more than three independent factors have to be reckoned with. There seems, however, no reason for such an assumption. It appears more probable that corresponding chromosomes undergo the same change in each case so that the factors are all homologous with each other, though of independent origin in the different races.

We may, therefore, account for the origin of the duplicate and triplicate "factors" for red in the Swedish wheats by assuming that successive mutations have occurred and that in each case the duplicate or triplicate condition has afterward become homozygous and stable through the repeated self-fertilization occurring in later generations.

Turning now to the history of *Œnothera rubricalyx*, it appears that the original monomerous condition has become dimerous in subsequent generations of culture. And it will be seen from the culture records that this has happened independently several times in different lines of descent.

It may be worth while first to recapitulate in briefest form the evidence for the original monomeric character of *Œ. rubricalyx*. The original mutant gave an F_1 offspring of 12 plants, 11 of which had red buds (R) and one green buds (r). Three of the former selfed produced F_2 families in which the ratios R:r were respectively 10:5, 14:6, and 33:11. The sum of these three families is 57:22 which is close to a 3:1 ratio and could not reasonably represent a 15:1 ratio, nor could either of the three ratios individually. Two plants descended from the F_2 family which yielded 33:11, a perfect 3:1 ratio were used to cross reciprocally with *Œ. grandiflora*, a green budded species of diverse habit. Since these plants were from a family which was obviously monomerous, the F_1 from the cross would either be all R (if the parent was homozygous) or R:r in equal numbers (if the parent was heterozygous). The numbers obtained were 30 R:28 r in one cross and 79 R: 71 r in the other. Hence the family which gave the ratio 33:11 was undoubtedly monomerous and up till that time a single mutation had taken place involving only one pair of chromosomes.

It was anticipated that the F_2 from *rubricalyx* × *grandiflora* and its reciprocal would again yield 3:1 ratios but it was found that in fact there were other ratios as well, the chief of which now appear to be 2:1, 4:1, 5:1 and 15:1. In my discussion of these extensive results[1] I was at first inclined to attribute them to an effect of the *grandiflora* parent in modifying the frequency of inheritance of the R character, and to conclude that since the cross with *grandiflora* had obviously modified the red-bud character R by dilution in many cases, it must also have modified the *frequency* with which R would appear. I have since grown a large series of F_3 families, the results of which are published in detail elsewhere.[2] In the present communication a further analysis of these F_2 and F_3 ratios will be made, from which it appears that the unexpected ratios obtained in these generations are probably not an effect of the cross with *Œ. grandiflora,* but they result in part from the subsequent occurrence of duplicate mutations in *rubricalyx.* Other ratios, such as 5:1 cannot, however, be fully explained in this way.

In this connection it seems desirable to point out that in the inheritance of any character there are two features to be taken into consideration: (1) The nature of the character, and (2) the mechanism of its distribution in the germ cells. Mendelian writers frequently ignore the former, and biometrical writers vitiate their case when they take no account of the latter; but in a complete account of the inheritance of any character both must be considered. As a matter of fact, although crossing with *grandiflora* probably does not modify the mechanism of transmission of R, yet it does seriously and permanently modify the character itself in some cases, as I have shown in previous publications.

We may now consider the ratios R:r in the F_2 and F_3 of *Œ. rubricalyx* × *grandiflora* and the reciprocal. A further study of

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[1] Gates, R. R., 1914, "Breeding Experiments which Show that Hybridization and Mutation are Independent Phenomena," *Zeitschrift f. Abst. u. Vererb.*, 11: 209–279, Figs. 25.

[2] "The Mutation Factor in Evolution," pp. 254 ff.

these ratios makes it evident that they nearly all fall remarkably close to three or four ratios. So close is the fit that it seems probable that several ratios, such as 5:1, are significant as such, though at present no complete explanation of them can be offered. I was formerly inclined to regard some of these ratios as the expression of merely quantitative differences without

TABLE II.

F_2 (*Oe. grandiflora* × *rubricalyx*).

Ratios.	Expectation.	Agreement.	Conclusion.
68 : 16	63.00 : 21 67.20 : 16.8	3 : 1 possible 4 : 1 very near	4 : 1
142 : 15	147.00 : 10	15 : 1	15 · 1
133 : 4	128.40 : 8.6	15 : 1	15 : 1
Total 275 : 19	275.60 : 18.4	15 : 1 perfect Hence 2 families 15 : 1 1 family 4 : 1	

F_2 (*Oe. rubricalyx* × *grandiflora*).

(a) 66 : 13	59.25 : 19.75 65.84 : 13.16	3 : 1 5 : 1 perfect	5 : 1
(b) 45 : 14	44.25 : 14.75	3 : 1 nearly perfect	3 : 1
(c) 47 : 3	Incomplete. In addition 9 dwarfs, 1 intermediate.		
(b) 134 : 44	133.50 : 44.5	3 : 1 perfect	3 : 1
(a) 67 : 13	66.70 : 13.3 60.00 : 20	5 : 1 perfect 3 : 1 unlikely	5 : 1
(a) 82 · 13	79.20 : 15.8 71.25 : 23.75 89.00 : 6	5 1 very near 3 : 1 very unlikely 15 : 1 " "	5 : 1
(a) 77 : 15	76.70 : 15.3 69.00 : 23 86.25 5.75	5 : 1 perfect 3 : 1 unlikely 15 : 1 very unlikely	5 : 1
45 : 14 134 : 44			
(b) 179 : 58	177.75 : 59.25	3 : 1 *very* close	3 : 1
66 : 13 67 : 13 82 : 13 77 : 15			
(a) 292 : 54	288.30 : 57.7 259.50 : 86.5 324.40 : 21.6	5 : 1 very close 3 : 1 unlikely 15 : 1 impossible[1] Hence in F_2 2 families 3 : 1 4 " 5 : 1 0 " constant	5 : 1

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[1] By "impossible" is meant that the chances against this interpretation, taken in connection with the other results, are so great that for practical purposes it need not be considered.

F_3 (*Oe. grandiflora* × *rubricalyx*).

Ratios.	Expectation.	Agreement.	Conclusion.
231 : 56	229.60 : 57.4	4 : 1 very near	4 : 1
	239.20 : 47.8	5 : 1 ?	
	191.30 : 95.7	3 : 1 impossible	
	268.10 : 18.9	15 : 1 "	
237 : 56	234.40 : 58.6	4 : 1 very near	4 : 1
	244.20 : 48.8	5 : 1 ?	
	219.75 : 73.25	3 : 1 improbable	
	274.70 · 18.3	15 : 1 impossible	
Total 468 : 112	464.00 : 116	4 : 1 very near	4 : 1
	483.30 : 96.7	5 : 1 improbable	
	435.00 : 145	3 1 improbable	
	543.75 36.25	15 · 1 impossible	
		Hence F_3 (*grandiflora* × *rubricalyx*) 2 families 4 : 1 Also 4 families constant R 3 " constant r 2 " intermediate in pigmentation of buds.	

F_3 (*Oe. rubricalyx* × *grandiflora*).

57 : 31	58.70 : 29.3	2 : 1 very near	2 : 1
	66.00 : 22	3 : 1 ?	
	82.50 : 5.5	15 : 1 impossible	
2 : 3		?	
22 : 6	21.00 : 7	3 : 1 very near	3 : 1
112 : 69	120.70 : 60.3	3 : 1 impossible	
	135.75 : 45.25	2 : 1 near?	2 : 1 ?
12 : 2		?	
182 : 29	176.00 : 35	5 : 1 near	
	168.80 : 42.2	4 : 1 impossible	5 : 1
	197.80 : 13.2	15 : 1 impossible	
4 : 2		?	
55 : 2	53.40 : 3.6	15 : 1 close	15 : 1
37 : 2	36.60 : 2.4	15 : 1 perfect	15 : 1
72 : 6	73.10 : 4.9	15 : 1 very near	15 : 1
59 : 1	56.25 : 3.75	15 : 1 not very close	15 : 1
Total 223 : 11	219.40 : 14.6	15 1 very close	15 : 1
79 : 37	77.30 : 38.7	2 : 1 very near	2 : 1 ?
	87.00 : 29	3 · 1 ?	
	108.75 : 7.25	15 : 1 impossible	
5 : 3		?	
80 : 34	85.50 : 28.5	3 1 near	
	76.00 : 38	2 : 1 nearer	2 : 1 ?
		Hence in F_3 *rubricalyx* × *grandiflora* Probably 4 families 2 : 1 ratio 1 family 3 : 1 " 1 " 5 : 1 " 4 families 15 : 1 " Also 2 families constant for R 8 " constant for r 1 family intermediate 186 plants.	

more precise significance, but particularly the ratios 5:1 and 15:1 in addition to 3:1 fall so closely into definite categories that the probability of there all being significant is great. The foregoing table contains the F_2 and F_3 ratios for the various families.

Considering these data as a whole, the ratios nearly all fall remarkably close to whole numbers. In the first column of Table II. are given the actual ratios obtained, in the second column the expectation for different ratios, and in the third column the conclusion as to the ratios probably represented in each case. Many of the families are larger than these of Nilsson-Ehle, and in general they appear to fit the various ratios more closely.

Considering first the F_2 families, it will be seen that those whose ratios are 3:1 or 15:1 are in perfect or almost perfect accord with expectation. This being the case, it seems probable that the 5:1 and 4:1 ratios obtained are significant as such, and in any case they cannot be considered merely wide departures from 3:1. Of the 5:1 ratios the first, second, and fourth are in perfect agreement with 5:1 while the other one is very close, as is also the sum of these four families (292:54). The significance of these facts is further heightened by the fact that three of these four families (the first, third and fourth) are derived from selfing different flowers of the same F_1 plant. This is shown in my original record of these experiments,[1] and it almost forces the conclusion that in this particular plant as well as others giving similar ratios, R gametes were being produced with greater frequency than r gametes in the ratio 5:3. There is, however, another explanation which will be considered later.

In the results of Nilsson-Ehle, on the other hand, the ratios do not fall clearly into such intermediate categories but tend to form a continuous series of ratios as Kajanus pointed out. Thus in one series of crosses[2] between black and white glumes involving only monohybrid ratios, the F_2 ratios in the 13 families actually range from 2.2:1 (323:144) to 4.1:1 (230:56), yet the total (2468:795) is fairly close to 3:1. One of these families contained 86

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[1] *Zeitschr. f. Abst. u. Vererb.*, 11, p. 236.

[2] "Kreuzungsuntersuchungen," I, p. 18.

black (B): 22 white (B). F_3 offspring were grown from each of these 108 plants and the results showed their composition to have been as follows: 36 BB:50Bb:22 bb. From this result Nilsson-Ehle concludes that there was a preponderance of "black" gametes over "white" ones. But a series of F_3 families in another cross gave the reverse condition, 26 BB:60Bb: 33 bb, from which the conclusion is drawn that white gametes were here more numerous than black ones. Even though these results offset each other yet they cannot be referred merely to chance fluctuations in ratios. But no further explanation of them was offered. It will be shown later that in my crosses of *Œ. rubricalyx* and *Œ. grandiflora* these deviating ratios do not offset each other but are all consistent with the hypothesis that R gametes are being produced with greater frequency than r gametes.

Returning now to Table II. the first ratio (68:16) is not a very bad fit for 3:1, although exceedingly close to 4:1. It might easily pass for 3:1 without further comment were it not for the fact that two other ratios in this table are in very close agreement with 4:1 while they depart very widely from 3:1. The sum of these two ratios (468:112) is very close to 4:1 while it is highly improbable as a 3:1 ratio, the more so since the actual 3:1 ratios are almost in precise agreement with expectation.

Among the three F_2 families from *Œ. grandiflora* × *rubricalyx*, two show a 15:1 ratio and one a 4:1 or perhaps a 3:1 ratio. Hence it might be supposed that the *rubricalyx* plant which was used as pollen parent, already possessed duplicate factors for red. But this was not the case. That plant was in fact heterozygous for a single factor, since when crossed with *grandiflora* it gave an F_1 of 79R : 71r, which is as near to equality as could be expected. The full history of the *rubricalyx* individuals used for this and the reciprocal cross has been given in pedigree form in another paper,[1] to which reference should be made. It may be said that in both cases they are descended from the family which contained 33R : 11r. One member of this family was pollinated by *nanella* and produced a family of 42 plants. One of the latter (No. IV., 2), which was a perfect *rubricalyx* in appearance but

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[1] Gates, *Zeitschr. f. Abst. u. Vererb.*, 11: opp. p. 216 and on p. 217.

carried dwarfing latent, was used to pollinate *Œ. grandiflora.* Since the F_2 offspring of this cross gave 15:1 ratios in two families, while the F_1 was a 1:1 ratio, duplicate mutations must have intervened between these two generations. The two plants which were the parents of the families containing 142 R: 15 r and 113 R: 4 r respectively must have possessed the duplicate factor in all their germ cells, so that they were heterozygous for R and R′. Their composition might then be written RrR′r′.

As pointed out earlier in this paper, such a condition might have arisen (*a*) through the transformation of a chromosome belonging to a second pair, (*b*) through an exchange of mates on the part of two pairs of chromosomes. We may now examine the comparative credibility of these two alternatives. There are certain difficulties with either hypothesis, one of which is that the transformation from the monomerous to the dimerous condition, whether effected by chemical or mechanical means, must apparently have taken place early in the ontogeny, before definitive germ cells are formed. The alternative hypothesis would be that all the germ cells had undergone the transformation simultaneously and independently, which one cannot believe possible.

There is, however, one consideration which makes it appear probable that the duplicate condition for R is not usually arrived at through a transformation of a new chromosome, but rather through a redistribution of the chromosomes. The 15:1 ratio can only be obtained from an RrR′r′ parent, in which both duplicate factors are heterozygous. It would therefore be necessary to assume when a 15:1 family is derived from a 3:1 family, that a chromosome belonging to a new pair had undergone a chemical transformation while its mate and the mate of the original modified chromosome were unaffected, *i. e.*, that the condition Rrr′r′ became altered directly to RrR′r′. This is very unlikely. On the other hand, as I showed long ago,[1] the chromosomes in *Œnothera* are very loosely paired during the reduction division, and moreover irregular chromosome distributions have been shown to occur at this time (as in the production of *Œ.* mut. *lata*). I also (*l. c.*) pointed out the probability

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[1] "A Study of Reduction in *Œnothera rubrinervis*," *Bot. Gazette*, 46: 1–34, pls. 3, 1908.

that exchanges of chromosomes of different pairs but without change in number would take place under these conditions. By such a mismating or exchange of mates on the part of two chromosome pairs, a plant which was homozygous (RR) for one factor would give rise to plants which were heterozygous for duplicate factors (RrR′r′). This is then what has probably occurred in the cases where plants from a 3:1 family have given rise to 15:1 ratios. The frequency with which such mismating occurs in *Œnothera* may thus be estimated.

It is known that the chromosomes of *Œnothera* are in pairs (doubtless of paternal and maternal origin) throughout the somatic divisions, and the paired arrangement is probably a feature of the first mitosis after fertilization. If, then, a plant which would have been homozygous for a single factor (RR) becomes transformed into one which is heterozygous for duplicate factors (RrR′r′) and so gives a ratio 15:1 in its offspring, the most likely assumption is that *at the time of fertilization* the two R chromosomes, instead of becoming paired with each other, each paired with another (r) chromosome. Hence in this case the regrouping of chromosomes probably occurred not during meiosis where it would have to occur simultaneously in all the germ cells, but as a feature of fertilization or the first mitosis of the embryo. It will be shown later, however, that mismatings of the chromosome pairs probably also occur during meiosis and so modify the 3:1 ratio. To sum up, it appears that when a 15:1 family is derived directly from a plant in a 3:1 family, the remating of the chromosomes must have occurred at fertilization or soon afterwards; but when, for example, a 4:1 or a 5:1 family is derived from a 3:1 family, this may be accounted for by a certain amount of remating of chromosomes during meiosis.

The method above described will also apply to the origin of duplicate and triplicate factors in wheat and is perhaps more probable than the successive chemical transformation of different chromosomes. There is, however, a method of testing between these two possibilities. If the duplicate condition arises through a regrouping of the chromosome pairs, then, as has been mentioned, a race or a plant homozygous (RR) for one factor will give rise to a plant heterozygous for two factors

(RrR′r′). On the other hand, if the chemical transformation of a fresh chromosome takes place in a homozygous monomeric plant (RR), then the dimerous individual derived from such a monomerous plant should have the constitution RRR′r′.[1] It would be possible to determine between these two alternatives by breeding tests. If the constitution of the plant is RrR′r′ its offspring should give a 15:1 ratio. If it is RRR′r′ they would all be red in F_1 and F_2. But plants having the former formula could also be produced by the mismating of chromosome-pairs during meiosis in RR plants.

If we now return to the table (p. 210) and examine the F_2 from the reciprocal cross (*rubricalyx* × *grandiflora*) we find a total absence of 15:1 ratios, showing that not only was the *rubricalyx* parent of this cross monomerous but its offspring remained so. The parent of this cross was a member (No. IV., 8) of the monomerous family 33:11. As will be seen from the table, two of the F_2 families from *rubricalyx* × *grandiflora* gave perfect or almost perfect 3:1 ratios. Four others gave 5:1 ratios, three of which were perfect and the other very close to expectation as already pointed out. I have at present no further explanation of these 5:1 ratios to offer, but it seems probable that their significance will later become apparent.

Ratios more or less in excess of 3:1 could be obtained from plants homozygous for one factor, if there was a tendency for mismating of the chromosomes in meiosis. But this will not account for the definiteness of the 5:1 ratios obtained.

Turning to the F_3 of *grandiflora* × *rubricalyx* the full data are given in my book (p. 255). Four families were constant for R, 3 constant for r, 2 families numbering respectively 283 and 20 plants bred true to an intermediate condition, and 2 families split in the ratio 4:1, as shown in the table (p. 211). The excess of R's in the last two families is a significant excess over 3:1, however it is brought about.

In the F_3 of *rubricalyx* × *grandiflora*, four families give ratios nearest 2:1, one family near 3:1, one near 5:1 and four very close to 15:1. Whatever the significance of the 2;1 and 5:1 ratios in

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[1] We have already found it highly improbable that a plant Rr could be directly transformed chemically into RrR′r′, since we should anticipate that the chromosome r would undergo a mutation before the chromosome r′.

these families, the appearance of 15:1 ratios in the F_3 of this cross is of much interest, since the F_2 contained no families which could reasonably be construed as containing duplicate factors, except the one having the incomplete ratio 47:3. Reference to the pedigree numbers[1] shows that the first two are derived from the F_2 family No. 60 in which the ratio is doubtful, the third is derived from selfing a plant in the F_2 family No. 62, and the fourth from selfing one in family No. 63. In these two families the ratios were respectively 67:13 and 82:13, both of which are shown (p. 210) to be very near 5:1 ratios. The appearance of these 15:1 ratios in F_2 from 5:1 families can be explained if we assume that independent duplicate mutations have occurred in the F_2 families 60, 62, and 63. This must happen as previously outlined, through a plant which is homozygous for one factor giving rise to a plant which is heterozygous for two; or in other words, through the rearrangement of a pair of homologous chromosomes so that they belong to different pairs.

Another point which will be explained by the present hypothesis is the difference in the depth of color in homozygous red-budded races. Thus in the F_3 families 93 and 95,[2] containing respectively 280 and 312 plants, the latter were constantly darker red than the former. The latter family was doubtless homozygous for duplicate factors (RRR′R′), or at least RRR′r′, since the family from which it was derived yielded 15:1 ratios. The former family was on the other hand probably homozygous for a single factor (RR) and hence not so densely red-pigmented.

It will thus be seen that in several instances 15:1 families have been obtained from the offspring of 3:1 or 5:1 families. All such cases can be explained by assuming that a duplicate mutation has intervened. The original mutation by which deep red buds in *Œnothera* first appeared is an extremely rare occurrence, having occurred but once in all cultures of *Œnothera*. When, however, a chromosome has once undergone this change it is reasonable to suppose that other chromosomes in the same nucleus could without difficulty take on an analogous transformation. The whole mechanism is, however, at hand in the

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[1] See "The Mutation Factor in Evolution," p. 256.

[2] *L. c.*, p. 255.

meiotic divisions, for transforming the original 3:1 ratio into a 15:1 by merely redistributing the chromosome pairs.

In concluding this paper it is desirable to compare the related but different results recently obtained by Honing,[1] with two varieties of *Canna indica* which are naturalized in Sumatra. One variety has green leaves while in the other the leaves have a broad red margin.

From the offspring of plants of the latter variety Honing obtained ratios red: green of 3:1, 9:7 and 27:37. The same ratios were obtained in crossing the two varieties. These ratios are accounted for by the hypothesis that the coöperation of three "factors" is necessary to produce the red margin. If these are located in chromosomes belonging to three different pairs, then the resulting ratio should be 27 red: 37 green, since the character can only appear in the presence of all three factors A, B, C. On the other hand, if all three factors are located in the same chromosome a 3:1 ratio would be obtained, while if two of them were in one chromosome and the third in a chromosome of a second pair, the ratio would be 9:7.

It was found that in certain cases plants in families having a 3:1 ratio gave rise in the next generation to a 9:7 or 27:37 family. In such cases one may assume that a mutation has taken place resulting in a redistribution of the determiners, the three which were present in one chromosome being rearranged so that they are in chromosomes belonging to two or three different pairs. So far as I am aware, this is the first experimental evidence that an actual rearrangement of the chromomeres in the chromosomes is one of the kinds of change which the nucleus may undergo, the case being somewhat different from Morgan's well-known phenomena of "crossing over" in *Drosophila.* Further experiments are necessary to test the nature of this evidence for the occurrence of mutations in which such a rearrangement of the nuclear material can take place.

SUMMARY.

Nilsson-Ehle was the first to show that duplicate and triplicate factors for red are present in certain strains of wheat. He

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[1] Honing, J. A., 1915, "Kreuzungsversuche mit Canna-Varietäten," *Rec. Trav. bot. Néerlandais*, Vol. 12: Livr. 1, pp. 26.

found, moreover, that the same strain may be in one case monomerous and in another case dimerous for this character; and that while, for example, Grenadier wheat possessed three independent units for red, Extra-Squarehead possessed only one. The origin of the original "factor" for red may be accounted for in the wheats as in *Œnothera rubricalyx*, through the chemical transformation of one chromosome or a pair of homologous chromosomes. The duplicate condition for the character R may have arisen (1) through a chemical mutation in a second pair of chromosomes, (2) through a re-mating of the chromosomes (RR) forming a homozygous pair. The latter method is for various reasons the more probable.

Although the original *Œnothera rubricalyx* was a monohybrid and continued so for at least two generations, yet in subsequent generations involved in crosses with *Œ. grandiflora*, 15:1 or di-hybrid ratios were derived from the offspring of members of 3:1 families. This can best be accounted for by supposing that in a plant (RR) homozygous for one factor, a re-grouping of the chromosome pairs occurred. This re-grouping involves merely an exchange of mates on the part of the chromosomes RR so that they now belong to different pairs. The formula for the plant may now be written RrR′r′, *i. e.*, the plant is heterozygous for two independent units for red and its offspring will give a 15:1 ratio.

The second mutation, producing the duplicate condition for R, is thus probably a purely mechanical process, while the original mutation which produced the "factor" R is a chemical change of wholly different nature. It is possible that in some cases the duplicate and triplicate conditions also arise through the chemical transformation of additional chromosomes.

When a 15:1 family arises from a 3:1 or 5:1 family, as has happened several times in *Œ. rubricalyx* hybrids, it is necessary to assume that the regrouping or remating of chromosome pairs which led from the monohybrid to the dihybrid condition, took place at fertilization, or at any rate early in the ontogeny, and is then handed down to the germ cells by mitosis. The chromosomes are known to be paired in the somatic divisions, and it seems probable that the manner of pairing set up in fertilization continues in this case throughout the ontogeny, though this is not true for all organisms. Otherwise it would be necessary to assume that when a plant in a 3:1 family gives rise to a 15:1 family all its germ cells have simultaneously undergone a mis-mating of the chromosome pairs during meiosis, a highly improbable event.

In the F_2 and F_3 hybrids of *Œ. rubricalyx* and *Œ. grandiflora*, in addition to 3:1 and 15:1 ratios, 2:1, 4:1 and 5:1 ratios occur. The 5:1 ratios at least seem to be significant, indicating that R and r gametes are regularly being produced in the ratio 5:3, or that a certain amount of re-grouping of the R chromosomes is regularly occurring during meiosis.