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by R. Ruggles Gates.**

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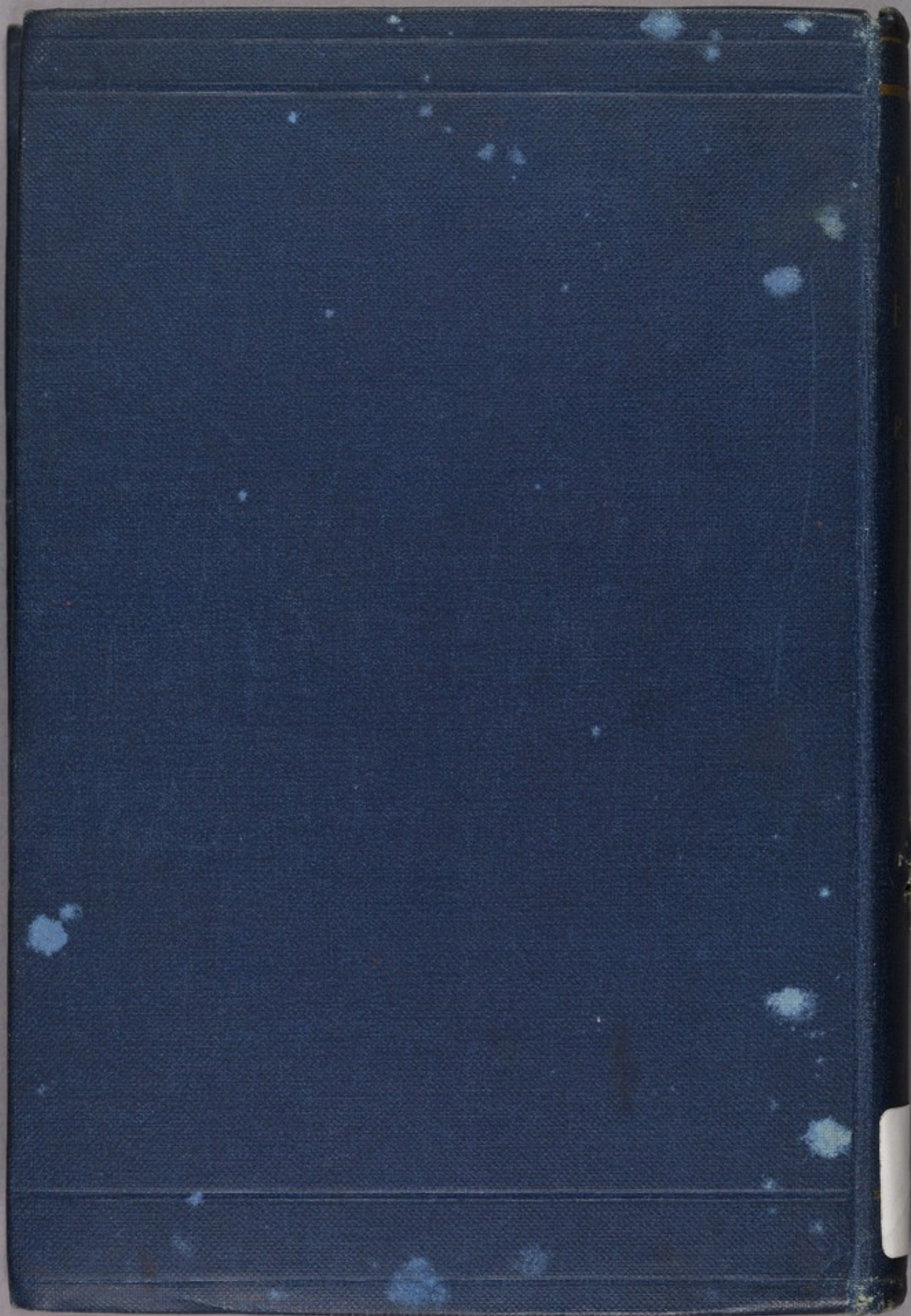
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THE
MUTATION FACTOR
IN EVOLUTION

WITH PARTICULAR REFERENCE
TO OENOTHERA

BY

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PREFACE

IN this book, which has been written at the invitation of the Editor of Messrs. Macmillan's Science Monograph Series, I have endeavoured to bring together all the facts which bear vitally upon the question of mutations. In doing so attention has been confined largely to the genus *Oenothera*, because it is with reference to this group of plants that most of the crucial questions concerning mutations have been debated and decided.

At one time it seemed probable that the numerous suggestions of Mendelians, that mutation was, after all, only a phenomenon of hybridism, might prove true. Out of deference to these views, I formerly ascribed rather more weight to crossing as a cause or source of mutations than I should do now. It will, I think, be apprehended from the many recent investigations of mutations, as well as from the contents of this book, that the conception of mutation as a process *sui generis* has been amply justified. Every line of investigation of the *Oenothera* mutations has strengthened this view, to the point of demonstration.

Historically, it has recently been shown, through a specimen of Michaux, that *Oe. Lamarckiana* has the same right as any other North American species to rank as an endemic element of the flora. Cytologically, it has been discovered that various nuclear changes take place in this species which cannot be explained in terms of Mendelian

unit-factors or any other hybrid process. The extensive hybridisation experiments have formed a third line of attack, and de Vries has shown that their results can only be co-ordinated and explained by assuming mutation as a distinct process. The convergence of these and other lines of evidence upon the question of mutations makes the conclusion irresistible that the mutation phenomena represent a well-defined type of variability which all evolutionists in future will have to reckon with.

The actual proof that germinal changes do occur has depended more upon the cytological work than anything else, and it is a promising sign that more investigations involving a comparison of internal and external structure in the study of variability and hybrids are now being undertaken. The precision of the nuclear processes is such that these comparisons are no longer vague and remote, as the layman supposes; and the recent advances in this subject make the field more promising and definite than ever. Since *Oe. mut. gigas* was shown to be a new species originating suddenly through tetraploidy, the number of comparable cases among wild plants and animals has increased amazingly, showing that this is an evolutionary process of much significance. It is probable that duplication of a single chromosome, as it occurs in *Oe. mut. lata*, will also be found in various other organisms.

It is obvious that, although marked germinal changes have now been shown to take place in many organisms and from a variety of causes, yet much difference of opinion will continue to exist regarding the precise place they should occupy in the hierarchy of evolutionary factors; but they can never again be considered negligible from this point of view, and the tendency to emphasise their importance grows continually stronger.

With greater understanding of mutations and the processes and agencies by means of which these changes take place, it is by no means chimerical to anticipate that they

will ultimately be brought under control, so that they may be experimentally produced and thus contribute enormously to the economic welfare of mankind. Every fact which leads to a better understanding of the changes involved or the means of producing them is a step in this direction.

Since my work with the *Oenothera* mutations began, in 1905, the investigations have taken me into every phase of the subject. The field is still rapidly developing, with many investigators taking part, and the last two years have been more prolific in results than ever before. The present book, in addition to summarising our knowledge of the subject, contains a large amount of hitherto unpublished matter from my own studies and experiments. These results are found in every chapter, but many others have been withheld for lack of space.

In the course of my researches I have received aid from various societies and many individuals which I wish gratefully to acknowledge. Several individual acknowledgments are made in the text, but I wish here specifically to thank a number of others. The Royal Society has made several grants of money, and also the British Association in 1913, and the Carnegie Institution of Washington in 1908. For facilities for growing the plants I have been indebted in different years to Professor John M. Coulter at the University of Chicago; Professor Frank R. Lillie, Director of the Marine Biological Laboratory, Woods Hole, Mass.; Professor Wm. Trelease, former Director of the Missouri Botanical Garden; Professor Wm. Bateson, F.R.S., at the John Innes Horticultural Institution, and Dr. E. J. Russell at the Rothamsted Experimental Station. Seeds have been kindly sent by many Botanical Gardens and also by Professor S. M. Tracy, of Biloxi, Mississippi; Professor R. Wilson Smith, of Toronto; Professor Aven Nelson, of Wyoming; Professor Hugo de Vries; Professor H. W. W. Pearson, of Cape Town, and many others.

For courtesies in connection with the examination of herbaria I am indebted to Sir David Prain, F.R.S., and Dr. O. Stapf, F.R.S., at Kew; Dr. A. B. Rendle, F.R.S., and Mr. E. G. Baker, F.L.S., at the British Museum (Natural History); Dr. B. Daydon Jackson at the Linnean Society; Professor A. C. Seward, F.R.S., and Dr. C. E. Moss, F.L.S., at Cambridge; and Professor S. H. Vines, F.R.S., at Oxford, where several most valuable specimens were found.

In connection with the publication of this book, I am indebted to the Council of the Linnean Society for the use of a number of blocks (Figs. 1, 2, 22-33, 37-39, 48-51, 54-55, 81, 82, 84); to the Clarendon Press for permission to copy figures from the *Annals of Botany*; to Messrs. J. and A. Churchill for permission to copy figures from the *Quarterly Journal of Microscopic Science*, and for the blocks for Figs. 59 and 60; to Gebrüder Borntraeger for supplying a number of blocks from the *Zeitschrift für ind. Abst. u. Vererbungslehre* (Figs. 34-36, 41, 58, 61, 79, 80, 85-96, 106, 111, 112); to the University of Chicago Press for permission to copy figures from the *Botanical Gazette*; to Dr. Geo. T. Moore for the loan of several blocks (Figs. 62-65) from the Reports of the Missouri Botanical Garden; and to the Executive Council of the State of Iowa for permission to copy certain figures from the Proceedings of the Iowa Academy of Science. Professor L. Blaringhem has also kindly given me the print for Fig. 16, and Mr. N. Heribert-Nilsson has sent the prints for Figs. 20 and 21. I also desire to express my thanks to Professor J. Bretland Farmer, F.R.S., for criticism and help in various ways. My indebtedness to the work of Professor de Vries will be obvious throughout the book. Finally, I am much indebted to Professor R. A. Gregory, Editor of the Series, for his help and care in passing the book through the press.

R. RUGGLES GATES.

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What next ? A tuft of evening primroses,
O'er which the mind may hover till it dozes ;
O'er which it well might take a pleasant sleep,
But that 'tis ever startled by the leap
Of buds into ripe flowers ; or by the flitting
Of divers moths, that aye their rest are quitting ;
Or by the moon lifting her silver rim
Above a cloud, and with a gradual swim
Coming into the blue with all her light.

JOHN KEATS : Early Poem,
(1815 or earlier).

THE MUTATION FACTOR IN EVOLUTION

WITH PARTICULAR REFERENCE TO OENOTHERA

CHAPTER I

INTRODUCTION

Evolutionary Factors

THE nature and causes of organic diversity are the problem of the evolutionist. The phenomena of heredity and variation are both unique in the organic kingdom, and both are equally necessary for an explanation of the evolutionary changes which all agree have taken place in geological time. For while variability leads immediately to diversity, heredity is the conservative factor which preserves, and so accumulates, the differences gained. Regarding the ultimate nature and cause of variability we still know very little. The bathmic theories, which now receive little support, would regard it as an inherent principle leading, not only to diversity, but to progressively increasing complexity. Others have regarded variability as purely a product of the environment acting upon the organism. Without adopting either view in its extreme form, one may hold that variability is the result of interaction between the organism and its environment in various ways not yet understood.

The determination of these methods of interaction, and their relation to phylogeny, appears to be the present

problem of evolution. The problem is tremendously complicated by the effects of organisms upon each other, as in the relations of mimicry and the obtaining of food. The effects which insects have had upon the evolution of the flower, and the complementary effects upon the insects themselves, are but one instance of this sort. It is obvious that when such interactions have been going on in the plant and animal kingdoms throughout geological time, it is almost impossible to disentangle these effects from any orthogenetic tendencies which may have existed except those which come into expression in large orders and over considerable periods of time.

Was it decreed by natural selection that there should be two kingdoms, plant and animal, the one "parasitic" upon the other? This would seem most probable, though a few bacteria with wholly different types of nutrition have survived to the present day. But within the plant kingdom, for example, the tendency towards the gradual reduction of the gametophyte and the increase in complexity and importance of the sporophyte may, we think, be legitimately regarded as an orthogenetic tendency, even though it results in part from an original inherent difference between sporophyte and gametophyte in the structure of their nuclei. The fact that in the Red Algæ, the tetrasporic (gametophyte) plants are no more complex than the carposporic (sporophyte) plants, though each gives rise to the other, shows that in a marine environment no increase in complexity need follow the change in nuclear structure. Similarly, the independent gradual and progressive development of horns in various families of mammals may be looked upon, with Osborn (292), as the result of an orthogenetic tendency, though the inherent cause is here of a totally different character. It may be that the Bergsonian type of creative evolution contains a more reasonable harmony of the bathmic and environmental views of evolution than has yet been

realised, though it is not within my province to consider the matter in this brief introductory sketch.

At any rate, biology has passed the stage when single evolutionary factors, no matter how insistently urged or how brilliantly advocated, can be held accountable for the great diversity of life which we see around us, or for the changeful panorama of organisms revealed in the rocks. The inheritance of acquired characters, natural selection, orthogenesis, mutation, and even crossing, have been at various times appealed to as universally applicable to the solution of the problems of species-origin. Curiously enough, the propounders of the various doctrines (with the exception of that of crossing) seldom believed in their universality, but fitted them into a niche along with other factors in their general scheme. Thus Darwin believed in the direct action of environment and the inheritance of the effects of use and disuse, though he assigned to natural selection the major *rôle* in species-differentiation. Had there been larger knowledge of discontinuity or alternative inheritance in his time, Darwin would doubtless have laid more stress upon sports or mutations as a method by which new species might originate; for his well-known objection to their efficacy was the fact that they would be swamped by blending with their parents in inheritance. But Neo-Darwinians, becoming over-impressed by one of the factors (albeit the most important factor) which Darwin himself recognised, frequently came to personify Natural Selection as the only efficient cause or means of specific differentiation. In the same way many Mendelians and some mutationists have failed to overcome the natural tendency to regard the arc within their vision in the investigation of discontinuity in inheritance as the whole circumference of the circle.

Certain writers, being greatly impressed by the numerous cases, such as those of many water plants, in which species

seem to have originated by direct adaptational response to a changed environment, have assumed this to be the universal factor of species modification. But even a superficial survey of plant and animal forms makes it obvious that countless specific differences exist which cannot be accounted for in this way, even though such an explanation seems quite adequate for a number of cases. It appears probable, however, from various ecological facts which need not be detailed here, such as the dwarf character of alpine species, that impressed modifications or direct responses to changed environment may in some cases become hereditary after many generations, though specific proof of this is not yet forthcoming. Perhaps it may be useful to regard temporary modifications as due to impressed cytoplasmic changes, which may in some cases finally become hereditary by effecting a permanent change in the constitution of the nucleus. But it must be borne in mind that such conditions may have originated, as de Vries believes, through the germinal change having occurred first and the new form having found its appropriate habitat afterwards.

Again, though the direct evidence for it is at present rather scanty, it is conceivable that the Lamarckian principle in cases of use and disuse may have applied to the modification of many species. And the principle of orthogenesis, whatever its explanation may be, appears to be necessary to account for the broader features of phylogeny in many phyla, and for the general progressive trend which evolution as a whole undoubtedly exhibits, at least in the main line of descent leading to mammals and man. By progress here is meant increase in complexity and in power of control over the environment.

It is now coming to be recognised that the various evolutionary factors above mentioned are by no means mutually exclusive, but they result from different phases of organic activity and have all probably played their part

in the infinitely complex result we call evolution. An understanding of the multifarious diversity of the earth's present flora and fauna requires also the recognition of the effects, *e.g.*, of geographical and physiological isolation, and no doubt also many features which have not yet been recognised in the activities of organisms. By evolutionary factors we therefore mean activities, of whatever nature, leading to specific diversity.

Though mutations are but one of the diversifying activities of organisms, they have the distinct advantage of being, not linear, but in many directions. Just as an alpine climber dangling over a chasm may, by changing his hold, swing himself on to a shelf from which he can make a fresh start in some other direction, so we may think of the organism trying many unconscious experiments in its offspring, some of which are hurled by the gravitational effect of natural selection into the abyss of extinction, while others with a more fortunate turn rest on a ledge of safety whence new essays of variability begin. The desire of the climber is to get to the top, but we cannot attribute any such fixed purpose to the organism, and it seems more reasonable to ascribe the increase in complexity associated with much of evolution to the chemical and structural complexity of the protoplasm and especially to its unique property of irritability.

On the other hand, only a tithe of the evolution we know has been progressive. Much of it has been retrogressive, and still more divergent. The causes of divergences and of progress are the things to be explained. Aside from the infinitely labyrinthine by-paths of digression and retrogression, the main high road of evolution, if there is one, can only be conjectured in a simplified way by projecting backwards to their hypothetical meeting points the main axes of the various phyla of organisms. When this is done, those meeting points are found to be for the most part lost

in the dawn of geological time. But they reveal enough to show that the high road, far from being a straight single or double track, has been tortuous in many directions which do not permit of expression in three dimensions as up or down, backwards or forwards, or even right or left. The relatively few phyla, such as the Angiosperms, Reptiles, Birds and Mammals, the origin of which is not shrouded in darkness, appear to show that each phylum advanced as a tidal inundation with a complexity of wave within wave or, to change the metaphor, as a meshwork of interwoven strands to form a cable.

Mutations

In this book we are concerned almost wholly with mutations and the *rôle* they have played in connection with specific diversity. Among recent writers, de Vries (423) has recognised that mutation does not furnish in itself a complete theory of evolution, and that it must be supplemented at least by natural selection and orthogenesis. Other writers have expressed a variety of opinions concerning mutations, from the extreme view that this is the only method of species-origin, to the equally extreme denial that mutations have any evolutionary value whatever.

The views of mutation which need concern us here are those which consider the nature of the behaviour in the *Oenotheras*. Formerly, speculations regarding these phenomena were rife because there were relatively few decisive facts to go upon. But the subsequent extensive cytological and breeding work has greatly narrowed the range of speculation and rendered untenable most of the early suggestions. Bateson (16) was one of the first to suggest, in 1902, that *Oe. Lamarckiana* is a hybrid splitting off various Mendelian recessive forms, and this view has since been expressed by others in a variety of

ways. That *Oe. Lamarckiana* has undergone crossing is, we think, undoubtedly true, at least of some races. But the idea that the mutants are merely Mendelian recombinations has been refuted by the cytological facts. The questions, therefore, remain, (1) What is the nature of the hybridity of *Oe. Lamarckiana*?¹ and (2) What is the relation between this condition and the phenomena of mutation? Various aspects of these questions will be answered in the following chapters. It may be said here, in answer to the first question, that although *Oe. Lamarckiana* has very probably undergone crossing of races (in which it is in agreement with many other wild species), yet there is no satisfactory evidence that it has been synthesised as the result of a cross between two other species.

Regarding the second question, it may be said that *Oe. Lamarckiana* is in a condition of "germinal instability," which may have resulted from the indirect effects of crossing on plants having the cytological peculiarities of the *Oenotheras*. The delicate balance of the loosely paired meiotic chromosomes has been disturbed, leading to the appearance of some of the most characteristic of the mutations. This germinal instability is probably an induced condition, which manifests itself in manifold departures from the parent form.

It must be stated quite clearly, however, that the mutants which occur are in no sense the reappearance of characters which were acquired through a cross. They are, on the contrary, the result of a distinct process, though the conditions under which that process may take place may have been induced, or at any rate, the process may have been rendered more easy, by previous crossing. This should be sufficient to show the superficiality of the view that when a plant is crossed, the

¹ Since this was written, the discovery that *Oe. Lamarckiana* was originally a wild species in North America precludes the possibility that it originated as a hybrid in cultivation.

only thing left for it to do is to split out the characters it received. Many writers apparently think that by branding a plant as a "hybrid" they have answered all the questions of heredity and evolution which its behaviour may propound. It should be remembered that crossing in nature is a common phenomenon, and that many wild species are hybrid in this sense. So true is this, that among open-pollinated plants the evolutionary unit is in reality not a single pure biotype, but a population containing a large number of closely related and freely intercrossing races. These races differ from each other in varying degrees, and hence the difficulties of the systematist when making a critical study of the species in such polymorphic genera.

Several writers have rashly concluded that because crossing has apparently led to polymorphism in certain genera, therefore crossing is the one and only efficient cause of this condition. Biologists appear to be more prone than other men of science to rush blindly to a universal affirmative, neglecting the logical chasms that so frequently yawn in their pathway. Let us apply the above idea to the conditions in a few polymorphic groups. Thus Rosen (317, 318) has shown by breeding experiments that new and constant forms, which are not Mendelian recombinations, can be produced by crosses between the many elementary species of *Erophila verna*. But it by no means follows either that all new species, even in *Erophila verna*, originate in this way, or that polymorphism is not also produced by other agencies. Multiplication of races also perhaps occurs in similar fashion in such genera as *Rosa*, *Rubus*, and *Crataegus*. Yet it is always open to experiment to prove that in these genera also new forms may arise through mutations.

If we turn now to the notoriously polymorphic genera *Hieracium* and *Antennaria*, the polymorphism is here connected with, and in the view of many writers caused by, the condition of apogamy. Obviously, in parthenogenetic

forms the polymorphic condition cannot be brought about by crossing, although it is of course possible to indulge in the argument that crossing may have taken place before the apogamous condition supervened.

Again, in the genus *Oenothera* itself, there appears to be the greatest amount of polymorphism among the small-flowered species of the *biennis* series, though these are close-pollinated, and rarely or never cross. To take an extreme example, in *Bacteria*, which no one suspects of crossing, not only is there great polymorphism aside from environmentally-produced fluctuations, but germinal changes or mutations occur, either spontaneously or after subjection to a variety of experimental stimuli.

Since, therefore, it must be conceded that germinal changes occur in the absence of crossing, it is obvious that hybridisation cannot be the efficient cause of all germinal change. But we may go a step further and say that, whether this be admitted or not, any new form appearing from a known hybrid or otherwise must be analysed to discover how it appeared. If cytological and experimental analysis shows that a germinal change has taken place, then it is immaterial from an evolutionary point of view whether it occurred in a cross-bred or a pure-bred race.

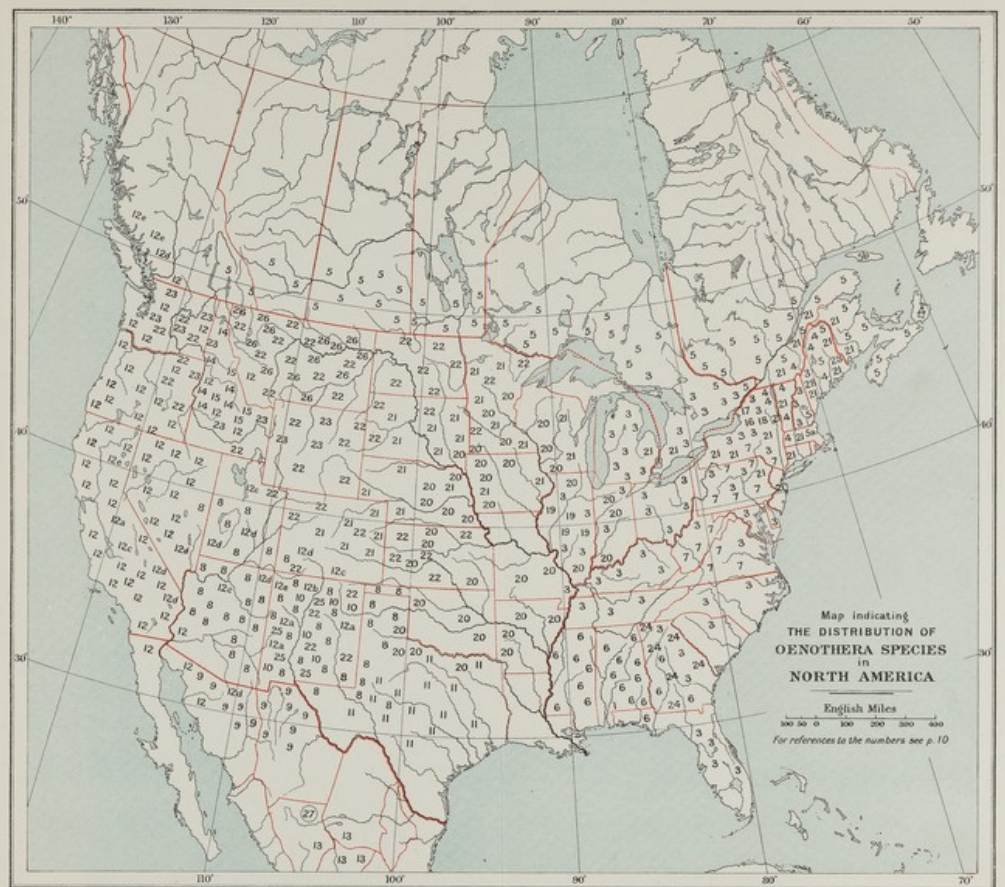
Such cases have been amply demonstrated by the cytological work in *Oenothera*. They show that germinal changes do take place. Polymorphism is not, then, a universal result of a single cause, but a condition which may be brought about by various agencies.

Finally, it may be pointed out that mutation is a composite process, and each mutation must therefore be considered by itself as regards its manner of origin and evolutionary significance. That many diverse types of change are involved in the origin of different mutants has been clearly shown by the recent work. It must not be forgotten, however, that all mutations are subject to the action of natural selection, and that all which survive must have passed through its sieve.

LIST OF SPECIES IN THE ONAGRA GROUP OF OENOTHERA.

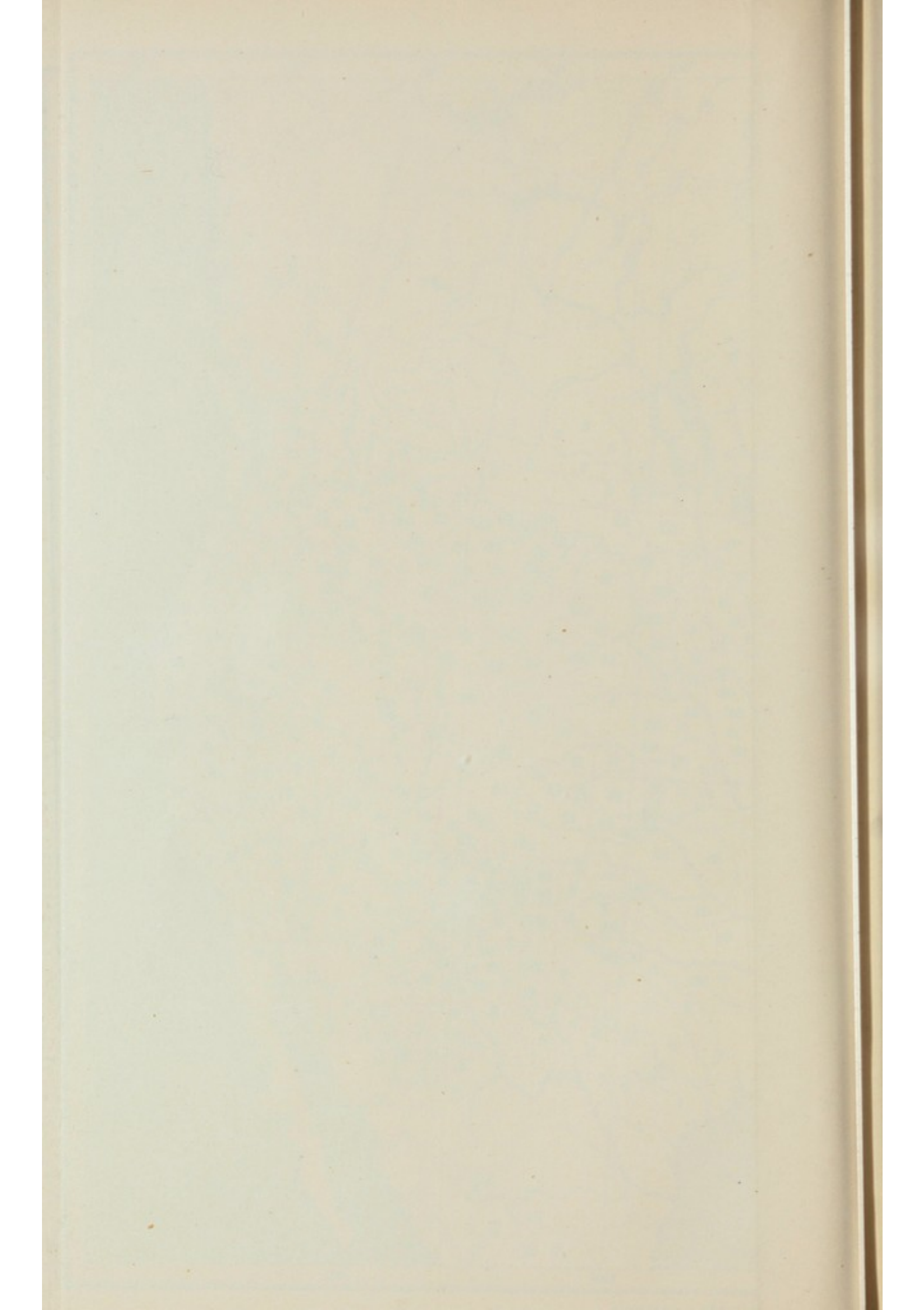
- | | |
|--|--|
| 1. <i>Oe. grandiflora</i> , Solander. | 12d. <i>Oe. Hookeri</i> var. <i>angustifolia</i> n. var. |
| 2. <i>Oe. Lamarckiana</i> , Ser. | |
| 2a. „ var. <i>cruciata</i> , Hort. | 12e. „ var. <i>parviflora</i> n. var. |
| 3. <i>Oe. biennis</i> , Linn. | 13. <i>Oe. Simsiana</i> , Ser. |
| 3a. „ var. <i>sulphurea</i> , de Vries. | 14. <i>Oe. MacBrideae</i> (Nelson), Heller. |
| 3b. „ var. <i>cruciata</i> , de Vries.
= var. <i>leptomeris</i> , Bartlett. | 15. <i>Oe. ornata</i> (Nelson), Rydberg. |
| 4. <i>Oe. cruciata</i> , Nutt. | 16. <i>Oe. angustissima</i> , Gates. |
| 5. <i>Oe. muricata</i> , Linn. | 17. <i>Oe. nutans</i> , Atkinson and Bartlett. |
| 5a. „ var. <i>canescens</i> , B. L. Robinson. | 18. <i>Oe. pycnocarpa</i> , Atkinson and Bartlett. |
| 5b. „ var. <i>parviflora</i> n. var. | 19. <i>Oe. canovirens</i> , Steele. |
| 6. <i>Oe. Tracyi</i> , Bartlett. | 20. <i>Oe. rhombipetala</i> , Nutt. |
| 7. <i>Oe. argillicola</i> , Mackenzie. | 21. <i>Oe. Oakesiana</i> (Robbins), S. Watson. |
| 8. <i>Oe. Jamesii</i> , T. & G. | 22. <i>Oe. strigosa</i> (Rydb.), Mack. and Bush. |
| 9. <i>Oe. macrosceles</i> , A. Gray. | 23. <i>Oe. cheradophila</i> , Bartlett. |
| 10. <i>Oe. macrosiphon</i> , Wooton and Standley. | 24. <i>Oe. heterophylla</i> , Spach. |
| 11. <i>Oe. Drummondii</i> , Hook. | 25. <i>Oe. procera</i> , Wooton and Standley. |
| 12. <i>Oe. Hookeri</i> , T. & G. | 26. <i>Oe. depressa</i> , Greene. |
| 12a. „ var. <i>irrigua</i> (Wooton and Standley), Gates n. comb. | 27. <i>Oe. Heribaudi</i> , Lévl. |
| 12b. „ var. <i>Hewetti</i> , Cockerell. | 28. <i>Oe. parviflora</i> , Linn. |
| 12c. „ var. <i>semiglabra</i> n. var. | |

Oe. longissima, Rydberg.*Oe. hirsutissima* (A. Gray), Rydberg.*Oe. subulifera*, Rydberg.*Oe. Cockerelli*, Bartlett, *in litt.**Oe. Millersi*, de Vries, *in litt.**Oe. franciscana*, Bartlett.*Oe. venusta*, Bartlett.„ var. *grisea*, Bartlett.*Oe. stenomeris*, Bartlett.*Oe. stenopetala*, Bicknell.*Oe. atrovirens*, Shull and Bartlett.*Oe. venosa*, Shull and Bartlett.



Map indicating
THE DISTRIBUTION OF
OENOTHERA SPECIES
in
NORTH AMERICA

English Miles
100 50 0 100 200 300 400
For references to the numbers see p. 10



CHAPTER II

CHARACTERS AND DISTRIBUTION OF THE OENOTHERAS

As a preliminary to the discussion of the mutation phenomena, as presented by the *Oenotheras*, we will first examine the group to which the mutating species belong. The species of the sub-genus *Onagra*, with which alone we are concerned, were confined to America in their original distribution, though now naturalised in many parts of the world. This group is almost entirely limited in range to North America, extending over Canada, the United States, and Mexico. There exists a great diversity of forms (many of which are as yet undescribed), scattered over the whole continent. These plants frequently abound in cultivated ground and sandy soils, and in the last three centuries they have become widely naturalised in Europe, in England, France, Holland, Germany, Spain, Italy, Lithuania, Russia, Caucasus, the Ural region of Siberia, Sweden, Norway, and elsewhere, on sand dunes, along railways, in abandoned fields, along river courses, and in similar situations, where they multiply and flourish greatly. They have also been introduced in South Africa, the Madeiras, Japan, and various other parts of the world,¹ and probably few plants have

¹ According to Haller (*Hist. Helvet.*), "*Oe. biennis*" was naturalised in several localities in Switzerland as early as 1768. Since there is a specimen of *Oe. Lamarckiana* from Switzerland in Herb. Henslow, collected about 1820, it is not impossible that the reference of Haller is to the same plant. Zwinger (*Theatrum Botanicum*, p. 974) speaks of *Oenothera* still earlier (1744) as cultivated in the gardens of Switzerland

been so widely naturalised. Several specimens of a type resembling *Oe. mut. rubrinervis* have been collected in Newfoundland, apparently wild and not naturalised.

The distribution of the species of *Oenothera* in America has no doubt been considerably altered since the advent of civilised man. In the group we are considering, the large-flowered forms are probably much less numerous and their ranges much more restricted now than three centuries ago when colonisation of North America began, while the small-flowered species seem to have held their own with, for the most part, little if any diminution in their range.

The accompanying list (p. 10) includes the recognised species in the *Onagra* group. There are several others the status of which is at present more or less obscure. Several new species, mostly segregates from *Oe. biennis*, L., and *Oe. Hookeri*, T. and G., have recently been described, and a number of others will doubtless be added in the next few years from critical experimental studies now in progress; for *Oe. biennis* in particular is represented by a host of geographic races, many of them rather local in occurrence. The general distribution of each species, so far as known,

and naturalised at Huningen near Basle. Barrelier (1714) seems to have seen it in Portugal, and his name, *Lusitanica* (see p. 67) indicates that he thought it came from there. Parkinson, in the *Theatrum* (1640), refers to *Oe. biennis* and two species of *Epilobium* as wild along roads and the borders of fields. Hence it was probably naturalised in England between 1629 (*Paradisus*) and 1640. Zanichelli (*Istoria delle piante de' lidi Veneti*, 1735) found it naturalised in certain places in Northern Italy. Some of these plants belonged to different races. Indeed, so widely were *Oenotheras* distributed that Spach in 1835 (*Hist. Bot. des Vég. Phan.*) believed them to be native and proposed for them the name *Oe. europea*. His conclusion, however, was certainly erroneous. A number of these references have been taken from A. De Candolle's famous *Géographie botanique raisonnée*, 1855.

In England, Watson in his *Cybele Britannica*, 1847, records "*Oe. biennis*" in eleven out of the eighteen areas into which he divides England, Wales, and Scotland. This included two areas of Wales, all those of England except the Trent region and the Lake region, and also the western lowlands of Scotland.

is given, and these are shown on the accompanying map. In this map the ranges indicated are of course only approximate, and *Oe. biennis* is considered in an inclusive sense.

1. *Oe. grandiflora*, Solander. (Fig. 1.)

Exsiccata.—1. Bartram's plants, "collected in Carolina, Florida and Georgia, 1773-6," fol. 10, 2 specimens, typical, petals about 35 mm., hypanthium slender, buds smooth and nearly glabrous except sepal tips, scattered long hairs on stem, leaves tapering to base. 2. Ait.

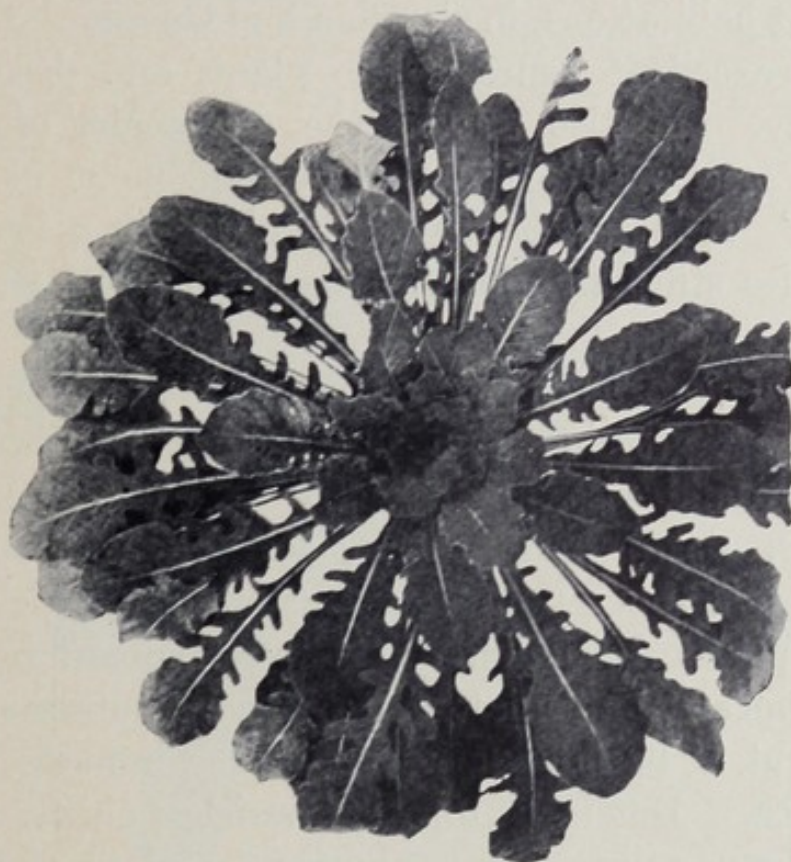


FIG. 1.—*Oe. grandiflora* race.

Hort. Kew. (B. Mus.). 3. *Oe. suaveolens*, Desf. S. Vicente, Madeira, Lowe, 1862 ("quite a weed"). 4. Herb. Demidoff, Pallas (petals 42 mm., hypanthium 48 mm., 2 mm. in diameter, buds stout, glabrous, a very luxuriant race). 5. Cobham Lodge, 1831 (style short, flowers smaller, bud cone 18 mm.). 6. Cobham Lodge, 1829. 7. Jardin des Plantes, Carré Chaptal, 1815. 8. Herb. Lindley (Cambridge), Hortus Hort. Soc., 1828, "*Oe. suaveolens*" (apparently a small-flowered variety of *Oe. grandiflora*, bud cone 11 mm.). 9. Waste ground near St. Botolph's Station, Colchester, 1881 (buds stout and perhaps squarish, sepals red as in mut. *rubrinervis*).

Now known to be indigenous only in Dixie Landing, and one or two other localities in Alabama, though there

are records under the name *Oe. grandiflora* from Ontario, where it is said to be common on good soil (Macoun, *Cat. Canadian Plants*), Michigan (*Cat. Wheeler and Smith*), and one locality in Minnesota (*Cat. Upham*, 1884). How closely the latter forms may be identified with the Alabama species is at present unknown. *Oe. grandiflora* was formerly indigenous to the general region of "Virginia," and as late as 1821 it was "native in woods and fields, and about habitations, in Carolina and Georgia."¹ Barton gives an excellent figure of the plant, and describes its variability. He also quotes the statement of Elliott² that the species is "certainly not indigenous in our low country." It is possible that careful search may discover this species still surviving in some portion of its eastern range.

Oe. grandiflora has been widely naturalised in Europe, and is now growing wild in England (Cheshire coast, Colchester, and elsewhere), many parts of France (*Oe. suaveolens*, Desf.) and other places on the Continent. Races of this species are also naturalised in such out-of-the-way places as Madeira. Its rapid spread in Europe might appear contradictory to the hypothesis of the curtailment of its boundaries under the influence of man in America. But in Europe it flourishes chiefly on sand dunes, along railway embankments, and in similar unoccupied places, where it has few competitors and is relatively undisturbed by man. In America, though flourishing on sandy soils, the *Oenotheras* do not appear to be particularly frequent on sand dunes. Unlike many other naturalised species, they have not changed their habitat in coming to Europe, since even in America they often flourish in cultivated or abandoned fields and by railways, where they frequently form a moving population.

¹ Barton, *Flora N. Amer.* Vol. 1. 1821.

² Elliott. *A Sketch of the Botany of South Carolina and Georgia.* The part containing *Oenothera* (Vol. 1, p. 441) was published in 1817.

2. *Oe. Lamarckiana*, Seringe. (Fig. 2.)

Exsiccata.—1. Switzerland. Mus. Henslow, Coll. Rev. James Dalton (1820-40), the exact counterpart of de Vries's race. 2. Garden Edw. Leeds, before 1876 (named "*Oe. muricata*"). 3. Herb. Hort. Kew, 1883. 4. Newfoundland, Capt. Cochrane (nearest mut. *rubrinervis*), petals 25 mm., leaves very narrow, 10-7 mm. wide. 5. Uxbridge, England, 1907 (buds with red stripes). 6. Garden in Reigate, Boulanger, 1907 (B. Mus.). 7. St. Anne's-on-Sea, Lancashire, 1907. 8. *Ibid.* (petals 19-24 mm., style short). 9. *Ibid.* (*rubrinervis*). 10. St. Cast, Brittany, 1907; these are hybrids = *Lamarckiana* × *biennis*.



FIG. 2.—*Oe. Lamarckiana*, Ser., de Vries's race.

This species is now known only naturalised and in cultivation, and was formerly supposed by some to have originated in gardens. This will be discussed in the next chapter.

Oe. Lamarckiana is the common evening primrose of English gardens everywhere, and has been extensively naturalised on the Lancashire coast for more than a century. A specimen in the Cambridge Herbarium, collected in Switzerland about 1820, appears to agree exactly with

de Vries's race. In the gardens of Southern Sweden, races belonging to *Oe. Lamarckiana* (some of which appear to agree closely with certain English garden races), occur commonly and are probably also naturalised in places. The variability and natural hybrids of this species have been studied by Boulanger and by de Vries on the coast of Brittany, where it freely intercrosses with *Oe. biennis*. Certain specimens from Newfoundland which appear to have been collected wild most nearly agree with *Oe. mut. rubrinervis*. And finally a specimen in the Kew Herbarium, collected in the vicinity of Tours in 1860, appears to be a hybrid between *Oe. Lamarckiana* and *Oe. muricata*.

In England, Baxter (*British Phanerogamous Botany*, Vol. 4, 1839) under the name "*Oe. biennis*" gives a figure which apparently belongs to *Oe. Lamarckiana*. He states its distribution to be as follows: Durham, on South Shields Ballast-hills, and near Sunderland; Essex, on Warley Common; Gloucestershire, near Bristol; Kent, on Shooter's Hill; Lancashire, at Crosby, Liverpool, Southport, and Formby; Somerset, near Bath; Suffolk, several areas near Woodbridge; Surrey, at Battersea and Coulsdon; Warwick, abundant on the banks of the Arrow; Wiltshire, near Great Bedwyn; Glamorganshire, near Swansea; and in Worcestershire. To these localities Deakin in the *Florigraphia Britannica*, 1857, adds the banks of the Don below Sheffield, Yorkshire. Of course, some of these records may be for other species than *Oe. Lamarckiana*, though this species seems to be most successful.

With regard to these records, it appears to be significant that the earlier English floras contain no mention of "*Oe. biennis*" as a wild plant, previous to the discovery of "millions" of these plants on the sandy coast north of Liverpool by Dr. Bostock and Mr. Shepherd about 1805. Thus Hull's *British Flora*, first edition, 1799, contains no *Oenotheras*, but the second edition, in

1808, refers to the above-mentioned discovery, which was first recorded in Sowerby's *English Botany* (Vol. 22, pl. 1534) in 1806. Again, Smith's *Flora Britannica*, 1800, contains no *Oenotheras*, but the *English Flora*, 1824, refers to the Liverpool plants. Hudson's *Flora Anglica*, three editions of which appeared respectively in 1762, 1778, and 1798, likewise makes no mention of *Oenothera*. It is, therefore, probable that *Oe. Lamarckiana* established itself on the Lancashire coast between 1785-1796, the approximate date of its introduction into Paris, and 1805, when it was observed in Lancashire in abundance. *Oe. grandiflora*, introduced into Kew in 1778, also flourishes near Birkenhead, but the date of its advent is not known.

2A. *Oe. Lamarckiana* var. *cruciata*

In gardens. A culture from Hort. Bremen in 1912 gave nine plants with cruciate petals and two with broad petals. In the previous year fifty-three plants were grown from the same packet of seeds. Only five of them bloomed, but these were all cruciate. The length of the petals was about 30 mm. On one plant both cruciate petals (7 mm. broad) and normal petals (32 mm. broad) were observed. The styles in this race are short, so that nearly all the flowers are self-pollinated.

3. *Oe. biennis*, Linnæus. (Fig. 3)

Exsiccata.—1. "A Hortus Siccus by Mr. George, London," fol. 459, *Lysimachia siliquosa latifolia virginiana magno flore* (petals 20 mm.). 2. Banister, Herb. Siccum, fol. 215, *Lysimachia siliquosa Virg. major* (petals 20 mm.). 3. "Plants Coll. in Virginia by Mr. Clark": flowers only, fol. 75 ("April") petals 20 mm., style short. 4. Flower, fol. 81 ("May") petals 25 mm., stigma certainly above anthers, petals emarginate, sepal tips short. 5. Flower, fol. 87 (petals 19 mm.). 6. Flower, fol. 98. ("Sept.") petals 18 mm., hypanthium 28 mm. 7. Herb. Sherard, *Onagra latifolia*, Inst. R. H. *Lysim. lutea cornic.* C.B. Pin., *Lysim. lutea cornic. non papposa Virg.*

major, *Lysim. Virg. altera*, *foliis latioribus*, *floribus luteis*, *majoribus* Cat. Alt., Raj. Hist. 862 (petals estimated about 25 mm.). 8. Herb. Sherard, 771 (petals 25 mm.). 9. Herb. Du Bois, *Onagra latifolia*, etc. 10. Herb. Morison (Fig. 3). 11. Plukenet, *Thesaurus Botanicus*, 1661, fol. 75. 12. Herb. Sloane, Vol. 22, fol. 51 ("Plants Coll. by Mr. Scott in Paris"). 13. Herb. Sloane, Vol. 309, fol. 115 (Uvedale, Herb. Rayanum). 14. Herb. Sloane, Vol. 57, fol. 8 and Vol. 58, fol. 196 (coll. by Courten from the King's Garden, Montpellier). 15. Herb.



FIG. 3.—*Lysimachia lutea corniculata non papposa*, *Virginiana major*. Morison Herb. = *Oe. biennis* Linn.

Sloane, Vol. 168, fol. 215 (Banister Coll.). 16. Herb. Sloane, Vol. 45, fol. 23 ("Plants Gathered about the Year 1660"). 17. Herb. Sloane, Vol. 139, fol. 11 (collection of Mary, Duchess of Beaufort, very luxuriant specimens, petals 29 mm.). 18. Herb. Sloane, Vol. 321, fol. 39 (Herb. Boerhaavianum). 19. Herb. Sloane, Vol. 333, fol. 15 ("Garden Plants and Flowers Gathered and Named by Dr. Uvedale"). 20. *Onagra latifolia* T. 302 (B. Mus.) Hort. Cliff. (stigma lobes 10 mm.). 21. *Onagra latifolia*, Tourn. Chelsea Garden (No.

1052), 1743. 22. Chelsea Garden (No. 2878), 1779, another race, petals 14 mm., leaves short with broad, cuneate base. 23. *Hortus Hyemalis* No. 68 (Hill's *Hist.*, p. 398). 24. Linn. Soc. Herb. (petals 15 mm.). 25. Hort. Kew (Brit. Mus.), 1781. 26. Entre St. Jean et Landeron, 1834 (petals 22 mm.). 27. Suffolk coast, 1811 (petals 18 mm.). 28. Mrs. J. Turner, 1806 (upper leaves elliptical). 29. Crosby, near Liverpool, 1825. 30. Near Woodbridge, England, 1810 (bud cone 14.5 mm.). 31. Herb. Rottlerianum, East Indies, 1821. 32. Herb. C. C. Babington, Crosby Warren, near Liverpool, 1837 (petals 17 mm.). 33. Woodbridge, Suffolk, 1829 (petals 15-20 mm.). 34. Gerd, near Bagnères, Pyrenees, 1824, Mus. Henslow. 35. Banks of the Rhine, Mus. Henslow. 36. Exmouth Sands, Rev. W. R. Crotch (petals 22 mm.). 37. Lake of Geneva, W. P. Hamond. 38. Crosby, near Liverpool, 1838 (type). 39. Near Southport, 1839 (petals 19 mm.). 40. Near Chester, Pennsylv., Townsend. Herb. Hook., 1867 (race with very large flowers, petals 25 mm.). 41. Hamburg, Herb. Aueswald. 42. Hagenau (Bas-Rhin). 43. Botzen, Herb. Mus. Tirolensi. 44. Near St. Petersburg, Herb. Balticum. 45. Near Berne, 1868. 46. Upsala, 1883. 47. Upsala, 1887 (?). 48. Bords du Lac, sous Lausanne, 1879. 49. Boitzenburg ad Albim, Herb. Hook. 50. Jacksonville, Florida, 1894 (a peculiar new species near *Oe. biennis*, having petals 15 mm. long, ovary 8 mm., capsules very short (14 mm.) and stout). 51. Oregon, Folmie (race with very narrow leaves, 10 mm.). 52. Georgeville, Quebec, 1903 (peculiar race, bud cone 13 mm.). 53. Acton (near London), 1907 (petals 20-11 mm.). 54. S. Kensington, 1907. 55. Kelowna, Brit. Columbia, 1909 (bud cone 12 mm.). 56. Heideiberg, 1829. 57. Holstein (petals 24 mm.).

If Bartlett's delimitation of *Oe. biennis* be accepted, and there is no doubt that it should be, then the race which has been common in Holland since the time of Linnæus, and is now frequently designated as the "European *biennis*," should be regarded as the type of the species. This particular race, which was probably the first *Oenothera* to be brought from America, is now, like *Oe. Lamarckiana*, no longer known to occur there, though de Vries found a specimen in the Herbarium of the University of Minnesota which appeared to be identical with it. On account of its close pollination, and for other reasons, it is certain that this *biennis* race has not been modified during the three centuries of its cultivation and naturalisation.

It seems to have been first naturalised in Holland, where it was already common in the time of Linnæus,

1737. This type, which bore the original name *Lysimachia lutea corniculata* of Bauhin, was certainly cultivated more frequently in gardens than any other of the early introductions, as shown by the numerous specimens in pre-Linnean collections. That it was a native of "Virginia" is not only indicated by the time of its introduction (1614) but by specimens of flowers afterwards collected there by "Mr. Clark." One of these flowers, having petals 25 mm. in length and a long style, perhaps represents a natural hybrid with a larger-flowered species.

There is much variability in the naturalised races belonging to *Oe. biennis*, which are now scattered all over Europe. The number of such races found on a given area of the Continent would not be so very much less than in many equal areas of North America. The origin of these many races in three hundred years from a few introductions is a very interesting question. Have they all originated through crossing, or have other agencies been at work? The latter alternative can now be positively asserted, at least in certain cases.

In England, races of *Oe. biennis* in the broader sense are wild in Lancashire, at Crosby, near Liverpool (1825), the Suffolk coast (1811), near Southport (1839), near Woodbridge (1810), at Exmouth Sands, and in Acton (1907) and South Kensington, and doubtless elsewhere. On the Continent I have collected various races in the vicinity of Berlin, and have examined specimens from Heidelberg (1829), Hamburg, Hagenau in Alsace-Lorraine, Botzen in the Austrian Tyrol, Upsala (1883), near St. Petersburg, near Berne (1868), Holstein, St. Jean (1834), Lake Lausanne (1879), Lake Geneva, banks of the Rhine (1830), and the Pyrenees (1824). On a specimen collected by A. Braun in 1849 in the vicinity of Freiburg, he states that hybrids between *Oe. biennis* and *Oe. muricata* are not infrequent in that vicinity.

3A. *Oe. biennis* var. *sulphurea*, de Vries

Exsiccata.—*Onagra latifolia flore dilutiore*. T. 302 Hort. Cliff.
Two specimens (B. Mus.).

This variety is also found in Holland and has also been observed by de Vries in Germany and Switzerland. It differs from the type of *biennis* only in having paler yellow flowers. It has been identified by Bartlett as one of the forms recognised in the early works of Hermann, Tournefort, and Linnæus. Whether it was introduced from America or originated in Europe as a mutation is unknown, but it has maintained its constancy ever since.¹ Curiously enough de Vries has found that *Oe. biennis* × *Oe. biennis sulphurea* gives *sulphurea*, and *Oe. biennis sulphurea* × *Oe. biennis* gives *biennis*. Thus both hybrids are patroclinous, and they remain constant in later generations. Hence it is impossible to determine whether they have been crossed with each other or not. On the other hand, in *Oe. Lamarckiana* × *Oe. biennis sulphurea* the ordinary deep yellow is fully dominant so that it alone appears, both in F₁ and F₂.

3B. *Oe. biennis cruciata*, de Vries, = *Oe. b.* var.
leptomeres, Bartlett

Exsiccatum.—*Oe. biennis* var. *cruciata*. British Columbia, 1909 (B. Mus.). (Cruciate var. of the *Oe. biennis* in that locality.)

Described by de Vries from Holland and since found in Germany (Lüneburg Heath). Probably originates repeatedly from *Oe. biennis* through mutation. It has given rise in culture to a dwarf mutant, *Oe. bien. cruc. nanella*, de V. A local cruciate variety of the race or sub-species of *Oe. biennis* found in British Columbia has no doubt originated there through a mutation, just as a similar variety of *Oe. Lamarckiana* has originated in cultivation.²

¹ Stomps (354) has recently shown that it appears as a mutation in cultures of the normal *Oe. biennis* in Holland.

² Bartlett (15B) has recently studied cruciate species or varieties from near Washington; Hudson Falls, N.Y.; Long Island; Mobile, Ala., and Springfield, Mo. (including a mutant, *Oe. stenomeres* mut. *lasiopetala*), and Bicknell (24A) *Oe. stenopetala* from Nantucket. These have all no doubt originated by independent mutations.

A constellation of closely related elementary species, which compose *Oe. biennis* in the broad sense, extends over a very wide range in America. The distribution is usually given as Labrador to Florida and westwards to the Mississippi, but in the more northern part of this range most of the forms should be included in *Oe. muricata*, which has smaller flowers than *Oe. biennis*.

4. *Oe. cruciata*, Nuttall

Exsiccata.—1. Cambridge, Mass. (Herb. Nuttall, B. Mus.). 2. Cobham Lodge, 1831. 3. Herb. Lindley, 1825.

Occurs from Maine and Vermont to Massachusetts and northern New York. It is a species having cruciate petals, and has very probably originated as a mutation, though its immediate ancestor is apparently not now found in the region. Cultures of de Vries and MacDougal from wild plants have shown that it contains several biotypes differing in width of petals, length of hypanthium, etc. One of the races grown by de Vries from near Lake George, N.Y., gave rise in both the first and second generations of cultures to a third form which was the same as one derived from Jaffrey, N. Hampshire. Whether this is an actual case of mutation, or merely the segregation of hybrid types, the experiments were not extensive enough to determine, though the latter appears more probable. The type of the species has bud cones 11 mm. in length, club-shaped, bracts rather broad. This appears to be the only cruciate form which has succeeded in establishing a considerable distribution for itself, though cruciate varieties of several other species have arisen, doubtless through independent mutations.

5. *Oe. muricata*, Linnaeus. (Figs. 4 and 5, cf. Fig. 14)

Exsiccata.—1. Herb. Du Bois, *Onagra angustifolia*, caule rubro, flore minore, Tournef., late flowers, bud cone 5 mm., hypanthium 14 mm., sepal tips not in contact. 2. Herb. Sherard, *Onagra angustifolia*,

I.R.H. *Lysim. angust. canadensis, corniculata*, H. R. Par. *Lysim. cornic. lutea Canad. minor seu angustifolia*, Mor. H. R. Bles. *Lysim. lutea cornic. non papposa Virg. minor*, H. Ox. 772 (petals 9–10 mm., stem-leaves 22–23 mm. wide). 3. 772₂, larger flowers (petals 18 mm. ?) and very narrow leaves (19–12 mm. wide). 4. Herb. Sherard, 774, petals 10 mm., ovary 6–8 mm. 5. Herb. Sloane, Vol. 309, fol. 116 (leaves narrow, 15 mm., bud cone 7 mm.). 6. Cherroke county

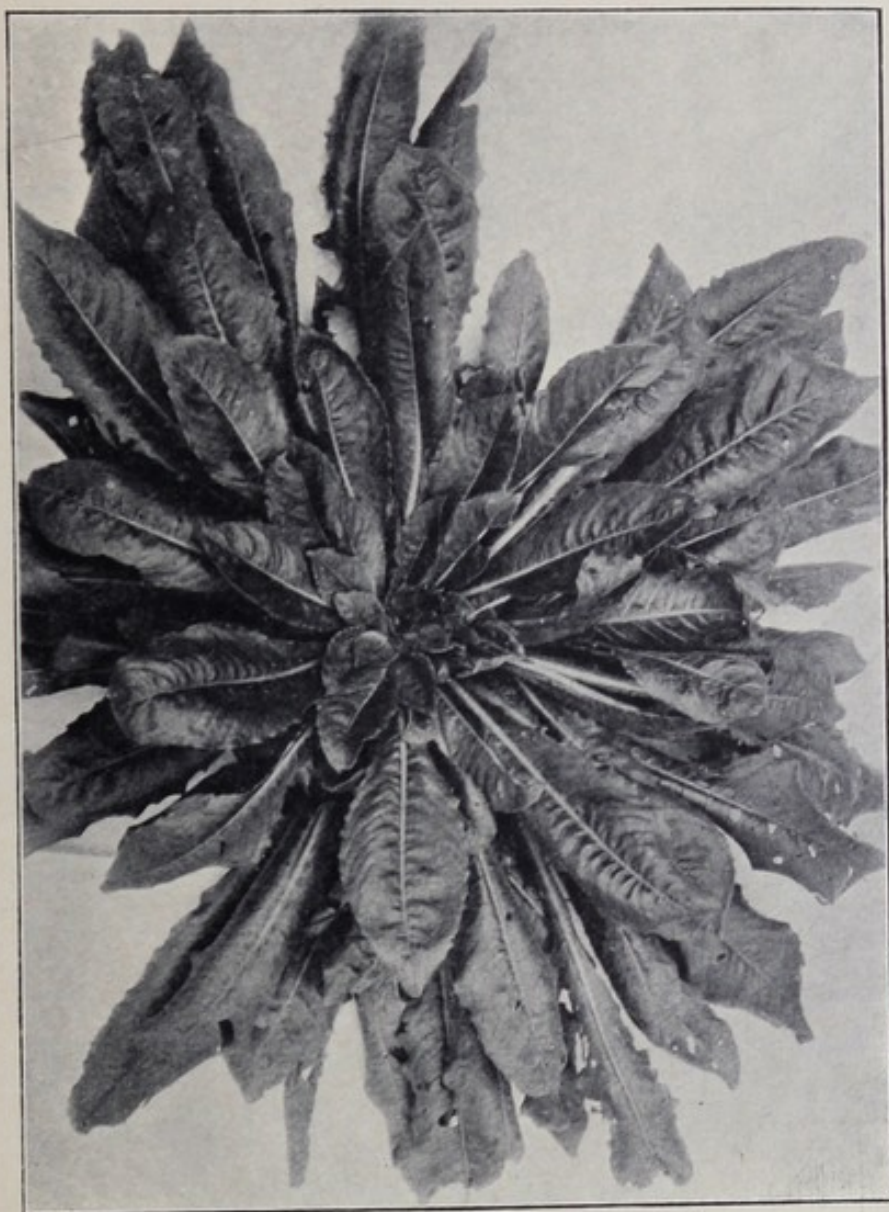


FIG. 4.—*Oe. muricata*, broad-leaved form
(from Middleton, Nova Scotia).

(Georgia), W. V. Turner, 1769; bud cone 10 mm., leaves narrow (10–12 mm.), stem red; Indian name, Outa kenoka = “red stalked, stand straight.” 7. Hudson’s Bay, Banks, 1773 (petals 10 mm., leaves narrow, 10–11 mm. wide). 8. Hort. Gotting., Murray, 1782 (petals 15 mm., buds nearly glabrous, style short as in *Oe. mut. brevistylis*). 9. Columbia river, near the sea. D. Douglas, 1825. 10. Plains of Red River, D. Douglas, 1827. 11. Linn. Soc. Herb. (bud cone 11 mm.).

12. Cobham Lodge, 1826. 13. Ruggisberg, 1830 (?) (bud cone 20 mm., stem muricate). 14. Near Freiburg, 1849. 15. Hudson's Bay, Banks (bud cone 13 mm., leaves narrow). 16. Red River, Douglas, 1827 (petals 15 mm.). 17. Herb. Lindley, N.W. America, Douglas (very narrow leaves). 18. Hamburg, 1842 (narrow leaves, petals 9 mm.).



FIG. 5.—*Oe. muricata*, narrow leaved form (from Winnipeg).

19. Colmar, France, 1841 (leaves very narrow, 8 mm.). 20. Holstein (petals 12 mm.). 21. Bord de la Moselle à Liverdun, Billot, 1861 (leaves very narrow, 9 mm.). 22. St. Trond, Limbg. 1865 (leaves 8 mm.). 23. Herb. Demidoff, Pallas, several specimens, petals 20–10 mm., leaves 16–9 mm. wide; hence probably hybrids = *biennis* × *muricata*. 24. Banks of Elbe, 1860. 25. Bei Hamburg, 1866 (petals

11 mm., leaves very narrow). 26. Lakes Winnipeg and Superior, Dr. Richardson, 1819-22 (petals 12 mm.). 27. St. Trond, Limbg. (petals 12 mm., leaves very narrow, 10 mm.). 28. Fort Assinaboyne, Drummond (?) (leaves fairly broad, petals 15 mm.). 29. Islands in Columbia River, B.C., Douglas (bud cone 12 mm.). 30. Lake Region, Ontario, 1877 (?) (bud cone 17 mm., leaves narrow, stem red). 31. Châtel, bord de la Moselle, 1885; forma *Mosellana* H. Waldner in litt. 32. Mülhausen in Alsace (petals 8 mm.). 33. Prairie, Carberry, Manitoba, Christy, 1883 (petals 13 mm., leaves narrow). 34. Islands in the Vistula at Warsaw, 1895 (very hairy with white pubescence). 35. Islands in the Vistula at Warsaw, 1895 (many long hairs). 36. Vienna, 1907. 37. Lithuania, 1898. 38. Etruria, Viareggio, 1908; flowers rather large, bud cone 17-18 mm., slender.

This species extends right across the continent in about latitude 42° - 50° , from Nova Scotia, New Brunswick and Gaspé to Ontario, Manitoba, and Saskatchewan, and probably also further north. I have obtained identical races from Nova Scotia and Winnipeg, and there appears to be much less diversity of types in this latitude than further south in the United States where the *biennis* races predominate. *Oe. muricata* races occur, however, from the Great Lakes to Missouri, Colorado, and northward. I found an interesting type of dimorphism in cultures both from Nova Scotia and Winnipeg. The same broad-leaved and narrow-leaved forms occurred in both localities (Figs. 4 and 5).

Oe. muricata canescens, Robinson

This is one of many sub-species of *Oe. muricata*. It occurs in Massachusetts, and I have grown very constant races of it from Wood's Hole, Mass. It should not be confounded with *Oe. strigosa*.

Oe. muricata, L., var. *parviflora* n. var.

Exsiccatum.—Jupiter River, Anticosti, John Macoun, 1883.

This variety is founded on a specimen in the British Museum which was collected by John Macoun on the Jupiter River, Anticosti, in 1883. It agrees with certain

racess of *Oe. muricata*, L., in its reddish, muricate stem and narrow leaves (12 mm. wide), but the flowers are as small as in *Oe. parviflora*, L. (petals 5 mm.).

Oe. muricata, like *biennis*, *Lamarckiana*, and *grandiflora*, is widely naturalised in Europe. I have seen specimens from Hamburg (1842), Holstein, the Moselle at Liverdun (1861), St. Trond, Limbg. (1865), Freiburg (1849), Warsaw (1895), the Elbe (1860), Vienna (1907), Lithuania (1898), Etruria (1908), Mülhausen in Alsace; Colmar, France (1841). According to the Rev. E. S. Marshall it is naturalised in England at Burnham-Berrow, N. Somerset.

Early herbarium specimens under the names *Onagra angustifolia*, *caule rubro*, *flore minore* and *Lysimachia corniculata lutea canadensis minor*, referring respectively to *Oe. muricata* and *Oe. angustissima*, indicate that narrow-leaved forms of *Oe. muricata* approached very close to the early representatives of *Oe. angustissima*, and that the two perhaps intercrossed.

6. *Oe. Tracyi*, Bartlett (11)

Known from Dixie Landing and Birmingham, Alabama, and the South Eastern States. In foliage it resembles *Oe. grandiflora*, but it has the small flowers of *Oe. biennis*. Its distribution would indicate that it is probably a derivative from *grandiflora*.

Species 7-13 have large flowers like *Oe. grandiflora* and *Oe. Lamarckiana*.

7. *Oe. argillicola*, Mackenzie

This is a very distinct, large-flowered species with very long and narrow leaves, discovered in New York in 1904. It occurs in southern New York, Maryland, and the mountains of Virginia and West Virginia.

8. *Oe. Jamesii*, Torrey and Gray

Exsiccata.—1. Engelmann cult., St. Louis, 1848 (B. Mus.). 2. Texas, Lindheimer, 1849–50 (petals 40 mm., hypanthium 70–110 mm.). 3. Organ Mountains, New Mexico, 1887 (?). 4. 14. New Mexico, 1900.

This species is less well known. It has foliage resembling *Oe. mut. rubrinervis*; habit decumbent; flowers yellow turning rose, bud cone conical, 35 mm. in length, hypanthium very long (5–11 cm.) and stout (4 mm. in diameter); abundant appressed pubescence. Found in Oklahoma and Utah to Texas, New Mexico, and Arizona.

9. *Oe. macrosceles*, A. Gray

Exsiccata.—1. Parras, Coahuila, Mexico, 1880 (petals 20 mm. turning purple, hypanthium 90 mm., ovary 15 mm., stigma barely above anthers, leaves narrow (7 mm. wide) nearly linear, almost entire, whole plant nearly glabrous).

Northern Mexico. Plant glabrous, stem erect, rosette-leaves spatulate-lanceolate with long petioles, ciliate; hypanthium very long, corolla 3 inches in diameter. Probably nearest *Oe. Jamesii*.

Oe. longissima, Rydb., from Utah, should be included here. Leaves and stem densely canescent, leaves entire, acute at both ends, hypanthium 10–12 cm., petals 4 cm., style scarcely exceeding the stamens. Differs from *Oe. macrosceles* in canescence and small bracts; and from *Oe. Jamesii* in longer, narrower, entire leaves, and in pubescence.

10. *Oe. macrosiphon*, Wooton and Standley

Exsiccata.—1. W. Texas to El Paso, C. Wright, 1849, Kew (petals 50 mm.). 2. Another specimen (petals 60 mm.).

Recently described from New Mexico. It is related to *Oe. Jamesii*, having the same habit, but it has much larger, deep yellow flowers (petals 50–55 mm. long) and the stems are pubescent with long hairs arising from papillæ.

11. *Oe. Drummondii*, Hooker

Texas. Soft-pubescent, decumbent; leaves ovate-elliptical or oblong; flowers large. Represented in culture by several races differing in flower-size, foliage and other features. *Oe. bifrons*, Don, appears to be closely related.

12. *Oe. Hookeri*, Torrey and Gray

Exsiccata.—1. Jardin des Plantes, Carrés Chaptal, 1815 (petals 32 mm., style short). 2. Herb. Lindley, Mexico, 1824. 3. New Mexico, 1847. 4. Vallée de Mexico, 1866 (?). 5. Utah, 1874 (?). 6. Vol. de Fuego, Guatemala, 1873. 7. Santa Cruz, California, 1884 (named *Oe. Lamarckiana*). Bodega, California, Barclay. 9. San Bernardino, 1896. 10. Santa Fé, New Mexico, 1897. 11. Parrott, S. Colorado, 1898. 12. Near Parrott, S. Colorado, 1898. 13. Sukodorf, Washington State, 1906.

This fine, large-flowered species (petals 40 mm.) occupies the whole Pacific coast region from Northern Mexico through California and northwards into British Columbia, eastward into Idaho and (as a rarity) Montana. This species also includes a number of distinct races, two of which, both having *Hookeri* foliage, I have compared under identical conditions of cultivation and proved their constancy. One of these, from San Bernardino, in Southern California, from seeds sent by Dr. S. B. Parish, produced a constant race with a tall central stem and lateral branches. The stems, buds, and leaves are strongly pubescent, the former with long, muricate hairs, though the papillæ from which these hairs arise are always green on the buds and frequently so on the stems. Race number two came from seeds collected by Miss H. A. Walker at Lake Merced, near San Francisco. It was also uniform, and differed constantly from the other race in the following particulars:—

(1) Markedly in habit, forming always at first a ring of very long basal shoots from the rosette and later a central stem which was usually shorter than the side shoots. The basal shoots are very tough in texture, but they develop a large collar at their base and are easily disarticulated from the main stem.

(2) In pubescence, the long hairs on the buds and stems being more numerous and spreading.

(3) Stems dark red and with many red papillæ.

(4) Conspicuous red papillæ on hypanthia.

(5) Buds red as in *rubrinervis* (colour pattern 5 with some red on the hypanthia). They were constantly green in race number one.

Race number two was also obtained independently from seeds of a plant in the herbarium of the Missouri Botanical Garden, collected in the same locality. Over 500 plants belonging to these races were grown in 1912.

These differences in habit, pubescence and coloration are very interesting on account of their constancy. They probably represent geographic races each adapted to its own local habitat. Race number one is the typical *Oe. Hookeri*, having soft pubescent foliage, upper stem-leaves about 2 cm. wide, rather blunt pointed, margin obscurely and distantly repand-denticulate. Race number two is apparently the same as *Oe. irrigua*, Wooton and Standley, recently described from New Mexico. But I should say that if the term variety is to be used at all, this form should be classed as a variety of *Hookeri*, not a species. I have so classed it in the list of species.

Oenothera Hookeri Hewetti, Cockerell (58, 59), comes close to var. *irrigua*, but differs in the following features: (1) in habit of growth, flowering the first year but reaching its full development the second year (it is possible that this feature may not be constant); (2) in pubescence, which is very sparse, greyish-green; (3) sepal tips long, reaching 10 mm.; (4) petals bright yellow, fading to apricot. This elementary species was observed by Dr. Cockerell at Rito de los Frijoles, New Mexico, in 1912, and described from a plant removed to his garden in Boulder, Colorado.

Three other varieties of *Oe. Hookeri* are here given names, on the basis of specimens in the British Museum. Var. *parviflora*, n. var., is based on a specimen from Kamloops, British Columbia, collected by John Macoun in 1889. The sheet bears the name *Oe. biennis* var. *hirsutissima*, Gray, which was the name formerly used to

designate all forms of *Oe. Hookeri*. The specimen has small flowers with short style (petals 14 mm., hypanthium 30 mm., ovary 12 mm.), but since it agrees with *Oe. Hookeri*, from which it has evidently been derived, in foliage and pubescence, it must be classed as a variety of that species and not of *Oe. biennis*. For some reason, smaller flowers are a necessity in the higher latitudes. Probably a small-flowered mutation appeared and was selected.

To this variety are referred the following :—

Exsiccata.—1. Herb. Lindley, N.W. America, Douglas, H.H.S. 1827 (?) (bud cone 25 mm., leaves with red midribs). 2. *Ibid.* Differs from last in having smaller flowers (bud cone 11 mm.) and buds nearly free from hairs. 3. "Columbia woods," Nutt. Herb. ("*Oe. mollis*") bud cone 14 mm. 4. New Mexico, Fendler, 1846 (bud cone 10 mm.). 5. California, Coulter (?) (petals 20 mm., leaves very narrow).

Oe. Hookeri var. *semiglabra*, n. var. is founded on a specimen collected in California by J. G. Lemmon in 1875, which bears the name *Oe. biennis* var. *grandiflora*. It agrees with the species, except in the absence of white pubescence. The buds are nearly glabrous (as in *Oe. grandiflora*) except for a short pubescence on the sepal tips and ovaries, and there are scattered long hairs arising from papillæ on the stem.

Three specimens are referred to it. 1. Rucker Valley, Arizona, 1881 (narrow leaves). 2. Salt Lake City, 1879. 3. Pagosa Springs, S. Colorado, 1899.

Oe. Hookeri var. *angustifolia*, n. var. is based on a specimen collected at Asphalt, Utah, in 1894 by Marcus E. Jones, with the name *Oe. biennis* var. *grandiflora* (Ait.), Lindl. It differs from the species in having (1) narrower stem-leaves (8-12 mm.) ; (2) slender, bright red stems ; (3) leaves nearly entire and very obscurely denticulate. These differences correspond in several respects with those between *Oe. Lamarckiana* and *Oe. mut. rubrinervis*. The petals are 35 mm. in length. *Onagra guttata*, Greene, n. sp. in Herb. Brit. Mus. from Kingston, New Mexico, in 1904, is referred to this variety with some doubt. It

may be worthy of specific rank, though in that case the name must be altered, for *guttata* is already occupied. The leaves differ in being very narrow (8-10 mm.), more pointed, and conspicuously repand-denticulate, the stems taller. Some forms of *Oe. strigosa* come very near this var. *angustifolia* except in having small flowers (petals 17 mm.). (Some of the specimens classed here may



Fig. 6.—*Oe. MacBrideae*.

perhaps belong properly with *Oe. MacBrideae* or *Oe. ornata*).

Exsiccata.—1. Lindley Herb., Douglas, British Columbia, 1825-7. 2. California, Douglas, 1833. 3. Nova California, D. Douglas, 1833. 4. New Mexico, 1847 (petals 30 mm.). 5. W. Texas to El Paso, 1849. 6. New Mexico, 1849. 7. Mex. Boundary Survey. 8. New Mexico, 1851. 9. Mt. California, Bridges. 10. Colorado, 1877. 11. Raton Mountains, Colorado, 1867. 12. Los Cuevas, Sonora, N.W. Mexico, 1890. 13. Yosemite Valley, 1891. 14. Asphalt, Utah, 1894. 15. San Bernardino, Calif., 1896 (?). 16. Utah, 1867. 17. Near Colonia Garcia, Chihuahua, Mexico, 1899. 18. Pagosa Springs, S. Colorado, 1899 (petals 28 mm.). 19. Griffins, Calif., 1902. 20. San Bernardino Co., 1902. 21. Barfoot Park, Arizona, 1906 (?).

Two other species, *Oe. franciscana*, Bartlett, and *Oe. venusta*, Bartlett (15), segregates from *Oe. Hookeri*, are described from California.

Oe. hirsutissima, Rydb., = *Oe. biennis* var. *hirsutissima*, Gray, has been considered a synonym of *Oe. Hookeri*, T. and G., but has shorter sepal tips (2 mm. instead of 4 mm.) and very long and loose pubescence on leaves and calyx. New Mexico and Colorado.

13. *Oe. Simsiana* Seringe

Exsiccata.—1. Mexico Valley, Schmitz, 1855 (?) (petals 25 mm., leaves rather narrow).

A Mexican species with large flowers but short style; it comes near to *Oe. Hookeri*. (See 253.)

Species 14–15 form a transition between *Oe. Hookeri* and certain small-flowered species related to *Oe. biennis*.

14. *Oe. MacBrideae* (Nelson) Heller (281)

Idaho. Fig. 6 shows rosette of this species in a uniform culture from seeds of Nelson. The plants have a short central stem with long basal branches. Buds closely set with long hairs from faint red papillæ, petals 44 mm. long, and base of stigma lobes usually some distance above the anthers.¹

15. *Oe. ornata* (Nelson) Rydberg (281)

Idaho. This species differs from the last in having smaller flowers (petals 25 mm.), though the style is long. The calyx and stem-tip are densely white hirsute-pubescent, and the stem-leaves narrowly oblong-lanceolate to linear-lanceolate.

Species 16–26 are segregates from *Oe. biennis sensu latiore*.

16. *Oe. angustissima*, Gates (144)

Exsiccata.—1. Petiver, Hort. Siccus Amer. Vol. 2., fol. 245 (bud cone 9 mm.). 2. Herb. Sloane, C. Schreutter, "Plantae collectae Padua," 1665, fol. 78, *Lysim. lutea corniculata*, *Lysim. Virginiana*. 3. Herb. Moris., *Lysim. lutea corniculata non papposa Virginiana minor*, Fig. 11, p. 55. 4. Herb. Sloane, Vol. 13, fol. 57, specimen 2 ("plants gathered at Paris by Moses Charas") *Lysimachia Virginiana* (bud cones 8 mm.).

¹ A type sheet of *Oe. MacBrideae* in Herb. Mo. Bot. Gard. contains two specimens having smaller flowers (petals 30–34 mm., hypanthium 50 mm.), one drying rose colour. Evidently the material contains several minor races.

Described from Ithaca, New York. It resembles *Oe. argillicola* in foliage, but has small flowers. It differs from the two following species from the same locality in the following characters: (1) the very long and narrow lanceolate leaves (24–26 mm. wide); (2) stem terete, nearly glabrous, upper part nutating; (3) sepal tips infra-terminal, hence separated in the bud, bright reddish.

17. *Oe. nutans*, Atkinson and Bartlett (13)

Described from Ithaca, N.Y. Its distinctive features are as follows: (1) rosette-leaves crinkled, red-spotted (5–6 cm. wide); (2) stem channelled; (3) sepal tips terminal, green; (4) bracts yellowish-green or nearly colourless, quickly *deciduous*; (5) flowers nodding when wilted.

18. *Oe. pycnocarpa*, Atkinson and Bartlett (13)

Described from Ithaca, N.Y. It is distinguished by the following features from *Oe. nutans*, to which it is nearly related: (1) rosette leaves flat or somewhat crinkled, green, outer ones deeply pinnatifid, (2) stem nearly terete; (3) petals firm, not wilting quickly.

19. *Oe. canovirens*, Steele

Described from Illinois. Differs from *Oe. biennis* markedly in foliage, which is crowded, the leaves being much shorter, densely cinereous-pubescent and blue-green, narrow (10–14 mm.), very acute; petals 10–14 mm.

20. *Oe. rhombipetala*, Nuttall

Exsiccata.—1. Texas, 1843. 2. Red River, Arkansas (petals 23 mm.). 3. Lexington, Kentucky, 1836 (?). 4. Fountaindale, Illinois, 1873 (petals 11 mm.). 5. Herb. Munroe, Chicago, 1875. 6. Jardin des Plantes, 1851 (petals 18 mm., leaves broadly lanceolate).

Indiana to Minnesota, Nebraska, Arkansas, and Texas. Differs from *Oe. biennis* in leaves linear-lanceolate (20 × 3 mm.), acute, inflorescence long and dense, petals rhombic-ovate.

21. *Oe. Oakesiana* (Robbins), S. Watson (Fig. 7)

Occurs from the St. John River, New Brunswick, and Quebec to Massachusetts, Rhode Island, Connecticut, New York, and westward to South Dakota, Minnesota and Colorado. Rosette-leaves symmetrically pinnate-veined, devoid of red, with a broad, white midrib; pubescence soft-appressed; sepal tips spreading; seeds large.

FIG. 7.—*Oe. Oakesiana*.

This species has a wide range, though the western form (which I have grown from St. Paul, Minnesota, and also from seeds sent by Dr. Ernst A. Bessey from Horseshoe Ranch, Estes Park, Colorado, at an altitude of 8,300 feet) differs from the Eastern plant as described by Vail, in certain particulars. The flowers are larger, petals 20×23 mm. (instead of $13-15 \times 12-14$ mm.), and the leaves differ somewhat in shape (cf. Fig. 7 with Pl. 15, MacDougal, Vail and Shull, 1907).

22. *Oe. strigosa* (Ryd.), Mackenzie and Bush

Exsiccata.—1. Leeds, North Dakota, 1909. 2. Pony, Montana, 1897. 3. Mammoth Hot Springs, 1899.

Occurs from Minnesota and Washington State to Kansas, New Mexico, and Utah. Most nearly related to *Oe. Hookeri*, from which it differs in its small flowers (petals 15–20 mm. long, some races 5 mm.), which are always pure yellow, and in its foliage. From *Oe. biennis* and *Oe. Oakesiana* it differs in the grayish, short-strigose pubescence. The foliage is grayish strigose, the rosette leaves obovate or spatulate and obtuse, the stem-leaves broadly oblanceolate, acute, and more or less wavy. Some forms of this species come very close to *Oe. Hookeri* var. *angustifolia*, differing only in the small flowers.

Var. *subulata*, Rydb., = *Oe. subulifera*, Rydb., has the sepals abruptly contracted into long subulate tips.

Oe. subulifera, Rydberg

Exsiccatum.—1. Forks of the Madison, Montana, 1897.

23. *Oe. cheradophila*, Bartlett (10)

Washington State and Wyoming. This species is a segregate from *Oe. strigosa*, from which it differs chiefly in having much smaller flowers (petals 8 mm. or less) with shorter sepal tips. Its foliage and pubescence resemble those of *Oe. Hookeri*.

24. *Oe. heterophylla*, Spach

Exsiccatum.—1. Bainbridge, Georgia, 1901. ?

Texas, Georgia. Nearest *Oe. rhombipetala*, Nutt. Rosette-leaves lanceolate, sinuate-pinnatifid, stem-leaves smaller and nearly entire, uppermost almost cordate; flowers few, often tripetalous, petals about 13 mm.

The author has grown races apparently belonging to this species or *Oe. rhombipetala* from seeds sent from Boulder, Colorado, by Prof. F. Ramalay, and also

from seeds collected by Prof. A. G. Ruggles in St. Paul, Minnesota.

25. *Oe. procera*, Wooton and Standley

To this species probably belongs a specimen at Kew, collected on the Gunnison Watershed, W. Central Colorado, in 1901. The petals are 14 mm. long, the sepals and hypanthium reddish, the leaves narrow (14 mm. wide), the stem pale reddish, long hairs scattered on stem and buds.

Recently described from New Mexico. It is related to *Oe. strigosa*, but has smaller flowers and different pubescence. The stems are simple, the stem-leaves mostly oblanceolate (15 mm. wide or less), narrowed at base to a slender petiole, bright green, thin, nearly entire; petals 12–14 mm. long, golden-yellow, fading purplish.

26. *Oe. depressa*, Greene

Montana. Resembles *Oe. strigosa*, but prostrate, leaves broader, much denser pubescence.

27. *Oe. Heribaudi*, Léveillé.

Mexico, near Puebla. Flowers very small, buds slender, 12 mm. in length, style long; foliage resembling *Oe. sinuata*, L., leaves lanceolate, short with cuneate base, margin repand-dentate; stem pale, covered, like young leaves, with soft pubescence; capsules short and stout (10–12 mm. in length).

28. *Oe. parviflora*, L. (see Fig. 13, p. 62)

Exsiccata.—1. Herb. J. M. Ferro (a Venetian apothecary), 1674, fol. 47, *Lysimachia Virginiana* (petals 5 mm., hypanthium 30 mm., ovary 12 mm.). 2. Pluk. Phytogr. Tab. 202. Fig. 7. *Lysim. lutea angustifolia Virginiana flore minore*, specimen, petals 5 mm. 3. Herb. Du Bois, "brought from Maryland by Mr. Wm. Vernon in 1698" (petals 10 mm.). 4. Herb. Du Bois, "in my garden at Mitcham" (petals 8–9 mm.). 5. Onagre Amer. fr. brevi. *Lysim. lutea angustifolia Virg. flore minore* Pluk. *Lysim. angust. Canad. altera caule rubro fl. minore* Schol. Bot. *Onagra angust. caule rubro fl. minore* (bud cone 5 mm. ovary 4 mm.) Fig. 13. 6. Ph. Miller, Chelsea Plants, fol. 69, *Onagra angustifolia, caule rubro, flore minori*. Inst. R.H. 302. 7. Herb. Du Bois, "sent from South Carolina by Mr. M. Catesby." (?) 8. Herb. Du Bois, "brought from Maryland by Dr. David Krieg, 1698." 9.

Herb. Sloane, Vol. 309, fol. 116, back. 10. Linn. Soc. Herb. 11. Canada, 1822. 12. Cobham Lodge, 1829. 13. Freiburg, 1834. 14. Brit. Mus., *Oe. parvifolia*, Hort. 15. Herb. Banks (bud cone 9 mm.). 16. Herb. Bishop Goodenough (bud cone 9 mm.). 17. Hort. Bot. Petropolitanus, 1867. 18. Herb. Lemann, M.D., 1852, Massachusetts. 19. Bermuda, 1873. 20. Garden Edw. Leeds, 1876. 21. Gouan, Herb. Hook.

“Canada to Virginia, rare” (Pursh, Fl. Am. Sept., 261, 1814). This species was long lost to the North American flora, until re-discovered at South Harpswell, Maine, in 1905. The rosette leaves are oblong-lanceolate, strongly denticulate, dark and shiny, mottled with red; buds club-shaped, sepal tips separate, petals 8 mm. long, cuneate; inflorescence dense. In the cultures of MacDougal the plants from Maine were identical with those from the Madrid Botanical Gardens, except that they matured more rapidly. Common near Washington.

This by no means exhausts the *Oenothera* forms now known from North America. Indeed, they are only beginning to be studied in sufficient detail to make possible an accurate survey of the species in their characters and distribution. De Vries (1913) has recently referred to or figured a number of new races, which may be mentioned here. They are mostly as yet undescribed. Among them is a small-flowered race from Manhattan, Kansas, the flowers of which seldom open. Two other races were obtained respectively from North Town Junction, near Minneapolis, and from Courtney on the banks of the Missouri.

Another subspecies of *Oe. muricata* was derived from Chicago, and one of *Oe. biennis* from the same locality. *Oe. strigosa* Cockerelli, Bartlett, in litt., is a race cultivated by de Vries from Boulder, Colorado, which stands between *Oe. muricata* and *Oe. strigosa*, but nearer the latter. *Oe. Millersi* was obtained by de Vries from Millers, Indiana. It stands in many respects between *Oe. muricata* and *Oe. cruciata*. Its leaves are bluish-green, darker and

broader than *Oe. muricata*. The inflorescence is very long and loose, the hypanthia and buds very thin, the fruits large and with a characteristic swelling at the base on the side next the leaf.

Dispersal, biology, and ecology of Oenothera.

Generalising from these and other data we may say that in more northern latitudes the small-flowered forms belonging to the *Oe. muricata* series predominate, while farther south a great variety of species in the *Oe. biennis* series, having somewhat larger flowers, is distributed over the east and middle of the continent. The large-flowered species are for the most part more southerly still in range—Virginia, Alabama, Texas, Utah, and Mexico—while the *Oe. Hookeri* series occupies the Pacific coast, and such intermediate species as *Oe. ornata* and *Oe. MacBrideae* occur in Idaho and adjacent States. But it is obvious that many of the species greatly overlap or are co-extensive with each other in distribution so that many parts of the continent are occupied by a considerable number of forms; and that any generalisations, except the broadest regarding distribution, are only very approximately correct (see map, p. 10).

The line separating the large-flowered species, such as *Oe. Lamarckiana*, Seringe, and *Oe. grandiflora*, Solander, from the small-flowered ones in the *biennis-muricata* series, is apparently a rather definite line of cleavage in the subgenus *Onagra*. The former group of species, in addition to having large flowers, have usually long styles and are therefore open-pollinated, while the small-flowered species have for the most part short styles, so that the stigma is surrounded by the anthers in the bud and self-pollination almost invariably occurs before the flower opens. Crosses are quite exceptional in such species under natural conditions. De Vries has shown that in

Oe. biennis the pollen tubes are half way down the style before the flower opens, so that the chances against cross-pollination taking place are very great, though it does occasionally occur.

The difference in flower-structure referred to above probably explains why the small-flowered group have better survived the depredations of man, and why they are now more numerous, both in races and in individuals, than the open-pollinated species. For in the self-pollinated (autogamous) species the development of flowers is sure to be followed by the production of seeds; but in open-pollinated (allogamous) species, pollination depends upon insects or the wind, and not infrequently fails to occur. The result is that in the former group the seed-production is enormously greater than in the latter. I have often observed this striking difference in cultures of large-flowered and small-flowered species grown side by side. It is, therefore, easy to see that with the increase of inimical conditions incident to the advent of civilisation, the allogamous forms would be the first of which the seed-production would fall below the requirements for their perpetuation, and they would therefore suffer curtailment of their distribution. Indeed, it seems probable that the autogamous races have always been more numerous and widespread than the allogamous ones, owing to their greater seed-production, which depends almost entirely upon the transfer of pollen from anthers to stigma.

An instructive experiment by which one can easily prove this difference and magnify it is by tying a large bag over the top of the stem of a plant of each type. In the short-styled species, if the bag be removed after several weeks, every flower will be seen to have set a full capsule of seeds. But in the long-styled species most of the flowers will have produced no seeds at all, while the remaining capsules will contain very few seeds, showing the failure of pollination to take place. Indeed,

in calm weather, in these conditions, under a bag seed-production totally fails.

It is obvious, then, that in the genus *Oenothera* continuous self-pollination, so far from being detrimental, is a great advantage, for the autogamous species are wider in range, more numerous in individuals, and show much more diversification of races than their allogamous relatives.

The statement sometimes made, that the open-pollinated species *require* cross-pollination for their greatest welfare, appears to be equally erroneous. Darwin and others after him have shown the advantage or the necessity of occasional crossing in many cases, and it has also been shown that the heterozygous condition, *e.g.*, in maize, is a direct and immediate stimulus to growth. Yet it seems quite certain that this condition is not universal and that in the genus *Oenothera* any such stimulus, if it exists at all, is greatly overbalanced by the advantage of a mechanism which will ensure self-pollination and therefore the production of seeds in all circumstances. The assertion that inbreeding of the *Oenotheras* in experimental work has resulted in their degeneration and partial sterility is without support in fact, for (1) there is no evidence whatever of their degeneration in culture, and (2) Geerts has shown that partial sterility is a widespread phenomenon, occurring in all branches of the *Onagraceæ*.

We are in agreement with the view of de Vries and Bartlett that the original home of the genus was in Central and South America, whence they have spread northwards since the retreat of the ice. No doubt a great deal of the diversification of species which has resulted in the present profusion of forms occurred during this migration northwards and expansion over the North American continent. Much light might be thrown on the probable nature of these changes by a study of the South American species, many of which are comparatively little known.

It would seem probable that these original progenitors of the present North American forms belonged either to the large-flowered series or to the medium-flowered *biennis* group. De Vries (425) inclines to the latter view, and supposes that the *biennis* array in the Middle States gave rise on the one hand to the more northerly smaller-flowered forms in the *muricata* series, and on the other to the large-flowered forms in the southern and western States. But to the writer the view seems at least equally tenable, that the large-flowered species were the earlier, and the passage northwards has been accompanied by successive reduction in the size of the flower. This would not, however, apply to the recently described *Oe. macrosiphon* which has extremely large flowers. Certainly, judging from present distribution, the species with smallest flowers seem to be not only the most hardy but the most northerly in their dispersal. We would, therefore, agree that the *muricata* series have been derived from the *biennis* series, but would consider it not unlikely that the latter may in turn have descended from the large-flowered open-pollinated forms still further south.

In either case, it is obvious that the habit of self-pollination has been a great advantage in the struggle for existence, to the forms that adopted it. From this it follows that there is no necessity for crossing, either to prevent degeneration or to induce variability. The self-pollinated forms have derived their great advantage from the increased seed-production, and there is no reason whatever for supposing that the continued inbreeding has exerted any contrary effect. Indeed, the autogamous species are, on the whole, decidedly more hardy and vigorous than the allogamous. They also, contrary to what might be expected, appear to be much more polymorphic. The source of this polymorphism, which is very pronounced in the *biennis* series, is not so clear. Probably geographic and climatic variation, with selection and mutation,

were all required to bring about the present condition of affairs, in which in some cases geographic races with local adaptations appear to occupy successive areas, while in other cases a number of equally adapted races occupy the same local area. It would also seem, from the phenomena of inheritance in this genus, that many new forms may have arisen through crossing, for new and constant hybrids are known to be produced in this way. It has been shown that the allogamous species undergo crossing in every generation, *e.g.*, *Oe. grandiflora* in Alabama, while even the autogamous species cross occasionally.

A few other biological and ecological features of the *Oenotheras* may be pointed out. The flowers open soon after sunset and generally fade more or less quickly on the following day. The sudden opening of the petals, particularly in the large-flowered species, is an interesting process and has been studied by several investigators. It appears to be a growth-response to falling temperature. The pressure developed from within first splits apart the sepals down one line, then the bud opens until the petals, which are wrapped about each other in convolute fashion, loosen to form a cylinder. By the rapid and sometimes almost instantaneous unrolling of this cylinder into the form of an inverted cone the sepals are reflexed and the petals then more slowly open out nearly flat. The whole process is accomplished more quickly than it can be described, and a field of *Oenotheras* after sundown with numbers of flowers popping open all over each plant is a notable sight. This reaction is more marked in hot than in temperate climates, and particularly on a cool evening after a hot day.

Each stem and branch produces a succession of flowers during the blooming season, which may continue for more than eight weeks. Usually one, but sometimes three or even more flowers open on each stem or branch in one evening. The flowers, particularly in the large-flowered

forms, decrease notably in size towards the latter part of the season. Since the style does not decrease in length as rapidly as the petals, it sometimes protrudes from the buds at the end of the season, and expands its stigma lobes before the bud opens. But such flowers are almost certain to be overtaken by frost before they can mature any seeds, so that the suggestion that this is an adaptation to secure occasional cross-pollination is without foundation. If there is any such adaptation in the *Oenotheras* at all, it is to be found in the short style of the small-flowered species to prevent crossing, or rather to obviate the dangers attendant upon open pollination !

The new flowers continue fresh through the night. In the fading, which begins on the following morning, unless the day is dull, the hypanthium or flower-stalk and the petals usually change colour somewhat. Frequently the base only of the petals becomes faintly tinged with pink, but in some species the whole petal becomes orange-coloured by the development of red anthocyanin in the yellow petal. This is true, for instance, of a species I have grown from the Madrid Botanical Garden under the name *Oe. spectabilis*.

The hypanthium is a characteristic organ of the flower in the genus *Oenothera*. It varies enormously in length in the different species, and it is not inconceivable that it may have arisen by a mutation, as MacDougal has suggested. The fact that when the young buds are parasitised by larvæ the hypanthium wholly fails to develop though the bud cones enlarge to their full size, and that aberrant individuals occasionally appear in cultures in which, among other peculiarities, the hypanthia are undeveloped, perhaps points to a similar conclusion. The striking manner in which the offspring of the original heterozygous *rubricalyx* mutant had either red or green hypanthia throughout also shows that the hypanthium clearly behaves as a unit structure, though

of course it does not *necessarily* follow that it originated as a unit. Thus, horns in cattle have apparently been suddenly lost in the polled breeds, and the hornless character is rather sharply alternative to horns in crosses, yet Osborn (292) has shown with much probability that horns in the Bovidæ, the Titanotheria and other groups were a gradual and continuous orthogenetic development.

To return to the hypanthium of *Oenothera*, at the base of the tube nectar is secreted which attracts insects. In North America the flowers when they open are frequented by large hawk moths (probably *Protoparce convolvuli*, Linn., or a related species)¹ which suck the nectar from the base of the hollow hypanthium by means of their enormously long probosces. During this process they aid in pollination of the long-styled forms, and masses of pollen may frequently be seen attached to their bodies. Next morning, when the flowers have already begun to wilt, they are visited by bees and other insects. Crosses of the large-flowered forms are in this way continually taking place, both in the wild and in gardens. The amount of such crossing in European gardens has probably been underestimated. The wind also takes some part in bringing the viscid strings of pollen from the anthers of a flower into occasional contact with its stigma, to which the pollen grains then adhere. But the sticky character of the pollen, which is held together in heavy masses, probably prevents the wind taking much part in the transfer of pollen from plant to plant.

The *Oenotheras* are apparently all biennial in their native localities, a rosette being formed in the first season either from seeds which have just been shed or from those which have passed the winter in the soil. In the following season a stem is formed and flowers and seeds produced.

¹ Hitchcock (187) found that *Oe. Missouriensis* (now usually placed in a separate genus, *Megapterium*) was visited by the sphinx moth *Deilephila lineata*.

But when any of these species are taken into culture they may be grown as annuals by beginning them under glass. With different conditions of culture, the habit and development of the plants vary enormously, and it is possible



Fig. 8.—*Oe. lata* in tropical conditions.
No internodes are formed.

even to transform some of them into perennials. Cultural conditions, of course, bring out many characters which would rarely or never have a chance to develop under the more rigorous conditions of competition with other vegetation.

The importance of recording the environmental conditions in all accurate experiments on heredity has been undervalued, but the *Oenotheras* furnish an apt case in which variations of the environment lead to surprising modifications in the development of the organism. Certain stages may be wholly omitted under one set of conditions of growth, which will appear fully developed in another set. Thus in the mature rosette of *Oe. grandiflora* (Fig. 1, p. 13), a characteristic type of leaf with deep basal lobes appears, but in ordinary cultures this stage is wholly omitted. To mention one other case, a culture of *Oenotheras* was grown (142) for twenty-two months in a tropical greenhouse under conditions of very high temperature and moisture content. In this environment the *Oe. Lamarckiana* forms nearly all continue to produce rosette-leaves, and in this way some of them formed stems several inches high but without internodes, the whole surface being covered with leaf bases (see Fig. 8). In fact, the modifications in growth which may be produced by varying the environment appear to be unlimited, but there appears to be no tendency for such modifications to be immediately inherited. The fundamental germ plasm remains the same, and is very little if at all affected. Hunger (193) has recently carried out experiments with *Oe. Lamarckiana* similar to those above mentioned. He grew his plants in the tropical climate of Saltiga, near Buitenzorg, Java, and found that they all remained rosettes and failed to form a stem or come into bloom. These experiments will be referred to again in Chapter IV.

The almost unlimited variety of distinct and constant races in the *Oenotheras* is no less striking than the diversity of reaction which may be obtained from any one race by modifications of its environment. In how far and under what conditions such "acquired characters" may become heritable is still one of the larger unsolved problems in plant evolution.

CHAPTER III

THE CULTURAL HISTORY OF OENOTHERA

BEFORE considering the present status of *Oe. Lamarckiana*, on which so much attention has been focussed, it is desirable to consider briefly the history of all the related forms in cultivation, so far as it can now be determined. As pointed out in previous pages, the distribution of the *Oenotheras* has been greatly changed in the last three centuries. Many forms are now, and have been for a century or more, widely distributed in Europe, and many have found places to flourish in South Africa, Australia, Japan, and other countries. Some of these races or species have (1) remained unmodified under conditions of cultivation or naturalisation. Others have either (2) been synthesised through crossing, or (3) been modified out of recognition, or (4) originated through mutation in their new habitats, or (5) have become extinct in their original home. It is probable that all these possibilities have been realised in different species. Thus *Oe. parviflora*, L., rediscovered in Maine in 1905, was shown by MacDougal (253) to be identical with a form long cultivated under that name in the Madrid Botanical Garden, though the Maine plants matured more rapidly. It is thus evident (as many other facts regarding cultivated plants have shown) that certain species may be cultivated for long periods without undergoing any structural modification. The physiological difference, in rate of development, may have been impressed on the species by continuous

TABLE I.—*Early*

Date.	Place.	Name.	Author.
1614	Padua?	Seeds from Virginia	—
1619	Basil	<i>Lysimachia lutea corniculata</i> ¹	C. Bauhin
1627	Venice	<i>Hyoscyamus Virginianus</i> ² .	Alpino
1628	Rome	<i>Lysimachia Americana</i> ³ . .	Columna in Hernandez
1629	London	<i>Lysimachia lutea siliquosa Virginiana</i> ¹	Parkinson
1640	London	<i>Lysimachia lutea siliquosa Virginiana</i>	Parkinson
1660	—	<i>Altera fol. latioribus flor. lut. majoribus</i>	—
1669	London	<i>Lysimachia corniculata minor lutea Canadensis</i>	Morison
1680	Oxford	<i>Lysimachia lutea corniculata non papposa Virginiana major</i>	Morison
		<i>Lysimachia lutea corniculata non papposa Virginiana minor</i>	Morison
1680	Oxford	<i>Lysimachia Virginiana latifolia lutea corniculata</i>	Morison
1680	Oxford	<i>Lysimachia Virginiana angustifolia corniculata</i>	Morison
1686	London	<i>Lysimachia lutea Virginiana</i>	Ray
1686	London	<i>Lysimachia Virginiana altera, foliis latioribus, floribus luteis, majoribus</i>	Ray
1694	Paris	<i>Onagra latifolia</i>	Tournefort
1694	Paris	<i>Onagra angustifolia</i>	Tournefort
1694	Paris	<i>Onagra angustifolia, caule rubro, flore minori</i>	Tournefort
1700	Paris	<i>Onagra latifolia, floribus amplis</i>	Tournefort
1714	Paris	<i>Lysimachia latifolia, spicata, lutea Lusitanica</i>	Barrelier
1714	Paris	<i>Lysimachia angustifolia, spicata, lutea Lusitanica</i>	Barrelier
1714	Paris	<i>Lysimachia lutea, corniculata latifolia Lusitanica</i>	Barrelier
1757	London	<i>Oenothera foliis lanceolatis, dentatis, caule hispido</i>	Miller
1757	London	<i>Oenothera foliis ovato-lanceolatis planis</i>	Miller

¹ Seeds from Padua. ² Seeds from an English physician, Dr. More.

references to *Oenothera*.

Work.		Identity of Species.
Pinax, pp. 245, 520 ..	Description	<i>Oe. biennis</i> , L.
De Plantis Exoticis ..	Description and plate	<i>Oe. biennis</i> , L. ?
Nova Plant., Anim. et Miner. Mexicanorum	Description and plate	<i>Oe. biennis</i> , L. ?
Paradisus	Description and plate	<i>Oe. biennis</i> , L.
Theatrum Botanicum .	Description and plate	<i>Oe. biennis</i> , L.
Cat. Altdorffinus ..	Name	Luxuriant <i>biennis</i> ?
Hort. Reg. Blesensis ..	Description	<i>Oe. muricata</i> , L.
Plant. Hist. Univ. Oxon., ii.	Description	<i>Oe. biennis</i> , L.
Plant. Hist. Univ. Oxon., ii.	Description	<i>Oe. angustissima</i> , Gates
Plant. Hist. Univ. Oxon., ii.	Plate	<i>Oe. biennis</i> , L.
Plant. Hist. Univ. Oxon., ii.	Sect. 3, t. 11, Fig. 7.	
Plant. Hist. Univ. Oxon., ii.	Sect. 3, t. 11, Fig. 8.	<i>Oe. angustissima</i>
Historia Plantarum, i.	Description	<i>Oe. biennis</i> , L.
Historia Plantarum, i.	Description	?
Élém. de Botanique ..	Listed	<i>Oe. biennis</i> , L.
Élém. de Botanique ..	Listed	<i>Oe. angustissima</i> , Gates
Élém. de Botanique ..	Listed	<i>Oe. muricata</i> , L., narrow- leaved race
Institutiones Rei Her- bariae	Listed	?
Plantae per Gall., Hisp. et Italiam observatae	Plate 989	<i>Oe. biennis</i> race
Plantae per Gall., Hisp. et Italiam observatae	Plate 990	<i>Oe. angustissima</i>
Plantae per Gall., Hisp. et Italiam observatae	Plate 1232	"Luxuriant <i>biennis</i> " ?
Figures of plants des- cribed in the <i>Gar- dener's Dictionary</i> , ii.	Plate 189, Fig. 1 ..	<i>Oe. muricata</i> , L.
Figures of plants des- cribed in the <i>Gar- dener's Dictionary</i> , ii.	Plate 189, Fig. 2 ..	<i>Oe. biennis</i> , L.

³ Seeds from Johannes Pona in Verona.⁴ Seeds from Virginia.

growth in the warmer climate of Spain with its longer growing season ; or the original Madrid plants may have been derived from a more southern latitude than Maine.

Cultivation of plants derived from seeds from botanical gardens makes it evident that much intercrossing often takes place, and it is very probable that some of the races now cultivated under garden names have originated in this way. Again, the "European *biennis*," which now flourishes in Holland and elsewhere and was the type of Linnæus's species, appears to be extinct in America. The same may be true of *Oe. Lamarckiana*, though in this case it is not improbable that the species may yet be found in the region of Virginia, West Virginia, Kentucky, or adjacent areas.

There was for some time a disposition to assume that *Oe. Lamarckiana* had originated as a garden hybrid because it could not be found in the wild condition, although several other *Oenothera* species, including *Oe. biennis*, were in precisely the same position. But the hopes or fears that *Oe. Lamarckiana* might turn out to have been synthesised by crossing in cultivation have been definitely laid at rest, first by the failure of Davis's (79, 80, 85) attempts to produce it in this manner, and finally by the discovery (426) at the Museum d'Histoire Naturelle in Paris of a specimen collected by Michaux in North America about 1796, which agrees exactly with *Oe. Lamarckiana*, Ser., in modern cultures.

Referring now to the history of the *Oenotheras* in Europe, Table I (p. 48) includes the more interesting historical references up to 1760.

The European history of *Oenothera* begins with the introduction of a form in 1614. The species has not been identified with certainty, but was very probably the same as that afterwards described by Caspar Bauhin in the *Pinax* (1623) under the name *Lysimachia lutea corniculata*, from seeds obtained from the botanical garden

at Padua in 1619. I formerly considered this more nearly related to *Oe. Lamarckiana*, though there was great difficulty in the identification, notwithstanding Bauhin's unusually lengthy description. Subsequent detailed study of this and many other records has modified my former identification of this and certain other forms, the examination of pre-Linnean herbarium specimens in particular having now made it possible to identify with certainty a considerable number of the pre-Linnean polynomials.

The identification of Bauhin's *Lysimachia lutea corniculata* was made possible by a specimen in the Morison Herbarium at Oxford. Photographs of this plant and of three other early specimens, kindly taken by Mr. H. Baker, are published here with the kind permission of Prof. S. H. Vines, F.R.S. The features of this specimen will be seen from Fig. 3 (p. 18). On the sheet is written "*Lysimachia lutea corniculata non papposa, Virginiana major*. Moris. Hist. Oxon. 2. 271. No. 7. *Lysimachia lutea corniculata*. C. B. P. 245." This is in the handwriting of Bobart the younger, who probably collected these specimens from plants grown in the Oxford botanic garden, and named them after the publication of Morison's *Plantarum Historia Universalis Oxoniensis*, Vol. 1 in 1680. The "2" on the sheet refers to pars secunda of Vol. 1. Pars prima was to have contained the trees but was never published. In 1886 the "2" was changed to 1 and the "No. 7" (referring to Morison's species number) added by the Rev. H. C. F. Garnsey, Fellow of Magdalen College. The description and measurements of this specimen are as follows:—rosette-leaf 20 cm. long to beginning of petiole, rather obtuse pointed, very broad (5.5 cm. greatest breadth), margin nearly entire, but obscurely and very distantly repand-denticulate, surface somewhat pubescent, midrib broad, probably white, blade perhaps slightly crinkled; upper stem-leaves 10.5–9 cm. in length

by 3.5–1.5 cm. in breadth; length of bud cone about 17 mm., petals crumpled but 18 mm. long, or probably somewhat longer, length of hypanthium 25–28 mm., thickness of hypanthium 1–1.5 mm., length of ovary 10–12 mm.; style short; capsules with scattered long hairs, none on hypanthium and rather few on sepals except the sepal tips.

Comparison of these measurements with Bartlett's description of the plant from Holland which he rightly regarded as the type of *Oe. biennis*, L., shows that the two are identical in almost every particular. *Lysimachia lutea corniculata* of Bauhin is therefore clearly a synonym of *Oe. biennis*, L., and is the same plant which by 1737, in the time of Linnæus, had become widely naturalised on the coast of Holland. The specimens of *Oenothera* in the Morison Herbarium are probably the earliest extant, since Bauhin's specimen no longer exists.

The specimen above-described shows that Bauhin's description in the appendix to the *Pinax* was inaccurate in its dimensions, which were evidently only guesses. Thus he says of the rosette leaves, "*latitudine unciam vix excedentia*," though the specimen shows the leaves to have been more than 2 inches wide. Similarly, the combined length of bud cone and hypanthium are stated to be 3 inches, though in reality they scarcely reached 2 inches; the length of the ovary is also exaggerated from $\frac{1}{2}$ an inch to $1\frac{1}{2}$ inches, and that of the capsule from 1 inch to 2–3 inches. The rosette leaves are described as thick, oblong, scarcely exceeding 1 inch in width, pale green and pointed, with a white midrib.

Parkinson's *Paradisus* (1629) contains an independent description of what was evidently the same plant, in which he refers to the "long and narrow pale green leaves" of the rosette; and the *Theatrum Botanicum* (1640) contains a figure of this plant. Parkinson gave the plant its English name—evening primrose. Prosper Alpin, in

his *De Plantis Exoticis* (1627), had also published a figure (see Fig. 9) of an *Oenothera* under the name *Hyoscyamus Virginianus*, from seeds obtained from an English phy-



FIG. 9.—*Hyoscyamus Virginianus*.
Alpin's *De Pl. Exot.*, p. 324.

sician, Dr. More. This is perhaps the same plant, but these drawings are too crude to be of much service in determining details of structure or even matters of relative

size. Columna (1628), in the *Nova Plantarum, Animalium Mexicanorum*, of Hernandez, described and figured what was probably a different race of *Oe. biennis* or *Oe. muricata*, under the name *Lysimachia Americana*. His rather inaccurate figure represents a plant with narrow leaves and mucronate petals. (See Fig. 10).

Gerarde's Herbal in 1633 copies Parkinson's figure



FIG. 10.—LEFT. *Lysimachia Americana*. Hernandez, *Nova. Plant., Anim. et Miner. Mex.*, p. 882.

RIGHT. Fig. 1232, Barrelier, *Plantae per Gall., Hisp. et Italianam observatae*.

(p. 475) and records several additional observations in his description. The plant is tall and with "many branches of an overworne colour, and a little hairie." The leaves are somewhat sinuate and the midribs whitish. The capsules grow to be "some 2 inches long, being thicker below, and sharper at the top, and somewhat twined"—an inaccurate description.

Morison, in his *Hortus Regius Blesensis* (1669), was one of the first to recognise various forms. In addition to *Lysimachia lutea corniculata* of Bauhin, he listed another species which was added to the London Garden between 1655 and 1660. This is named *Lysimachia corniculata minor lutea Canadensis*, and was probably the second



FIG. 11.—*Lysimachia lutea corniculata non papposa Virginiana minor*, Morison Herb. = *Oe. angustissima*.

Oenothera species to be introduced into Europe. It was evidently a race of *Oe. angustissima*, Gates.

The evidence for this identification is found in another valuable specimen in the Morison Herbarium at Oxford (see Fig. 11). On this specimen is written in the hand of Bobart, "*Lysimachia lutea corniculata non papposa Virginiana minor*. Moris. H. Ox., 271. *Lysimachia siliquosa*

Virginiana Tradescanti, Park." Soon afterwards (for it is in the same ink), Bobart, evidently through some misapprehension, changed the word "minor" to "major." The dot over the original *i* can be plainly seen. In 1886 the Rev. Garnsey intercalated the "1" and "No. 7", which should have been No. 8. It is obvious that Morison used the terms *Virginiana* and *Canadensis* interchangeably and that the *Lysimachia lutea corniculata* and *Lysimachia*



FIG. 12.—LEFT, *Lysimachia Virginiana latifolia, lutea, corniculata*.
Morison, *Hist. Pl. Univ. Oxon.*, = *Oe. biennis*.
RIGHT, *Lysim. Virginiana angustifolia, corniculata* = *Oe. angustissima*.

corniculata minor lutea Canadensis seu angustifolia of the *Hortus Blesensis* were the same respectively as *Lysimachia lutea corniculata non papposa Virginiana major* and *Lysimachia lutea corniculata non papposa Virginiana minor* of the *Hist. Oxon.* The third "Lysimachia" of the *Hort. Bles.*, *Lysim. lutea flore globoso*, Park. Ger., is not an *Oenothera*.

The two species of Morison above-mentioned are figured by him in *Hist. Oxon.*, sect. 3, tab. 11 (see Fig. 12), under the names *Lysimachia Virginiana latifolia*, *lutea*, *corniculata* and *Lysimachia Virginiana angustifolia*, *corniculata*. The first has already been identified from the specimen as the type of *Oe. biennis*, L. The second, having smaller flowers and narrower leaves, I formerly classed with *Oe. muricata*, L., before such very narrow-leaved species as *Oe. angustissima* were known to exist. Morison's specimen, however, evidently agrees with the latter species in all but two points, and must therefore be classed with it.

A glance at the specimen shows it to be remarkably like *Oe. angustissima*, Gates (144), described from Ithaca, New York, in 1913. Bartlett (13) refers to two forms closely allied to *Oe. angustissima* occurring in Maryland and Virginia, the source from which, no doubt, the ancestors of this specimen came. Although the specimen differs in certain particulars from *Oe. angustissima*, yet the differences are not so great as to justify its exclusion from that species. The description of the specimen (Fig. 11) is as follows: rosette-leaf, or lower stem-leaf, 15 cm. long, acute pointed, 15 mm. greatest width, margin faintly repand-denticulate; stem-leaves proportionally long and narrow (width 15–10 mm.) with apparently reddish midribs, surface covered with scattered pubescence; inflorescence rather loose; flowers very small, style short, length of petals 12 mm., length of hypanthium 21–23 mm., thickness of hypanthium 1.5 mm., length of ovary 12 mm.; ovaries and sepals densely covered with long hairs arising from papillæ, very few on hypanthium; stem bearing considerable pubescence of long type of hair.

Comparison with my description of *Oe. angustissima* shows that practically the only differences are in the smaller flowers (petals 12 mm. instead of 15–20 mm.) and greater pubescence of this specimen. Morison was therefore

the first to describe this species, in 1669. Another specimen is to be found in the British Museum (Natural History). A volume of rare plants of Veslinzius, Alpinus, and others contains a collection of specimens made by C. Schreutter at Padua in 1665. Among them is *Oe. angustissima* under the names *Lysimachia lutea corniculata* and *Lysim. Virginiana*. This species was probably introduced into Padua about the time Morison obtained it. The small flowers and rather weak growth of this plant probably led to its total extinction in gardens before the time of Linnæus, so that it escaped description by him and only attained binomial rank in 1913. It was, however, in cultivation in Paris as late as 1714 (Barrelier). All the other species, except perhaps *Oe. parviflora*, escaped from cultivation and soon became naturalised in many places, while *Oe. parviflora* itself has been retained in gardens to the present day.

The first volume of Robert Morison's *Plantarum Historia Universalis Oxoniensis*, published at Oxford in 1680, contains the full description of Bauhin's plant with a few alterations, under the name *Lysimachia lutea corniculata non papposa*¹ *Virginiana major*. To this is added a short description of another Oenothera, *Lysimachia lutea corniculata non papposa Virginiana minor*, which is described as differing in having leaves about half as wide, flowers much smaller, and shorter stems. This is the plant represented by the specimen in Fig. 11. The two species known to Morison were thus *Oe. biennis*, L., and *Oe. angustissima*.

Among the 17th century MSS. in the British Museum, Bloomsbury (Manuscript Department), one (Sloane 5282) is a large volume bearing the title "A book containing herbs, flowers and trees either growing wild or cultivated in gardens in England especially near London, etc." It is anonymous, dated about 1684, and contains a valuable

¹ *Non papposa* contrasts the seeds of Oenothera with the genus *Epilobium*.

collection of coloured drawings. Among the latter, which are apparently natural size and are without names, is (fol. 36) a flowering shoot of *Oenothera*. The bracts are rather narrow, the flower about 4 cm. in diameter, evidently representing *Lysimachia lutea Virginiana*, the type of the modern *Oe. biennis*, L. This is perhaps the earliest coloured drawing of an *Oenothera* extant.

The *Flora Altdorffina*, a catalogue of polynomial names of plants grown in the botanic garden at Altdorff near Nuremberg, in 1660, recognised two species, (a) the plant of Bauhin, and (b) *altera fol. latioribus flor. luteis majoribus*, for which it gives Alpin's plant as a synonym. But Alpin's drawing (see Fig. 9, p. 53) would seem to indicate that that plant had quite small flowers. The second species of the *Flora Altdorffina* appears to be different from either of Morison's species, and it was described by Ray. In 1686 Ray published his *Historia Plantarum*, which contained, under the name *Lysimachia lutea Virginiana*, a description of Bauhin's plant, copied from Morison, but with many emendations and additions. He makes no mention of Morison's smaller species, but gives a short description of another species as follows:—

11. *Lysimachia Virginiana altera, foliis latioribus, floribus luteis majoribus, Cat. Altdorff.*

Haec praecedente elatior est & major, ut quae humanum interdum altitudinem multum superet, foliis latioribus, & pro magnitudine brevioribus, ad margines minus sinuatis & propemodum aequalibus; floribus etiam multo amplioribus. In hortis nostris frequentior est praecedente.

Ray undoubtedly grew this species, which he states differs from the first one in being taller and larger, sometimes much higher than a man, with broader and relatively shorter leaves the margins of which are less sinuate and nearly entire, the flowers much larger.¹

¹ At St. Anne's-on-the-Sea in 1910 I observed a rather constant race in an unused back-yard, which most resembled a very luxuriant *Oe. mut. rubrinervis*. Its average height exceeded that of a man and its flowers were correspondingly large.

The concluding remark of Ray, "In hortis nostris frequentior est praecedente" would seem to show that its large flowers quickly brought it into favour in England, for Morison makes no mention of it in 1680. This species remains something of a mystery. It may have been only a large-flowered *Oe. biennis*, or it may have belonged nearer *Oe. grandiflora* or *Oe. Lamarckiana*; and it is worthy of note that L'Heritier in his MS. description of *Oe. grandiflora*, written about 1788, says "Conf. *Onagra latifolia floribus amplis*. Tourn. inst. 302."

Unfortunately, Ray's herbarium in the British Museum (Natural History) contains no specimens of this species, so its exact characters will probably never be settled. It must have been introduced into the garden at Altdorff at some time previous to 1660, and would appear to have been brought to England between about 1680 and 1686. Otherwise it seems difficult to account for the fact that Morison evidently did not grow it. Nevertheless, these two references, in *Cat. Altdorff*. and in Ray, seem to prove conclusively that a large-flowered *Oenothera* had already been brought to Europe before 1660. The complete absence of specimens from all the herbaria in which other *Oenothera* species are well represented, in contrast to Ray's statement that it is more frequent in gardens, is, however, a very mysterious circumstance. But there can be no doubt that Ray grew it himself.

In the third volume of the *Historia Plantarum* (1704), Ray refers to two other *Oenotheras* in addition to the two described in Vol. 1. The reference to the first of these is as follows:—

"*Lysimachia lutea Virginiana angustifolia, flore minori* Pluk. Phyt. T. 202. f. 7. An *Lysim. angustifolia Canadensis, altera, caule rubro, flore minore* Schol. Bot. ?"

This plant was very probably the *Lysim. corniculata lutea Canadensis minor seu angustifolia* of Morison, = *Oe. angustissima*, though there is no specimen to prove this.

The last species listed by Ray is *Lysimachia lutea corniculata*, *flore sulphureo*, Hort. Lugd. Bat., recently shown by Bartlett to be *Oe. biennis* var. *sulphurea*, de Vries.

The view that *Lysim. Virginiana altera*, *foliis latioribus*, *floribus luteis majoribus*, may have been merely a more luxuriant form of *Lysimachia lutea corniculata* was suggested by a specimen in the Duchess of Beaufort's collection in the Sloane Herbarium under the name *Lysimachia lutea Virginiana*. It is precisely like the type of the latter species (early specimens of which show very little variation) except that it is much larger in all its parts. The petals in ordinary specimens only vary in length from 18 to 20 mm. The specimen in question has several flowers, in all of which the petals are about 29 mm. in length. But the short style and the shape of the leaves proclaim it merely *Oe. biennis* of a larger growth. All the specimens in the Duchess of Beaufort's collection are large. Is it possible that the large size of this plant, and the increase in length of petals from 20 to 29 mm., are merely a result of intensive cultivation combined perhaps with selection? This hypothesis does not, however, completely solve the difficulty, for the name given is that of Ray's first species, and not of the second, which, he says, is more common in gardens. This hypothesis would also necessarily assume that Ray was mistaken in the other differences which he pointed out, and it is further in conflict with the fact that the *Cat. Altdorff.* recognised these two things as separate species.

That *Oe. parviflora*, L., was also an early arrival in Europe is shown by a specimen in the Sherardian Herbarium at Oxford, herewith reproduced (Fig. 13), and another specimen in Plukenet's herbarium at the British Museum. On the label of the Oxford specimen is written "*Onagre Amer. fr. brevi.*"

"*Lysimachia lutea, angustifolia, virginiana, flore minore.*
Pluk. Almag. 235. Tab. 202. f. 7.

"*Lysimachia angustifolia*, *Canadensis altera*, *caule rubro*, *flore minore* Schol. Bot. 44.

"*Onagra angustifolia*, *caule rubro*, *flore minore*. I.R.H. 302. 772₃."

As shown by Fig. 13, the flowers are extremely small, the bud cone being only 5 mm. in length, ovary 4 mm. in length, hypanthium 20 mm.; inflorescence compact; stem-leaves short (9.5–10 cm.), very narrow (14–16 mm.),



FIG. 13.—*Lysimachia lutea*, *angustifolia*, *Virginiana*, *flore minore*, Morison Herb., = *Oe. parviflora*, L.

margin distinctly repand-denticulate, points rather broad. This agrees with Vail's description of *Oe. parviflora*, L., in practically all particulars except the remarkably short ovaries, which measure only 4 mm. instead of 8 or 9 mm. in length.

There are two small specimens of this species in Plukenet's collection. Their description is as follows:—bud cone 5 mm. in length, petals 5 mm., hypanthium 32 mm., ovary 11 mm.; some long hairs on buds and stem; width of stem-leaves about 9 mm. Plukenet's figure in the *Almagestum* (1696) was probably drawn from this specimen. He further remarks (p. 235):—"Hujus plantae

siliqua in corniculam non extenditur," from which it may be inferred that the plants failed to set seeds though the flowers are self-pollinating.

The pre-Linnean polynomial, *Lysimachia lutea angustifolia Virginiana flore minore*, is therefore clearly identified by these specimens and figures, as *Oe. parviflora*, L. *Onagra angustifolia*, *caule rubro*, *flore minore* of Tournefort, was in some cases referred to the same species, but it would

seem that strictly this name belonged to certain races of what we now know as *Oe. muricata*, L. Plukenet recognises his plant as most nearly related to *Lysimachia angustifolia Canadensis altera, caule rubro, flore minore*, Schol. Botan. 44, which is presumably the same as Tournefort's *Onagra angustifolia caule rubro, flore minore*. The conspicuous red muricate stem of these races of *Oe. muricata* is the most striking distinction from *Oe. parviflora*, and this difference is represented in the polynomial names.

That races of *Oe. muricata*, L., were among the early introductions is shown by several specimens in the Sherard and Du Bois collections at Oxford. These include both narrow-leaved and broad-leaved specimens. We have found precisely the same dimorphism in plants of *Oe. muricata* collected both from Nova Scotia and Winnipeg. One of the sheets from the Sherard Herbarium bears the following label: "*Onagra angustifolia*, I.R.H. 302.

"*Lysimachia angustifolia, Canadensis, corniculata*, H.R. Par.

"*Lysimachia corniculata, lutea Canadensis, minor seu angustifolia*, Mor. H.R. Bles.

"*Lysimachia lutea corniculata non papposa Virginiana minor*, H.Ox. II. 271." Also the number 772.

It was hence considered incorrectly to be the same as the species we now call *Oe. angustissima*. The specimen has fairly broad leaves, a rosette-leaf 23.5 cm. long \times 4.1 cm. wide, repand-denticulate; stem-leaves 21–23 mm. wide; flowers small (petals 9–10 mm.). It is to be considered as a broad-leaved type of *Oe. muricata*, L.

The next specimen (see Fig. 14) bears only the number 772₂, indicating that it belongs to the previous sheet. This plant represents a narrow-leaved form of *Oe. muricata*. The rosette-leaves are respectively 30 cm. \times 3.1 cm. and 24 cm. \times 3.4 cm.; stem-leaves very narrow (19–12 mm. wide, about 11 cm. long); length of bud cone 15 mm., petals 18? mm.; pubescence as in *Oe. muricata*.

A specimen in the Du Bois collection at Oxford, which belongs to the type of *Oe. muricata*, bears the following label: "*Onagra angustifolia*, caule rubro, flore minore. Tournef. 302" and "From Mr. Stonestreet." The sheet bears a long, narrow, rosette-leaf about 24 cm. long, 4 cm. greatest width, with probably red midribs. The stem bears conspicuous long hairs, arising from red papillæ;



FIG. 14.—Herb. Morison.
A narrow-leaved race of *Oe. muricata*, L.

the shoot is in fruit, so the flowers are late ones and are very small (length of bud cone 5 mm.), length of hypanthium 14 mm., sepal tips not in contact. The above polynomial therefore in some cases refers to races of *Oe. muricata*, L., and such specimens as this show that races existed which were intermediate between *Oe. muricata* and *Oe. angustissima* in width of leaf and size of flower. The

Du Bois specimens were supplied by Krieg and Vernon from Maryland, Mark Catesby from S. Carolina, and others, between 1690 and 1723.

Before Tournefort's *Institutiones* (1700) the following species were therefore known, as shown by herbarium specimens chiefly at Oxford and in the British Museum :— (1) *Oe. biennis*, (2) *Oe. angustissima*, (3) *Oe. parviflora*, (4) *Oe. muricata*; and from the description it is certain that a larger-flowered species had also been cultivated. The latter appears from specimens to have been the exact counterpart of *Oe. biennis*, but much larger in all its parts. However, since all such specimens bore the names attached to the true *Oe. biennis*, and since there are apparently no specimens extant bearing the name *Lysimachia Virginiana altera, foliis latioribus, floribus luteis majoribus*, it may be that the latter really represented a distinct large-flowered species. But this conclusion is difficult to reconcile with the fact that Ray states this species to be commoner in gardens, while in point of fact the preserved specimens under this name all belong either to ordinary *biennis* or to the "luxuriant *biennis*." If one adopts the conclusion that the large-flowered form was in fact a different species, then the total absence of specimens remains a mystery. On the other hand, if one concludes that the form in question was a luxuriant *biennis*, then why was the name of the ordinary *biennis* always applied to it?

Tournefort, in the *Éléments de Botanique* (1694), lists three species of *Oenothera*.

Onagra latifolia. Lysimachia lutea corniculata, C.B. Pin.

Onagra angustifolia. Lysimachia angustifolia Canadensis corniculata, H.R.P.

Onagra angustifolia caule rubro, flore minori.

In his *Institutiones Rei Herbariæ* (1700) the list of *Onagra* species has been increased to nine, but of these only the first five are *Oenotheras*, as follows :

(1) *Onagra latifolia*. *Lysimachia lutea corniculata*, C.B. Pin. 245.

(2) *Onagra latifolia*, flore dilutior. *Lysimachia corniculata non papposa*, *Virginiana major*, flore sulphureo, H.L. Bat.

(3) *Onagra latifolia*, floribus amplis. *Lysimachia Virginiana*, altera, foliis latioribus, floribus luteis, majoribus, Cat. Altdorff.

(4) *Onagra angustifolia*. *Lysimachia angustifolia*, *Canadensis*, *corniculata*, H.R.Par. *Lysimachia Corniculata*, *lutea*, *Canadensis*, minor seu *angustifolia*, Mor. H.R. Bles.

(5) *Onagra angustifolia*, caule rubro, flore minori.

These five species may now be identified as follows:—

(1) *Oenothera biennis*, L. The Holland *biennis* ("European *biennis*").

(2) *Oe. biennis* var. *sulphurea*, de Vries. The first recognition of this form seems to have been in Hermannus, *Hort. Acad. Lugduno-Batavi Cat.* 1687. It differs from the type, according to de Vries, only in having paler flowers, and must either have been contained in the original seeds of *Lysimachia lutea corniculata* or have originated by a mutation since.¹

(3) A distinct larger-flowered species or a luxuriant *Oe. biennis*.

¹ One of the specimens in the British Museum, marked *Onagra latifolia flore dilutior*, Tourn., and believed to be the plant referred to by Linnæus in *Hort. Cliff.*, evidently represents *Oe. biennis* var. *sulphurea*. Curiously enough, five flowers of some other kind are attached to the sheet as though they belonged to the specimen. These flowers differ so markedly from those of the specimen that it is not even certain that they belong to an *Oenothera*, though we know of no other genus to which they can be referred. If they represent an *Oenothera* they must have originated by a very wide mutation. Their description is as follows:—hypanthium very long (45–60 mm.), 1.5 mm. thick, bearing scattered hairs, sepals narrow (3 mm. at base), short (12 mm.), no free sepal tips, stigma above anthers, stigma lobes very short (2 mm.) and imperfectly formed. The stigmas seem to resemble those of *Oe. brevistylis*, but the sepals are wholly different from those of any other *Oenothera* known.

(4) Belongs to *Oe. angustissima*, Gates.

(5) This belongs strictly to *Oe. muricata*, L., though *Oe. parviflora*, L., is sometimes referred to it in the early literature. The correct authenticated polynomial for *Oe. parviflora*, L., is *Lysimachia lutea, angustifolia, Virginiana, flore minore*, Pluk. Almag.

This includes nearly all the larger species now known from Eastern North America.

Barrelier (whose drawings are a great advance on those of his predecessors), in his *Plantae per Galliam, Hispaniam et Italiam observatae* (1714), gives very instructive figures of three species, with a new terminology, as follows:—

(1) Pl. 989. *Lysimachia latifolia, spicata, lutea, Lusitanica*, with the synonym *Onagra angustifolia*. Inst. R. Herb. 302.

(2) Pl. 990. *Lysimachia angustifolia, spicata, lutea Lusitanica*, with the synonym *Onagra angustifolia caule rubro, flore minore*. Inst. R. Herb. 302.

(3) Pl. 1232. *Lysimachia lutea, corniculata, latifolia, Lusitanica*, with the synonym *Onagra latifolia, floribus amplis*. Inst. R. Herb. 302.

On account of their interest, these figures of Barrelier are here produced (Figs. 15 and 10, right). His synonymy is obviously incorrect as regards the first two species. Thus *Onagra angustifolia* of Tournefort we have shown to belong to *Oe. angustissima*, while Barrelier's figure 989 shows that this plant belonged to a race of *Oe. biennis* or perhaps *Oe. muricata*. It must be remembered that *Oe. biennis* and *Oe. angustissima* had both been in cultivation since at least 1669, and that *Oe. muricata* was introduced before 1700. Although these are all small-flowered species, it is probable that they crossed occasionally during the period of cultivation up to 1714, and this may have led to the confusion in Barrelier's synonymy. His figure 990 can be referred with certainty to *Oe. angustissima*, though the synonym he gives belongs to *Oe.*

muricata. Pl. 990 shows particularly well the long and loose inflorescence, narrow leaves, and the emarginate and plicate petals of *Oe. angustissima*, the flowers being evidently quite small (12 mm.) as in Morison's race. I formerly, before *Oe. angustissima* had been rediscovered and described, regarded this figure as referring to a narrow-leaved race of *Oe. muricata*.

Barrelier's third species, represented in Pl. 1232 (Fig.



FIG. 15.—Barrelier, *Plantae per Gall., Hisp. et Ital. observatae*.

FIG. 989 = *Oe. biennis*, or perhaps *Oe. muricata*.

FIG. 990 = *Oe. angustissima*.

10, p. 54) is apparently the mysterious plant of Ray and the *Cat. Altdorff*. I formerly regarded it as certain that this was a large-flowered species, probably nearest *Oe. Lamarckiana*. Though that hypothesis is by no means disproved, yet it does not now rest on as firm a basis as before. A critical comparison of the figure with the other two of Barrelier seems to indicate that the flowers were

certainly larger than in the other two species; and the foliage, with leaves sessile and rather broad at the base, seems to resemble that of *Lamarckiana* rather than *grandiflora*. But the entire absence of specimens is a serious drawback to this interpretation.

The only references to the history of this species are the name in *Cat. Altdorff*. (1660), the description in Ray (1686) and the figure of Barrelier (1714). As pointed out earlier in this chapter, this figure 1232 may represent merely *Onagra latifolia* (*Lysim. lutea corniculata*) of a larger growth, in other words a luxuriant *Oe. biennis*. In that case *Onagra latifolia floribus amplis* will not really belong to the large-flowered series at all, but this explanation does not appear to be a satisfactory one either. (See in this connection 154A, p. 385.)

This *Oenothera* with large flowers must have come from the Virginia-Carolina region, and we know from Barton's *Flora of North America*, in which a good figure is given, that *Oe. grandiflora* survived there as late as 1821. Pursh, in his *Flor. Amer. Septen.* (1814), had also described an *Oe. grandiflora*. Chapman, in his *Flora of the Southern United States* (1897), says of *Oe. biennis* in this area that it may be "hairy, hirsute or smoothish," that the earliest leaves are often pinnatifid, the flowers "large," and that it "varies greatly in pubescence and size of flower." It seems, therefore, reasonable to suppose that search will reveal new large-flowered races in this region, and the pinnatifid rosette-leaves are a feature of *Oe. grandiflora*.

In 1735, Zanichelli (*Istoria delle piante de' lidi Veneti*) gives figures of two *Oenotheras* as follows:

I. *Onagra latifolia*, Tav. 112.

II. *Onagra angustifolia*, Tav. 47.

The first is probably a race of *Oe. biennis* having rather small flowers and rather narrow leaves. The second figure represents a plant with larger flowers and smaller, narrow leaves.

It is a curious fact that although Tournefort had recognised five forms which we might now class as four species and a variety, and Barrelier had clearly figured three species belonging apparently to (1) *biennis*, (2) *angustissima*, and (3) a very large-flowered *biennis*, or *Lamarckiana*-like species, yet Linnæus in the *Hortus Cliffortianus*, 1737, only described one. This was doubtless the *biennis* of the Holland sand dunes, as Bartlett has pointed out,—the only *Oenothera* apparently with which Linnæus was then familiar. He also recognised the var. *sulphurea*. He cited figure 1232 of Barrelier (see Fig. 12, p. 56) as belonging to this species and for some time ignored the existence of the other species which had been brought to Europe. Some of these species were afterwards described in successive editions of the *Species Plantarum*.

The only pre-Linnean species not ultimately described by Linnæus were apparently *Lysimachia lutea corniculata non papposa Virginiana minor* of Morison, which is now *Oe. angustissima*; and *Onagra latifolia, floribus amplis*, of Tournefort, which he recognised as a variety of *Oe. biennis* and which appears now to have been a *biennis* with exceptionally large flowers. His failure to describe the first of these was probably, as already suggested, because it had disappeared from gardens and had failed to naturalise itself. Similarly, it seems probable that on the Continent the other species was very little grown in gardens (an inference which is justified by the very few early references to it) and that Linnæus therefore perhaps never made its acquaintance. The only places where this species is known to have been grown are at Altdorff, Germany, in the garden of Ray at Cambridge, and in Barrelier's garden in Paris.

It must be said that the pre-Linnean botanists were more critical in their discrimination of *Oenothera* species than was Linnæus himself, and that his failure at first to recognise more than one species led to much confusion.

This confusion was perhaps increased by contemporary crossing between the various species.

In the eighth edition of the *Gardener's Dictionary*, 1768, Miller applied binomial names to five species of *Oenothera*. Those which concern us are (1) *Oe. biennis*, taken from Linnæus, (2) *Oe. angustifolia*, and (3) *Oe. glabra*. The second is a synonym for *Oe. muricata*, the name given by Linnæus in the previous year. The third species in the absence of specimens cannot be identified, but it may have belonged to *Oe. angustissima*.

It required the stimulus of a fresh discovery of *Oe. grandiflora* in Alabama by Bartram to direct attention once more to a distinction which seems to have been recognised by Barrelier in 1714, and by Ray in 1686, namely, the distinction between large-flowered and small-flowered forms. Bartram sailed from Philadelphia in 1773 in search of rare and useful plants. He discovered *Oe. grandiflora* on the Alabama River, and the species was introduced into Kew in 1778 through seeds from Dr. John Fothergill, who fitted out the expedition. It was studied by Solander, and a very brief description published in *Hortus Kewensis*, 1789. An unpublished figure of the plant, by L'Heritier, seems to have been lost, though a full manuscript description by the latter, written about the same time, has been preserved and was recently published (139), as well as the notes of Solander (138).

In 1796, Lamarck described an *Oenothera* in his *Dictionnaire* under the name *Oe. grandiflora*, from plants grown at the Museum d'Histoire Naturelle in Paris. Seringe recognised this species as different from the *grandiflora* of Solander introduced from Alabama, and changed the name to *Oe. Lamarckiana*. The source of Lamarck's plant has until recently been obscure. We were inclined to believe that it was descended from the large-flowered plant of Barrelier (Fig. 10, right) and many reports of its hybrid origin have been circulated. But de Vries

(426) has recently cleared up the matter by the important discovery that a specimen collected by Michaux in Eastern North America about the end of the eighteenth century, and now in the Paris herbarium, is identical with *Oe. Lamarckiana*, Ser., as now known from his



FIG. 16.—*Oe. Lamarckiana*, specimen collected by Michaux in North America. From a photograph by Prof. L. Blaringhem.

cultures and from Lancashire. The upper part of this specimen, from a photograph kindly supplied by Prof. L. Blaringhem (see 34), is shown in Fig. 16. It apparently leaves no doubt that *Oe. Lamarckiana* as we now know it originally grew wild in North America. The

peculiarities of pubescence, foliage, and buds and flowers are precisely those of present cultures of that species.

Michaux was in the habit of collecting seeds along with his specimens, and it is therefore highly probable, if not certain, that Lamarck described his species from plants grown directly from seeds collected in America by Michaux. The ancestry of *Oe. Lamarckiana* is thus fully as well authenticated as that of *Oe. biennis* or any other early species of *Oenothera*, and the theory of its hybrid origin in culture appears to be finally disposed of.

It is possible that the Swedish and the Isle of Wight races of *Oe. Lamarckiana* (referred to later) were derived from an independent source, conceivably descended from Barrelier's plant, but this is mere conjecture. It is also possible that they are modified races produced by crossing with *Oe. grandiflora*, though such an hypothesis is to be considered with great reserve. This "modified" *Lamarckiana* is now common everywhere in English gardens.

Among the naturalised forms along the coast of Lancashire is *Lamarckiana* which has been shown by the studies of Bailey (6), MacDougal (247), and the writer (123, 145) to be identical with the type of the species. *Oe. biennis* races also occur here, as well as races probably belonging to what is now known as *Oe. suaveolens*, Desf., in distinction from *Oe. grandiflora*, Solander. As early as 1806 millions of these plants grew in this locality, and the plate of Sowerby (see Fig. 17), with its stout buds and long style, indicates that *Lamarckiana* was the particular plant figured. How it reached this locality so soon after being received in Paris from Michaux, is not at present known.

Davis (81, 83, 84) recently attempted to throw doubt upon the correctness of de Vries's identification of the race of his cultures with the type-specimens of *Oe. Lamarckiana*, Ser., in Paris. But the identification of de Vries has since been fully vindicated (426), both by the re-examination of these specimens and by the discovery of the specimen

of Michaux. As is well known, the cultures of de Vries are descended from seeds originally derived from Messrs. Carter and Company in London in 1860 and naturalised at Hilversum. These seeds were supposed to have been



FIG. 17.
Sowerby's English Botany, Vol. 22,
pl. 1534. 1806.
Probably = *Oe. Lamarckiana*.

introduced from Texas. But it is much more probable, as Davis suggests, that they were derived from some naturalised locality in England, presumably the Lancashire coast. Mr. F. A. Gardiner, the present director

of the firm of Messrs. Carter, finds no difficulty with this hypothesis, since mistakes may easily arise regarding the original habitat of a new introduction.

It has usually been assumed that the *Oe. grandiflora* introduced from Alabama in 1778 was the first large-flowered form to come to Europe, but we have already seen (p. 61) that a form with petals about 30 mm. in length was in cultivation as early as 1660. This is presumably the same as the *Onagra latifolia, floribus amplis*, of Tournefort (1700) and corresponds to the second species described by Ray in 1686. However, since the herbarium specimens of this plant all bear the various *biennis* names, it is probable that it was merely a *biennis* race of larger growth, and not in the *Lamarckiana-grandiflora* series at all. Barrelier's figure would bear this interpretation. We have recently (154A) seen on the Lancashire coast near Hightown a colony of *Oe. biennis*, certain members of which probably represented this race.

De Vries (427) has recently shown that *Oe. suaveolens*, Desf., is not a synonym of *Oe. grandiflora*, Solander, but a separate species. It is naturalised in many parts of Western France, and some of the races in Lancashire should perhaps be classed with it rather than with *grandiflora*.

Since typical *Oe. grandiflora* races occurred in Carolina as late as 1821, it is necessary to assume that the range of the *grandiflora* of Alabama originally extended eastward to the Atlantic coast. It seems not improbable that *Oe. Lamarckiana* was another member of this eastern complex of forms (though not extending so far east), and that it may yet be found somewhere in the region of West Virginia or Kentucky. As a wild species we should certainly expect it, on account of its rate of development and climatic reactions, to be more northerly in range than *Oe. grandiflora*.

If it is once admitted (and we think it cannot be denied) that *Oe. grandiflora* formerly extended eastward into Carolina and Virginia, then *Oe. Lamarckiana*, *Oe. grandiflora*, and *Oe. biennis* might all have occurred wild in portions of this region; and it is reasonable to suppose that these species must have intercrossed where their boundaries overlapped, just as *Oe. grandiflora* and *Oe. Tracyi* now intercross in Alabama. Does it seem unreasonable to picture in parts of West Virginia and Carolina such overlapping areas with an original population of interbreeding large-flowered forms belonging to *grandiflora*, *Lamarckiana*, and *biennis* with various intermediates, in addition to the various smaller-flowered species? The early specimen collected in Virginia by Mr. Clark (see p. 17), having petals 25 mm. in length and a long style, is significant in this connection.

A cogent argument against the direct synthesis of *Lamarckiana* by a fusion of the germ plasms of *biennis* and *grandiflora*, though it has never been used and is now unnecessary, is the fact that the mutants from *Lamarckiana* all form a constellation around their parent and, so far as known, not one of them tends to approach *biennis* or *grandiflora* in any feature.

Tower's (377) success in producing, by the free intercrossing of three species, a fusion race which bred true but threw off occasional aberrant forms, lent colour to the belief that a similar process might have gone on in the production of *Oe. Lamarckiana*. In 1905 Tower placed equal numbers of three species of potato beetles, *Leptinotarsa decemlineata*, *L. oblongata* and *L. multi-taeniata*, together in an isolated locality in Mexico. The records which were kept of them from time to time showed that by 1907 only one type—a blended hybrid type—survived, the pure species having been gradually supplanted by the new race. This blended type in subsequent pedigree cultures bred true except for sporadic mutations. The

characters of these mutants are, however, not described, and it is not stated whether they are reversions towards the parental species or variations in other directions. It is possible that irregularities in chromosome distribution may explain some of these sporadic variations in *Leptinotarsa*, as in *Oenothera*.

Any study of the history of *Oe. Lamarckiana* must take into account the fact that, like other wild species,



FIG. 18.—*Oe. Lamarckiana*, race from the Isle of Wight.

such as *Oe. grandiflora*, it contains a number of independent races or elementary species. The strain studied by de Vries is only one of several which are known to exist. We are not now speaking of the mutants, but of the various known races from different sources, which must be classed with *Oe. Lamarckiana* in the strict sense and yet which differ from each other constantly in various features

such as pubescence and foliage. The races at present known may be enumerated as follows :—

(1) A race which was obtained from a garden in the Isle of Wight. This is certainly distinct from (2) the *Lamarckiana* of de Vries's cultures, and yet it must be



FIG. 19.—Isle of Wight race of *Oe. Lamarckiana*.

classed in the same species. (cf. Figs. 2, p. 15, and 18, p. 77).

The Amsterdam *Lamarckiana* is exactly duplicated by some of the *Oenotheras* from the coast of Lancashire, records of which go back to 1805. The writer's culture of the Isle of Wight race consisted of sixteen plants, which grew

to maturity in 1912 and contained two types in equal numbers. Fig. 19 shows a full-grown plant. Type I had red midribs in the rosette-leaves and a strong development of red on the ventral surface of the petioles of the stem-leaves. The foliage was very little crinkled, but otherwise resembled that of de Vries's race. In Type II the midribs and petioles were wholly without pigment, and the leaves were more crinkled than in Type I, but less so than in de Vries's race. A careful series of measurements showed that there was no difference in the length or width of the leaves in these two types. The buds agreed with those of de Vries's race in size, but differed in being less squarish and having few long hairs—characters which bring them somewhat nearer *Oe. grandiflora*. In Type I the buds agree with those of *rubrinervis* in coloration, having red streaks; in Type II the streaks on the sepals are paler. Otherwise the two types of my culture were in precise agreement.

Types I and II, above mentioned, do not therefore correspond to the *rubrinervis* and *Lamarckiana* of de Vries, but they agree with the red-nerved and white-nerved "pure lines" found by Heribert-Nilsson in his Swedish race of *Lamarckiana*. Heribert-Nilsson found that his white-nerved "line" had shorter fruits (average length 24–25 mm.) than the red-nerved one (average length 28–38 mm.). The difference between these lines appears to be a Mendelian unit-difference, in which the "red" character behaves as a dominant. The appearance of equal numbers of the corresponding types in my culture would be explained if it was derived from an individual of Type II crossed with a heterozygous plant of Type I. A comparison between the behaviour of these two types when crossed and that of *Lamarckiana* and *rubrinervis*, serves to emphasise the difference between mutations and hybrid combinations. It should be pointed out that this is the only Mendelian character which Heribert-

Nilsson succeeded in demonstrating in *Oenothera Lamarckiana*, and is the sole basis for his sweeping Mendelian hypothesis of mutation.

(3) The race already mentioned, which Heribert-Nilsson (184) obtained from a garden in Almaröd, in Southern Sweden, in 1907 (Fig. 20), is not identical with the Isle of Wight race, though both show the same heterozygous condition with regard to one character. It differs from the *Lamarckiana* of de Vries in the following features,

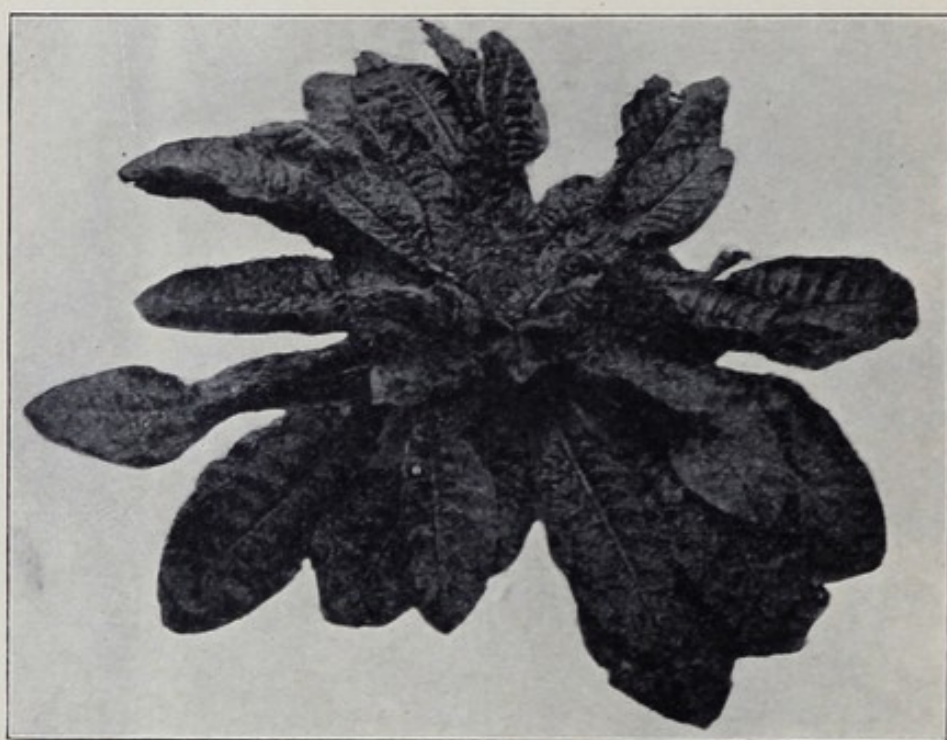


FIG. 20.—*Oe. Lamarckiana*, race from Sweden. Cf. Figs. 2 and 18. From a photograph by Heribert-Nilsson.

according to Heribert-Nilsson: (a) It is less strongly biennial. (b) The rosettes are not so large and have fewer leaves. (c) The sepals are coloured with brownish-red pigment. (d) The fruits have four deep red lines of pigment. It is greatly to be hoped that Swedish botanists will trace the history and source of this race by means of early records and specimens. Fig. 21 represents a narrower-leaved variant corresponding to *rubrinervis*.

Observations of the *Oenotheras* in English gardens

show that there are various races of *Lamarckiana* which seed themselves from year to year. Some of these have much-crinkled leaves and come near the race of de Vries's experiments; others, such as the Isle of Wight race, are less crinkled, and still others which are but little crinkled and have few long hairs on their buds, are distinctly nearer *grandiflora*.

Another race (4) of *Lamarckiana*, derived from a private garden in St. Louis, Mo. (145), differs quantitatively from the race of de Vries in many features when grown under the same conditions (see Fig. 22). In this race the

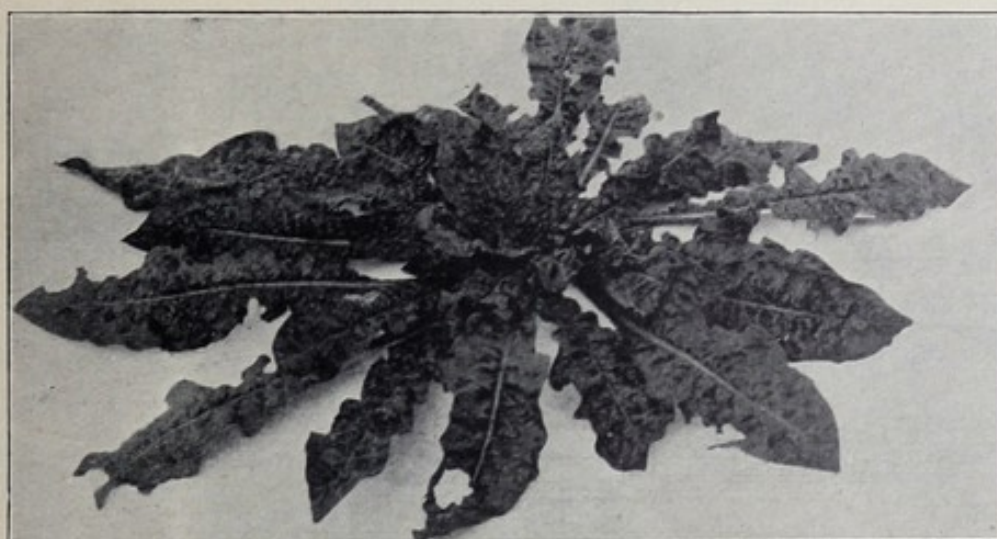


FIG. 21.—*Oe. Lamarckiana* from Sweden. Narrower-leaved variation resembling *Oe. mut. rubrinervis*. From a photograph by Heribert-Nilsson.

rosettes are much larger with decidedly broader, rather more crinkled leaves. The stem-leaves vary from ovate, tapering at both ends, and petiolate, to sessile with broad and aurate base; and the buds have fewer long hairs. The general aspect of this race is hence quite different from any of the others. This race produced a dwarf and a narrow-leaved mutant in cultures.

Of these four races, all except the last stand between the *Oe. Lamarckiana*, Ser., of de Vries's cultures and *Oe. grandiflora*, Solander, in various features. The last accentuates certain features of de Vries's race, such as

the crinkling of the leaves, but it, too, comes nearer *grandiflora* in having less hairy buds.

The *Oenotheras* in cultivation in botanical gardens include a number of races belonging to *Lamarckiana*, under such names as *Oe. biennis* and *Oe. biennis grandiflora*. These are often very variable, and have obviously undergone crossing. Sometimes they are cultivated under garden names such as *Oe. erythrosepala* and *Oe. hungarica*,



FIG. 22. — *Oe. Lamarckiana*, race from a garden in St. Louis, Mo.

and they often show mutations similar to those of the de Vries series.

It is thus clear that *Oe. Lamarckiana*, like other species, contains a number of elementary species and races differing from each other in varying degrees. It does not seem probable that these races have originated independently through hybrid synthesis. They may be merely forms produced by crossing at different times and under different conditions, of one original type endemic to North America.

Their similarity to each other indicates that they probably had a common origin, however the subsequent divergences have taken place. *Oe. grandiflora* as it now grows in the Alabama locality has also been found by Davis (79) to contain a number of separate biotypes, as well as the hybrids with *Oe. Tracyi* described by de Vries and Bartlett (422).

The differences between these *Lamarckiana* races do not correspond to those between the mutants—they are more quantitative and less qualitative in character than the latter—hence it does not seem probable that they have originated by the same process of mutation that these races themselves all exhibit. If we compare together (1) the various species of *Oenothera*, (2) the mutants of *Lamarckiana* with their parents, and (3) the various biotypes or races of *Lamarckiana*, we find the differences of different orders in the three cases. The differentiating features of the species are usually the most conspicuous, though some species are much more distinct and distant from their nearest neighbours than others. But a mutant like *gigas* or *lata*, if found wild, would be considered as worthy of specific rank as any of them, and the same is perhaps true of certain other mutants. The biotypes of *Lamarckiana*, however, certainly differ less from each other than do *Oenothera* species or, in some cases, the mutants. They seem to indicate rather the kind of diversity which is usually found in an interbreeding population of forms belonging to one Linnæan species.

SUMMARY

In summarising the results of this chapter, we find that the history of nearly all the species of *Oenothera* introduced into Europe has now been carefully traced and the pre-Linnean polynomial names identified. In

this way much light has been thrown upon the original distribution and characters of these species in North America, as well as upon their subsequent history in Europe. *Oe. biennis* was the first form to be introduced, followed by a race of *Oe. angustissima*, and soon afterwards by *Oe. parviflora* and *Oe. muricata*. There is evidence of various races and intermediate forms between some of these species. Of the early species, the *Onagra latifolia, floribus amplis* of Tournefort has until now remained obscure, but it was probably a larger-flowered race of *Oe. biennis*. This conclusion is confirmed by the recent examination of a Lancashire colony of *Oe. biennis* in which some individuals had larger flowers and broader leaves, thus corresponding fully with *Onagra latifolia, floribus amplis*.

In 1778 *Oe. grandiflora* was introduced into Kew from Alabama, and between 1785 and 1796 Michaux collected *Oe. Lamarckiana* in the Eastern States and it was introduced into the Jardin des Plantes in Paris. By 1805 it was apparently flourishing on the coast of Lancashire, and in 1860 it was brought into commerce, probably from this source, by Messrs. Carter. The cultures of de Vries are descended from these commercial seeds, but the Swedish race of *Lamarckiana*, as well as the forms now common in English gardens, differ in several features and must have come from another source or been modified by crossing with *grandiflora*.

CHAPTER IV

DESCRIPTION OF THE MUTATION PHENOMENA IN *Oe. Lamarckiana*

MUCH has been learned of the mutations of *Oe. Lamarckiana* since the publication of de Vries's *Mutations-theorie* in 1901, and it therefore seems desirable that a fresh and compact account of them should be presented here. This will be illustrated for the most part with figures from our own experiments, and will include summaries of the results of several investigators. The various races or biotypes of *Oe. Lamarckiana* have already been considered in the previous chapter. We will now describe briefly the characters of the different mutants of the de Vriesian race, to get a picture of their relationships. Under each are also summarised the breeding experiments which show the frequency of their occurrence and the nature of their inheritance calculated largely from de Vries's data.

Oe. Lamarckiana, Ser. De Vries's race. (Figs. 2, 23, 24, 25). Rosette-leaves rather broadly lanceolate, crinkled, pointed; lower stem-leaves petiolate, upper becoming gradually nearly or quite sessile, usually with a broad, aurate base. Buds quadrangular, style exceeding the stamens. Petals about 40–50¹ mm. in length and 50 mm. in breadth, obcordate and more or less deeply emarginate; bud cone 35–40 mm. in length and 9–9·5 mm. in diameter at base, hypanthium 30–36 mm. long, 3 mm. in diameter,

¹ The measurements given are chiefly from the author's own cultures.

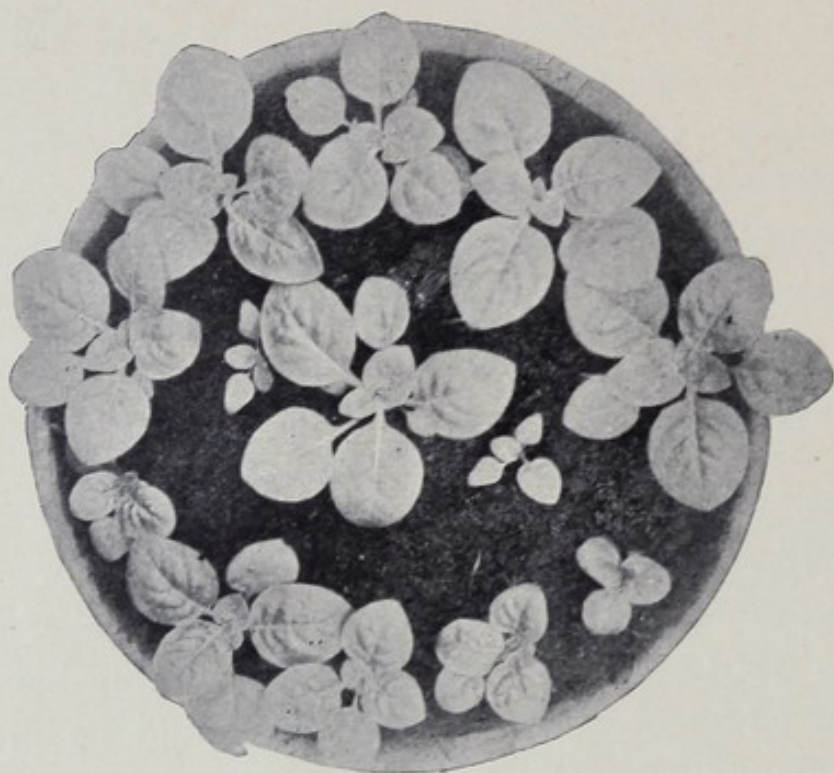


FIG. 23.—Young seedlings of *Oe. Lamarckiana*.



FIG. 24.—*Oe. Lamarckiana*, selected leaves from mature rosettes, showing range of fluctuation.

ovary 10–11 mm. long, 3.5 mm. in diameter, sepals yellowish-green or with fine reddish lines near their border. Fruits 15–34 mm. in length. There appear to be two types of branching. Some individuals form a ring of basal shoots which under some conditions become almost vertical. They flower relatively late. Others do not



FIG. 25.—*Oe. Lamarckiana*, full-grown plant.

form a ring of basal branches, and flower somewhat earlier. These differences do not seem to be inherited.

The frequency of the occurrence of mutants from *Oe. Lamarckiana* and their relative viability are matters of much interest. De Vries has given his extensive results in *The Mutation Theory*, Vol. 1, pp. 224 *et seq.*, so they need only be summarised here. From nine rosettes of

Lamarckiana which were taken from the disused potato field at Hilversum in 1886 the "Lamarckiana family I" is descended. Up till 1899 it consisted of seven generations of *Lamarckiana* offspring (grown at first as biennials) descended from these original rosettes. The total offspring were as follows:

TABLE II.
Frequency of mutations from *Lamarckiana*.

	"Family" I.	Per cent.	"Family" II.	Per cent.
<i>Lamarckiana</i>	53,000	—	10,000	—
<i>oblonga</i>	350	0.66	69	0.65
<i>lata</i>	229	0.43	168	1.58
<i>nanella</i>	158	0.3	111	1.05
<i>albida</i>	56	0.105	255	2.40
<i>rubrinervis</i>	32	0.06	1	0.009
<i>scintillans</i>	8	0.015	1	0.009
<i>gigas</i>	1	0.0019	0	
<i>elliptica</i>	0		7	0.066
<i>leptocarpa</i>	0		2	0.019

The total mutants in family I amounted to 1.55 per cent. They vary greatly in frequency, *oblonga* being the most frequent and *gigas* the most rare in its occurrence. Within narrower limits there were also variations in frequency from year to year. These are probably not wholly to be accounted for by differences in observation. Thus in three successive years (1895-7) the percentage of *lata* mutants was respectively 0.509, 1.69 and 0.27. In the same years the frequency of *oblonga* was respectively 1.23, 1.61 and 1.56 per cent. Hence the fluctuation in the frequency of *lata* is much greater than in that of *oblonga*. This is probably correlated with a difference in the manner of origin of these two mutants, as shown by cytological study (see p. 179). It is probable that the cytological processes involved in the origin of *lata* would be much more sensitive to climatic conditions than in the case of *oblonga*.

In family II, which was grown in 1895, the total number of mutants was 5.8 per cent., and it will be seen that the frequencies, particularly of *lata*, *nanella*, and *albida*, differ considerably from those of family I, being higher in every case.

De Vries has shown that the mutants, with the exception of *nanella* and perhaps *elliptica*, have a greater viability than the mother form. He sowed the seed very thickly, —75 c.c. of seed on 4 sq. metres of soil—and found that only 350 germinated out of a possible 37,500. But these included 135 mutants, or nearly 40 per cent., distributed as shown in column A. Column B shows the number

	A.	B.
<i>Oe. albida</i>	64	95
<i>Oe. oblonga</i>	9	30
<i>Oe. rubrinervis</i>	1	0
<i>Oe. nanella</i>	0	55
<i>Oe. lata</i>	61	54
	<hr/> 135	<hr/> 234

of mutants produced in the same area from 5 other packets of seeds more thinly sown. The 234 mutants which they produced was only 5 per cent. of the number which germinated. The seeds used were five years old. It is evident that though the absolute number of seeds which germinated successfully was reduced in the first case from 70 to 5 per cent. of seed, yet the percentage of mutants from the seeds which did germinate rose from 5 to 40 per cent. This result was probably due partly to the age of the seeds and partly to the greater crowding in the first sowing, both conditions being conducive to the survival of the mutants rather than the parent form. We have also found that when very few seeds of a culture germinate, owing to the age of the seeds, they almost invariably contain a large percentage of mutants. This result is important and unexpected, but there is no doubt that some of the mutants at least have an increased viability.

Seeds of *Oe. Lamarckiana* wherever obtained show similar results in the production of mutations. Thus we have grown various races of this species from several of the botanical gardens and have always found it give rise to mutants, and de Vries has had the same experience. Again, the St. Louis race of *Lamarckiana* (see p. 81) produced in 132 individuals one dwarf and one narrow-leaved mutant. The next generation, containing 63 plants, was very uniform except for the occurrence of two dwarfs and one *rubrinervis*-like plant, with shorter and narrower leaves. Commercial seed gives like records. De Vries grew 2,000 plants from seeds of *Lamarckiana* obtained from Haage and Schmidt of Erfurt, and found that they contained 1 *rubrinervis*, 1 *oblonga*, and 3 *nanella*, a total of 0.25 per cent. MacDougal (253) grew 3,500 seedlings from seeds of de Vilmorin. They contained 14 *nanella*, 3 *scintillans*, 1 *albida*, 1 *oblonga*, and several other divergent individuals.

Schouten (333) grew 522 plants from commercial seeds of Messrs. Tubergen in Haarlem, and found 502 typical *Lamarckiana*, 6 doubtful or abnormal, and 14 mutants as follows: 6 *brevistylis*, 7 *lata*, one of which was pale green and with leaves horizontal instead of hanging down against the stem, 1 *nanella*, 3 *gigas* and 1 *rubrinervis*. This is equivalent to about 2.68 per cent. of mutants.

Similarly, Hunger (193) has recently grown cultures of *Oe. Lamarckiana* at Salatiga, in Java. His seeds were obtained from two plants taken as rosettes from Hilversum, Holland, by de Vries, and self-pollinated in 1907. In the tropical climate of Java with its abundance of rain, Hunger obtained an increase in the percentage of germination from 14 per cent. (in Holland) to 32-34 per cent. In the offspring, numbering 1,950 plants, appeared 4 *nanella*, 20 *lata*, 5 *gigas*, 9 *oblonga*, 3 *lata-nanella*, 6 *oblonga-nanella*, 2 *rubrinervis*, 5 *scintillans*, 3 *elliptica*, 3 *subovata*, and in addition seven new mutants,

making about 8 per cent. of mutations in all. This included 5 *gigas* individuals, or 0.25 per cent., a greatly increased frequency for *gigas*. The considerable increase in the number of mutations is attributed to the higher percentage of germination, and particularly to the fact that the mutated seeds probably survived the high

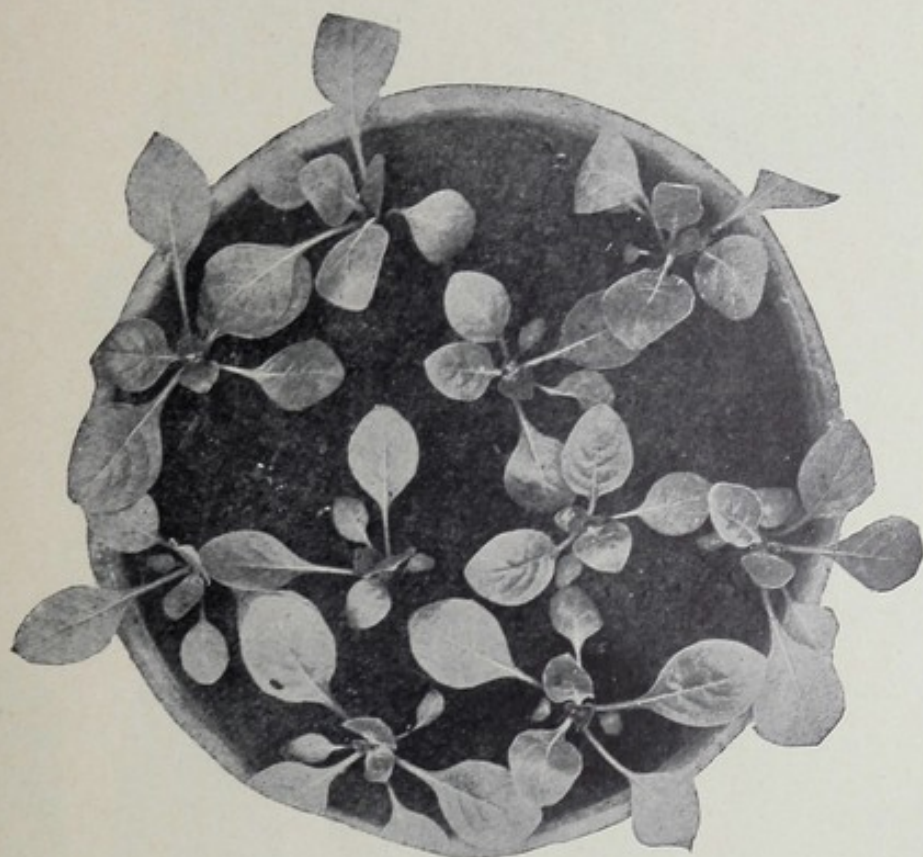


FIG. 26.—*Oe. brevistylis*, young seedlings.

temperatures experienced in transport to Java better than the normal seeds.

Oe. brevistylis, de Vries. (Figs. 26, 27, 28, 29).

Rosette-leaves similar to those of *Lamarckiana*, but rather broader and with very obtuse, rounded tips. The bracts are also broader and more rounded than in *Lamarckiana*, and the sepal tips very short; the style only reaches to the top of the corolla tube, and the stigma is misshapen. The ovaries are almost wholly sterile. This may be because pollen fails to germinate on the stigma, but the ovary may also be abnormal, for peculiarly

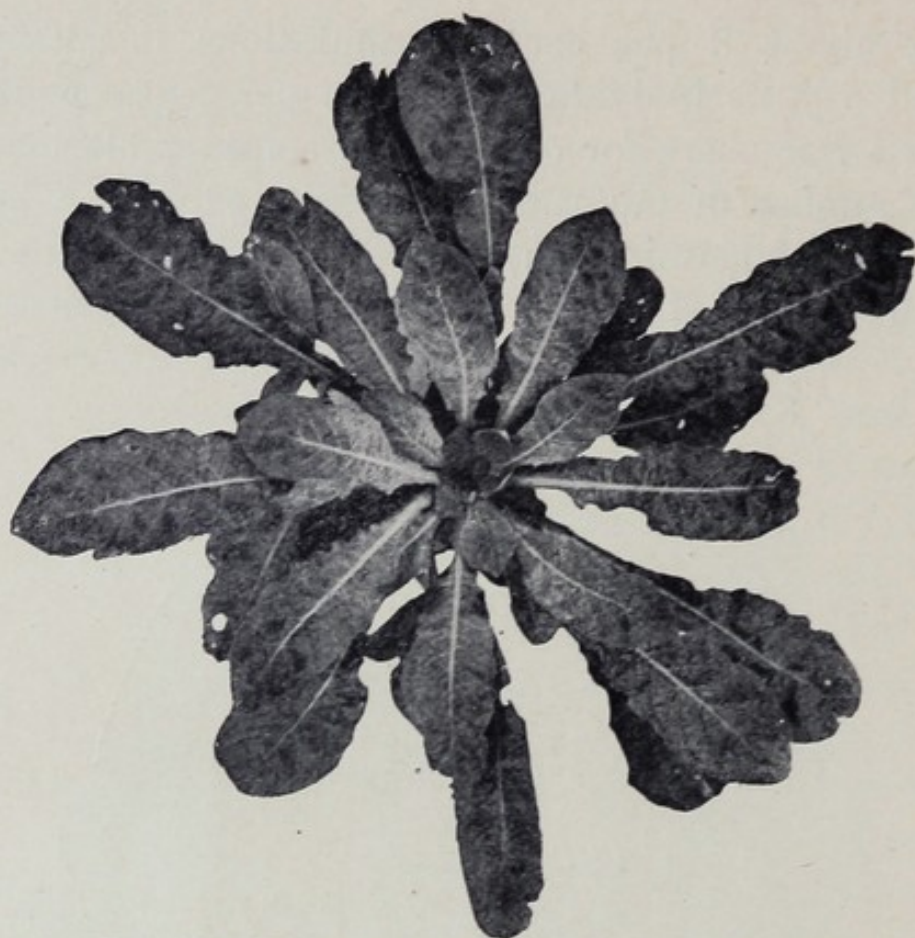


FIG. 27.—*Oe. brevistylis*, rosette (cf. Fig. 2, p. 15).



FIG. 28.—*Oe. brevistylis*, selected rosette leaves showing range of fluctuation (cf. Fig. 24, p. 86).

developed and of course functionless stomata frequently occur on the inner face of the ovary wall, where they seldom or never occur in the other forms examined.

This type was originally found growing wild with *Lamarckiana* at Hilversum by de Vries, but has since been obtained by Schouten in commercial seeds, so it has very probably originated as a mutant. It produces plenty of pollen, though very few seeds can be obtained from it, but de Vries succeeded in selfing five plants. These in 1898 yielded 175 plants, all *brevistylis*, showing that it breeds true. *Brevistylis* is usually propagated



FIG. 29. — *Oe. brevistylis*, buds showing short sepal tips.

by crossing its pollen with *Lamarckiana*. In this way it is shown to be probably a simple Mendelian recessive, though there are sometimes considerable departures from the expected ratios. *Lamarckiana* and *brevistylis* should thus give 25 per cent. *brevistylis* in F_2 , and the heterozygous *Lamarckianas* of the F_1 crossed back with *brevistylis* should give 50 per cent. of each type. A packet of seeds from de Vries, which had been crossed back in this way for several generations, gave, in 1909, 56 *Lamarckiana* and 32 *brevistylis*, besides 3 *lata* and 1 *rubrinervis* (?). Two of the *Lamarckianas* were selfed and produced *Lamarckiana*

and *brevistylis* plants in the ratios respectively of 22 : 4 and 12 : 3.

There is thus rather wide departure from the expected Mendelian ratios. Such departures appear to be characteristic of the *Oenotheras*. Schouten, from seeds of *Lamarckiana* \times *brevistylis* \times *brevistylis* obtained 39 *Lamarckiana* and 30 *brevistylis*, or 43.5 per cent. *brevistylis*. Of the 39 *Lamarckiana* plants, one differed from the rest in having cordate petals of cartilaginous texture, thus resembling a certain form of *lævifolia*. Its style was also shorter, and the stigma finger-shaped. This plant was selfed and gave in 1907 the following offspring :—

<i>brevistylis</i>	20 plants.	31.75 %
<i>Lamarckiana</i>	37	58.73 „
<i>lævifolia</i>	3	4.76
<i>lævifolia-brevistylis</i>	2	3.18
<i>lævifolia nanella</i> (dwarf <i>lævifolia</i>)	..	1	1.59

63

The *lævifolia-brevistylis* plant Schouten (333) considers to be a mutant combination, produced by the union of germ cells one of which has mutated into *lævifolia* and the other into *brevistylis*. According to this conception the plant is therefore both a double mutant and at the same time a hybrid. It resembled *lævifolia* in (a) the red colour on the stem, (b) the light green foliage, (c) in having the tops of the buds bent near the periphery of the inflorescence, (d) in form and texture of the petals. It agreed more nearly with *brevistylis* in (a) the bracts, (b) the rounded tops of the buds, (c) the form of the ovary and fruit, (d) the short style with leaf-like stigma lobes. Schouten argues that this plant cannot be a "hybrid" because short style is recessive to long; but extended experience shows how variable is the phenomenon of dominance in *Oenothera*.¹ The total of 6 mutants in

¹ Thus in 1912 we made the cross *rubricalyx* \times *brevistylis*, and although from 229 seeds only 2 plants developed in the following year, these

63, or 9.5 per cent., also points to a probable admixture of *lævifolia* pollen, for the percentage of mutants is ordinarily not above 5 per cent.

Of the *brevistylis* plants referred to above in *Oe. Lamarckiana* × *brevistylis*, two showed chloranthly, one of these being also peculiar in having a very short style, so that the stigma only reached half-way to the top of the flower tube. The latter was filled with nectar in which the stigma was immersed. The flower tube was slit open, and several flowers thus self-pollinated yielded nine plants, the latter all normal *brevistylis*. Hence this peculiar variation was uninherited.

Open-pollinated capsules from the other *brevistylis* plants above-mentioned yielded the following:—

<i>brevistylis</i>	123	plants.	50	%
<i>Lamarckiana</i>	47	„	19.11	„
<i>rubrinervis</i>	74	„	30.08	„
<i>lævifolia</i>	1	„	0.41	„
<i>rubrinervis-brevistylis</i>	1	„	0.41	„
						246			

Lamarckiana, *rubrinervis* and *lævifolia* grew near by, and doubtless furnished much of the pollen. The *rubrinervis-brevistylis* plant had (a) the form of leaves and stem, and the brittleness in all organs characteristic of *rubrinervis*, (b) the bracts, buds, style, stigma, and ovary of

grew to maturity and were intermediate in nearly every respect. One formed a small plant, with small, pointed, nearly smooth leaves having white midribs. This plant bloomed early (July 1). The buds were intermediate between *rubricalyx* and *brevistylis*, i.e., with the red colour pattern 7 on the sepals and red blotches on the hypanthium. The hypanthium on wilting turned uniformly dark red. The sepal tips were also shorter than in *rubricalyx*, showing distinctly the effect of *brevistylis*, and the length of style was again intermediate, the anthers surrounding the (normal) stigma and self-pollinating the flower as in *Oe. biennis*. The other plant differed in developing much more slowly (in bloom Sept. 1), having leaves crinkled, more like *rubricalyx* though with broader points (*brevistylis*), and somewhat redder buds, otherwise agreeing with the first plant. Thus one was intermediate, though aberrant in certain features, while the other was in certain particulars nearer *rubricalyx*.

brevistylis. Hence it was essentially a short-styled *rubrinervis*. Schouten considers the plant a combination-mutant and not a hybrid, *i.e.*, that it came from a germ cell of *brevistylis* which had mutated into *rubrinervis*, crossed with one which had remained normal. But it is not clear that a combination-mutant derived from germ cells which had mutated respectively into *rubrinervis* and *brevistylis* would be a different product from an



FIG. 30.—*Oe. laevifolia*, rosette.

ordinary cross between these two forms. A double mutant must be regarded also as a hybrid, even though it was derived from the self-pollination of an individual plant. The interpretation of these combination forms or double mutants was formerly obscure, but is now, we think, clear and will be referred to again later.

Oe. laevifolia de Vries (Figs. 30, 31).

Leaves more or less free from crinkling, rosette-leaves more narrowly lanceolate than in *Lamarckiana*, stem-

leaves standing out rather stiffly from the stem, narrower and more or less furrow-shaped. Petals usually as in *Lamarckiana* emarginate or sometimes truncate, but in weak plants they are sometimes elliptical.



FIG. 31.—*Oe. laevifolia*, mature plant.
(cf. Fig. 25, p. 87.)

The exact status and origin of this form remain somewhat obscure. It was also discovered by de Vries at Hilversum, but never appeared as a mutant in his cultures, though it has since occurred in the experiments of Schouten, and forms more or less resembling it have also appeared

in our own cultures. We have found this type to be variable in such features as width of leaf and amount of crinkling. It is doubtful whether all the forms mentioned below in the work of Schouten as belonging to *lævifolia* should be so relegated. From his description it would seem that the mean type of his *lævifolia* differed somewhat from that of de Vries.

Schouten (333) states that he obtained *lævifolia* as a mutant (1) from *gigas*, (2) from *Lamarckiana* × *Lamarckiana brevistylis*. It is probable, however, that the first was one of the narrow-leaved forms of *gigas*. In 1906 he grew 260 plants of *lævifolia*, which were all like the parent except three. Of these, two were *lævifolia nanella*, i.e., dwarfs having the same symptoms of sickness as *nanella*, but like *lævifolia* in the form and colour of their leaves and petals. The third was *lævifolia-salicifolia*. It had smaller leaves than *lævifolia*, and smaller flowers which were nearer *biennis*. The petals were heart-shaped, anthers conspicuously orange-coloured, pollen grains few. This plant gave a few seeds when selfed, but was entirely sterile when crossed with *lævifolia* pollen. The offspring proved to be

<i>lævifolia</i>	22
<i>scintillans</i>	6
<i>lævifolia-salicifolia</i> ..	1
unknown	1
	<hr/>
	30

Hence *lævifolia-salicifolia* is a hybrid between *lævifolia* and *scintillans* which it resembles.

Oe. mut. rubrinervis, de Vries. (Cf. figs. 32, 33).

Foliage greyish-green in colour, leaves somewhat narrower and less crinkled than in *Lamarckiana*; usually with red midribs, particularly on the rosette leaves; sepals with red stripes of varying width (see the series of buds 1-7, in 137, coloured plate), hypanthium green; stems brittle, owing to less development of bast-fibres.

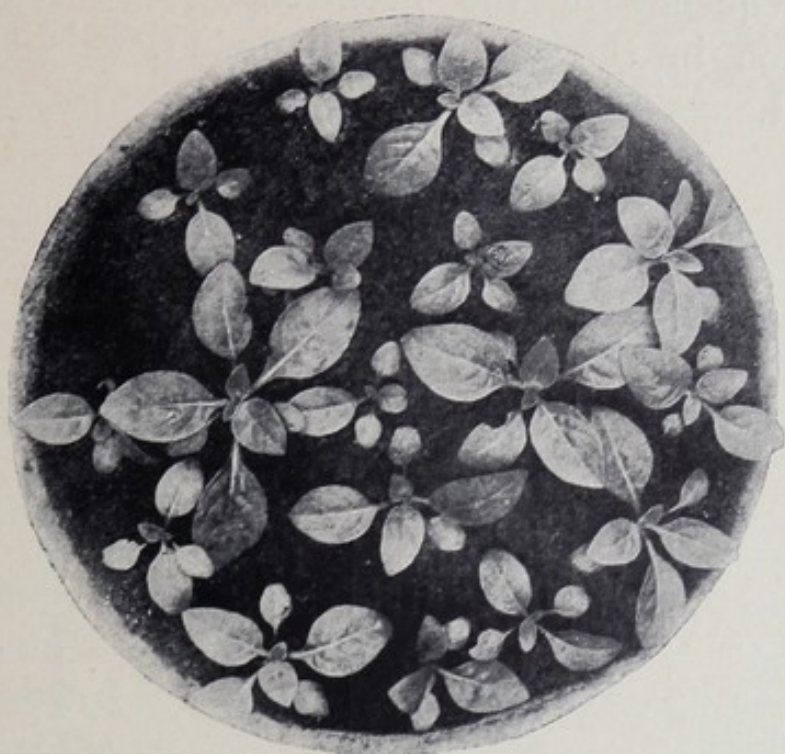


FIG. 32.—*Oe. mut. rubricalyx*, seedlings.
(cf. Figs. 23 and 26.)

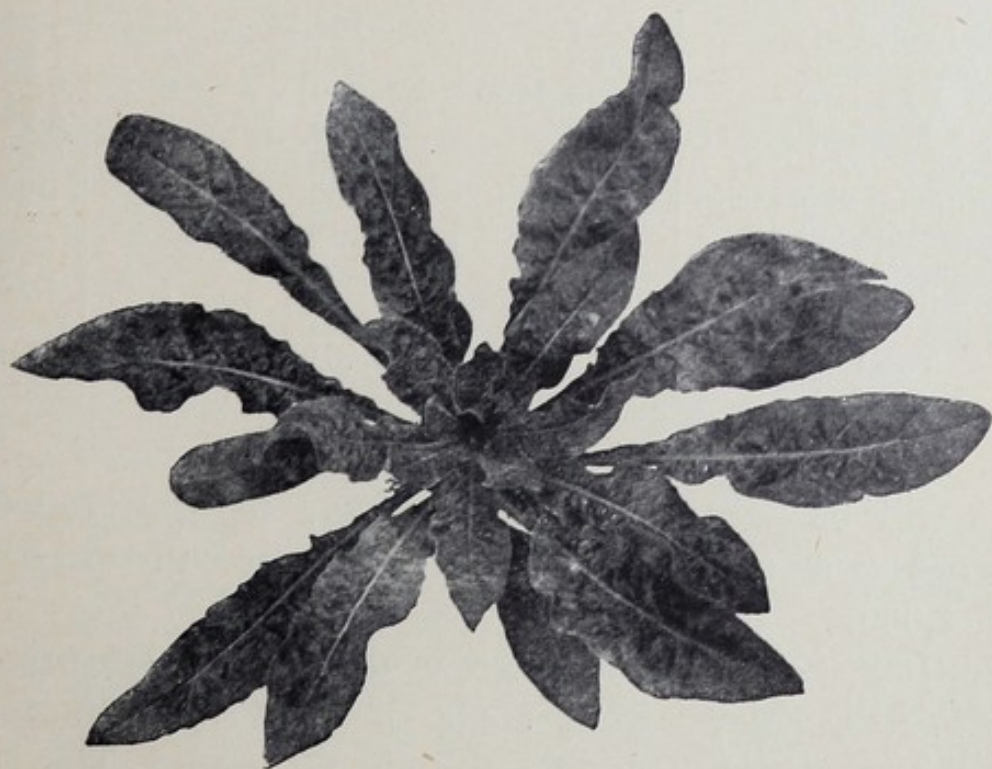


FIG. 33.—*Oe. mut. rubricalyx*, rosette.

The frequency of the occurrence of *rubrinervis* as a mutation in the cultures of de Vries is shown in Table III.

TABLE III.

Mutations of *rubrinervis* from *Lamarckiana*.

Pedigree.	Year.	Total number of plants.	Number of <i>rubrinervis</i> .	Per cent.
<i>Lamarckiana</i> family	{ 1890, 1895, 1896, 1897	33,800	32	0.094
Branch of same ..	1895-6	10,000	9	0.09
<i>Oe. laevifolia</i>	1889 & 1894	—	(4)	—
<i>Oe. lata</i>	1900	2,000	3	0.15
<i>Oe. oblonga</i>	1897	45	1	—
<i>Lamarckiana</i> × <i>nanella</i>	1897	1,051	2	0.19
<i>lata</i> × <i>nanella</i>	1895, 1900	222	2	0.90
<i>Lamarckiana</i> from the field	1889	—	(1)	—
Total	47,118	49	0.104
<i>Lamarckiana</i> , bien-nial culture	1897	164	2	1.22
<i>Oe. lata</i> mutant ..	1896	326	4	1.23
<i>Lata</i> × <i>Lamarckiana</i>	1898, 1900	750	2	0.27
<i>lata</i> × <i>brevistylis</i> ..	1896	266	1	0.38
<i>nanella</i> × <i>brevistylis</i> .	1895	270	1	0.37
<i>scintillans</i> × <i>nanella</i>	1898	95	1	1.05
<i>Lamarckiana</i> (from <i>Lamarckiana</i> × <i>scintillans</i>)	1900	80	1	1.25
Total	1,951	12	0.615

It will be seen that the frequency of appearance of *rubrinervis* as a mutation is, in the larger cultures, about 1 in 1,000.

In 1906 Schouten (333) grew about 1,200 offspring of *rubrinervis*, chiefly from seeds of de Vries, but partly from commercial seeds of a firm in Haarlem. The latter yielded most of the aberrant forms. The results were as follows (Table IV):

TABLE IV.
Offspring of *Oe. rubrinervis*.

Offspring.	Number of plants.	Per cent.
<i>rubrinervis</i>	1,097	95.89
<i>rubrinervis</i> with "gigas-fruits" ..	6	0.52
<i>Oe. blanda</i>	36	3.14
<i>laevifolia</i>	4	0.35
<i>rubrinervis-lata</i> ..	1	0.083
	1,144	

Oe. blanda is a form which, according to Schouten, differs from *rubrinervis* in being larger and taller, with longer internodes and larger fruits. It varied in numbers, in different families, from 0.37 per cent. to 12.60 per cent. The *rubrinervis-lata* resembled *lata* in the rounded tips of the leaves, the rounded buds and the male sterility, while it was like *rubrinervis* in the brittleness of all parts, the zigzag stem and the form of the leaves. No doubt this plant was a 15-chromosome mutant from *rubrinervis*.

This plant was selfed and produced about 350 plants, and about 50 more were grown from open-pollinated seeds, as follows (Table V):

TABLE V.
Offspring of *Oe. rubrinervis lata*.

	Selfed.	Open- pollinated.
<i>Lamarckiana</i>	0	1
<i>rubrinervis</i>	310	40
<i>Lamarckiana lata</i>	0	5
<i>rubrinervis lata</i>	32	2
<i>candelabrifomis</i>	1	0
<i>rubrinervis-scintillans</i> ? ..	1	1
unknown	4	0
	348	49

Oe. candelabrifomis, Schouten, is a presumed mutant the rosette-leaves of which have the form of a furrow,

longer and narrower than in *rubrinervis*, darker coloured and shining. The internodes are long and thin; the flowers nearly as small as in *biennis*, and the anthers are so little above the stigma that self-pollination takes place. The petals are funnel-shaped, less pleated than in typical *rubrinervis*, the inflorescence long and loose with small, dark yellow flowers.

This is one of the few cases in which large-flowered forms have given rise to individuals with small flowers, and it is possible that the plant may perhaps have come from a chance cross with *biennis*. One or two similar cases have been obtained in cultures from Birkenhead, but they are certainly rare occurrences.

De Vries (425) has recently recognised under the name *subrobusta* a form of *rubrinervis* which differs in being less brittle. It produces about 20 per cent. of the brittle *rubrinervis* in its offspring. In crosses with other mutants *rubrinervis* produces an F_1 containing from 27 per cent. to 80 per cent. *subrobusta*.

Oe. mut. rubricalyx, Gates (Figs. 32—36).

This differs from *rubrinervis* only in pigmentation, its hypanthia and sepals are red throughout, including the median ridge of the sepals, which is always green in *rubrinervis*. The ventral surface of the petiole of the rosette-leaves and, to a less extent of the bracts, is also red. The increase in anthocyanin production extends to nearly every part of the plant, even the nucellus cells of the ovule containing sufficient in their cell sap to make them pink when examined under the microscope. The stems are also suffused with red, especially towards the top. Morphologically *rubricalyx* is identical with *rubrinervis*, from which it originated suddenly by a heterozygous mutation in my cultures of 1907. It has occurred but once in all cultures, so far as known, and no wild species in this section of the genus has similar pigmentation. It is almost the only marked colour variation which has

appeared during the three centuries in which these *Oenotheras* have been in cultivation.

Oe. mut. rubricalyx originated in a pure culture of *Oe. mut. rubrinervis* at the University of Chicago in 1907. Four *rubrinervis* individuals of the previous generation selfed gave 112 offspring, all of which were like the parent except the *rubricalyx* mutant and two somewhat doubtful rosettes. The origin of this mutant is therefore accurately



FIG. 34. *Oe. mut. rubricalyx*, rosette.

known. Fortunately the writer happened to be making a special study of the variability in pigmentation of the buds in the very culture of *rubrinervis* in which the *novum* appeared. The range of variation in the *rubrinervis* population numbering in all more than 1,000 plants was found to be absolutely continuous, while a marked gap separated the extreme of pigmentation in *rubrinervis* from that of the *rubricalyx* individual. The offspring of the *rubricalyx* plant, moreover, showed no tendency to regress towards

rubrinervis. Instead they split into two sharply distinct classes belonging respectively to *rubricalyx* and *rubrinervis*. The number of survivors in the first generation of offspring was too small to determine a ratio (11 *rubricalyx*,¹ 1 *rubrinervis*, but three of these *rubricalyx* plants selfed gave in the



FIG. 35.—*Oe. mut. rubricalyx*,
full-grown plant.

second generation the ratios respectively of 10:5, 14:6 and 33 : 11. These four ratios make a total of 68 *rubricalyx*

¹ There is now no doubt that two rosettes which were formerly classed as "doubtful," because they showed only a small amount of ventral red, were really *rubricalyx*, as it has been found that when there is even a trace of ventral red on the rosettes the plants invariably develop the characteristic red buds.

to 23 *rubrinervis*, which is a very close approximation to a 3:1 ratio.¹

It is thus clear that the original *rubricalyx* mutant was heterozygous, having originated through the union of a normal germ cell with a mutated germ cell possessing the new dominant character. The difference between *rubricalyx* and *rubrinervis* is thus a simple monohybrid difference according to Mendelian methods of interpretation. It is not necessary to suppose that *rubricalyx* has acquired

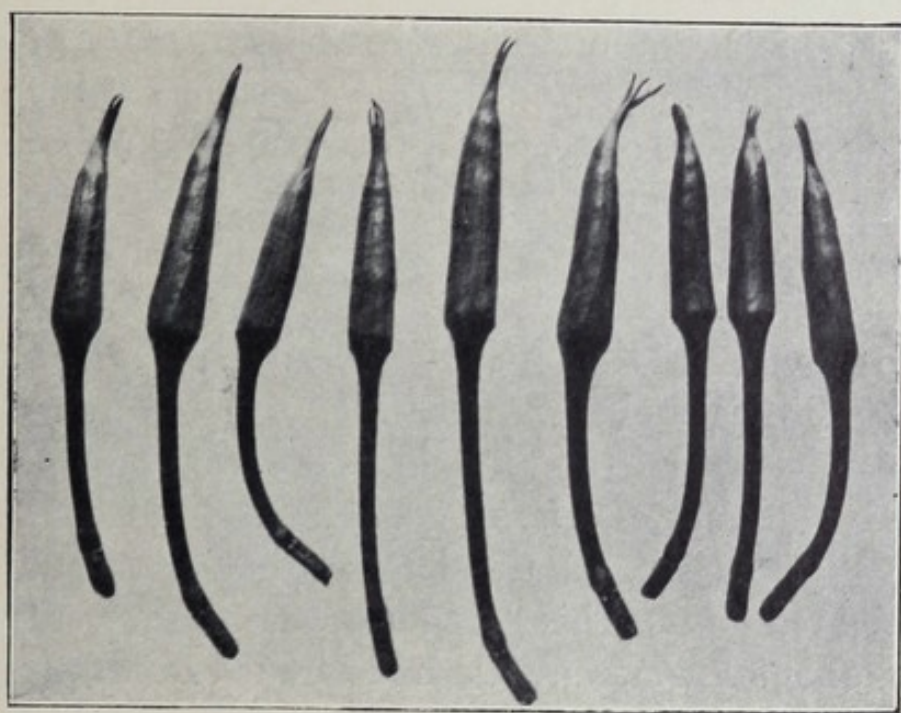


FIG. 36.—*Oe. mut. rubricalyx*, buds.

an additional unit-character, except as a matter of convenience in describing the crossing experiments. In reality, all it is possible to say is that a particular germ cell underwent a germinal change of such a nature that in development the resulting organism produced an enormously increased quantity of anthocyanin.

That *rubricalyx* originated from such a germinal change in one cell, and not from gradual accumulation, through

¹ It is necessary to emphasise the fact that by no possibility can *any* of these ratios (except perhaps 11:1 which is too small to be considered by itself) be construed as 15:1.

crossing of several individuals having each a "factor" for slightly increased pigment-production (as certain writers, notwithstanding the facts to the contrary, have attempted to suppose), is a fact of considerable significance. Its truth is shown, not only by the 3 : 1 ratios above mentioned, but by the following facts. Certain heterozygous plants from the culture from which the ratio 33 : 11 was obtained, were used to cross reciprocally with *Oe. grandiflora*. In the F_1 of the cross *rubricalyx* \times *grandiflora* the ratio of plants with red buds to those with green buds was 30 : 28, or almost exactly the anticipated equality on the supposition that the heterozygous parent was producing two types of germ cells in equal numbers, and was therefore a simple Mendelian hybrid for *one* unit-character difference. In the reciprocal cross, *grandiflora* \times *rubricalyx*, in an F_1 of 147 plants only 58 bloomed, but these were in the ratio 34 red-budded : 24 green-budded. Provisional determination of the whole family from examination of the rosettes gave 42 red, 71 without red, and 37 doubtful, showing only traces of red. It is certain that nearly all the latter at least would have developed red buds. This being the case, there were in the culture about 79 potentially red-budded and 71 green-budded. This is again a near approach to equality, and proves further that the *rubricalyx* parent was a simple monohybrid. Indeed, on the Mendelian's own method of interpretation, this conclusion is irrefutable.

The peculiarities of the later generations from these crosses will be considered in Chapter VII. In the third generation of selfed plants from the original mutant we obtained a pure race of 200 plants, the mother plant having evidently been homozygous for red. It happened that in previous generations we had bred only from heterozygous plants, which are indistinguishable from homozygotes except in the deeper red of the latter, and even this

can only be determined by close inspection in certain cases. The 200 plants grown in this family in 1912 were remarkably uniform in every feature, with the exception of two plants, one of which was somewhat aberrant in foliage and the other was small, having furrow-shaped leaves with white midribs. The seeds from this pure race were

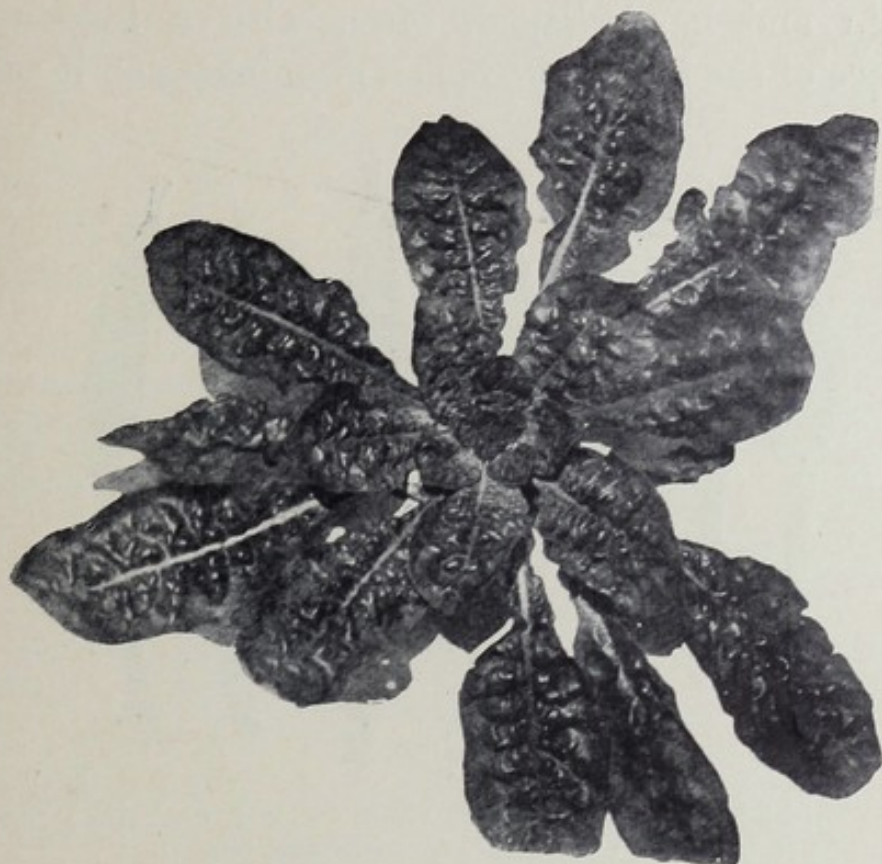


FIG. 37.—*Oe. mut. lata*, rosette (cf. Fig. 2, p. 15).

acquired by Messrs. Sutton and Sons, who are selling it under the name "Afterglow."

Oe. mut. lata, de Vries. (Figs. 37, 38.)

Rosette leaves shorter and more crinkled than in *Oe. Lamarckiana*, the pits being large and deep; the tips of the rosette leaves are characteristically very broad and rounded, the lower stem-leaves being also blunt-pointed, the upper ones obtuse. These broad, obtuse or rounded points are much more exaggerated than in *brevistylis*,

and the foliage is also lighter green. The stems of *lata* are short and usually more or less decumbent, with irregular branches, the top of a stem often hanging over to one side. The buds are peculiarly stout and barrel-shaped, usually with a protrusion or hernia on one side due to the crumpling of the petals within. The sepals rarely if ever show any coloration. The stigma is peculiarly ill-shapen and hand-shaped, often with a tendency to confluence of the lobes, but pollen germinates on it readily.

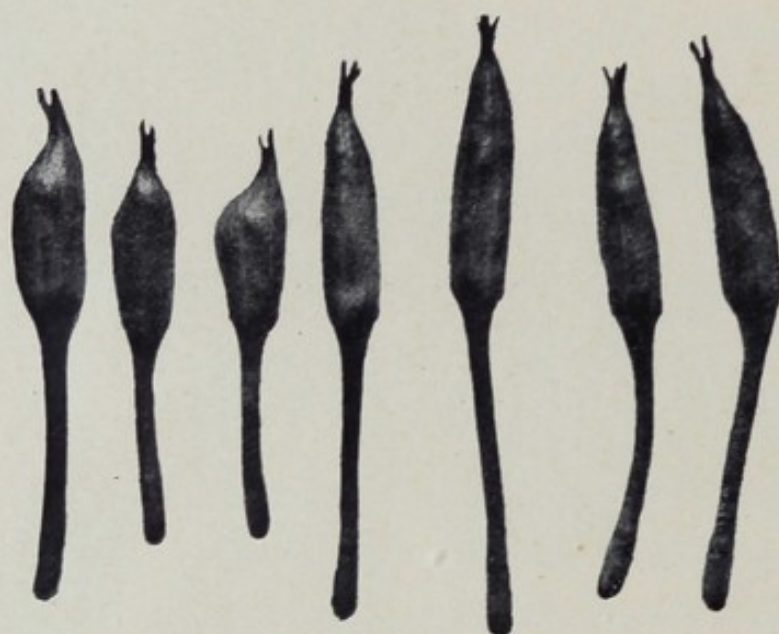


FIG. 38.—Three buds on the left, *Oe. lata*, de Vries ; four buds on the right, *Oe. semilata*, Gates.

The capsules are short and thick, containing relatively few seeds, and the pollen is wholly or almost wholly sterile. These remarkable peculiarities are associated with the presence of 15 instead of 14 chromosomes (see Chapter VI).

Oe. mut. lata has occurred a number of times in my cultures, and when derived from the *Lamarckiana* of de Vries's cultures it appears to be remarkably constant in appearance. Table VI summarises its occurrence in the experiments of de Vries. It was the first mutant to be recognised—in 1887.

TABLE VI.
Mutations of *lata* from *Lamarckiana*.

	Year.	Total.	<i>lata</i> .	% <i>lata</i> .
I.—From <i>Oe. Lamarckiana</i> .				
<i>Lamarck.</i> family	1888-90	25,000	8	0.03
„ „	1895	14,000	73	0.5
„ „	1896	8,000	142	1.8
„ „	1897-99	35,000	6	0.2
A lateral branch	1895	10,000	168	1.7
An annual culture	1897	4,132	11	0.3
A biennial culture	1897	164	8	5.0
II.—From crosses.				
<i>Lamarck.</i> × <i>nanella</i>	1897-99	8,283	22	0.3
<i>Lamarck.</i> × <i>gigas</i>	1899	100	2	2.0
<i>Lamarck.</i> × <i>biennis</i>	1900	80	1	1.0
<i>Lamarck.</i> (from crosses) ..	1896	4,600	7	0.2
III.—From other families.				
<i>Lamarck.</i> from <i>lævifolia</i> ..	1889	400	3	0.8
<i>lævifolia</i>	1894	1,500	2	0.1
<i>rubrinervis</i>	1894	96	2	2.0
<i>scintillans</i>	1896-9	7,872	38	0.5
Total		119,227	493	0.413

In our own cultures it has appeared as follows :—

TABLE VII.
Lata mutants.

	Total.	<i>lata</i> .
From <i>Oe. Lamarckiana</i>	117	2
„ <i>Oe. Lamarckiana</i> × <i>brevistylis</i>	92	3
„ <i>Oe. rubrinervis</i>	96	1
„ <i>Oe. rubrinervis</i> × <i>nanella</i> ..	42	1
„ <i>Oe. rubrinervis</i> × <i>Lamarckiana</i> (from <i>lata</i> × <i>Lamarckiana</i>)	64	1
	411	8 = 1.95% ¹

We have also obtained *lata*, or *semilata* rosettes from *rubricalyx* in the following circumstances. Four pots were very thickly sown in January with seeds of pure

¹ This cannot be directly compared with Table VI, since certain families not containing *lata* were not included here.

homozygous *rubricalyx*, and having germinated in large numbers were left to struggle and survive if they could. It was July before the survivors were finally planted out, and they did not develop beyond the rosette stage. From the two less thickly sown pots a total of 12 *rubricalyx* rosettes developed, while the two more thickly sown produced 6 *rubricalyx*, and 3 *lata* or *semilata* having also red pigment on the ventral surface of the midribs as in *rubricalyx*. The large proportion (14·3 per cent. of *semilata* mutants in this small number (21) of survivors) indicates that in close competition the mutant has the better chance of surviving. This result is somewhat surprising, for the condition of *semilata* with an extra unpaired chromosome might easily be looked upon as an abnormality leading to weakness in the organism.

Oe. lata is easily identified, even as a young rosette or seedling. The proportion of *latas* varies in different families from 0·1 per cent. to 1·8 per cent., with an average frequency of about 0·5 per cent. In families of 8,000, 10,000, and 14,000 plants respectively, the percentages were 1·8 per cent., 1·7 per cent., and 0·5 per cent., while in one small culture of 164 plants the number of *latas* ran up to 5 per cent. This fluctuation we now know depends upon the frequency with which both members of a pair of chromosomes are carried to the same germ cell in meiosis. Hence the peculiarities of *lata* do not arise through a new distribution of Mendelian unit-characters, but they depend upon the occurrence of an irregular meiotic division.

When *lata* is crossed back with *Lamarckiana*, the offspring consist of the two forms in varying numbers, the percentage of *lata* varying from 4 per cent. to 45 per cent. with an average of 22 per cent. Since the extra chromosome in *lata* usually passes undivided into one germ cell in meiosis, there should result equal numbers of germ cells having seven and eight chromosomes. The fact that

the *lata* offspring in *lata* \times *Lamarckiana* number less than 50 per cent. shows that megaspores with seven chromosomes usually have a better chance to survive than those with eight chromosomes. Occasionally, however, the number surviving is even more than 50 per cent. Thus de Vries (1913) records that *lata* \times *biennis* yielded 53 per cent. *lata* in 258 plants, while *lata* \times *biennis cruciata* gave 60 per cent.

Other mutants amounting to 2-5 per cent. are also produced in the offspring of *lata*. In the fourth generation of *lata* pollinated by *Lamarckiana* derived from the same mother plant, certain of the *lata* flowers were found by de Vries to have sufficient pollen to make possible their self-pollination. These yielded 442 offspring, of which 33 per cent. were *lata* and 4 per cent. mutants, and the next generation, obtained in the same way, produced 32 per cent. *lata*. Similarly, MacDougal, by selfing certain *lata*-like plants, derived from seeds of *Oe. Lamarckiana* from Birkenhead, obtained a progeny containing 80 *Lamarckiana*, 10 *lata*, 1 *albida*, and 3 *oblonga*. The mutant *lata* is therefore inconstant, reverting to *Lamarckiana* and producing a high percentage of other mutations as well. This is connected with the cytological behaviour, which will be described later.

The further hereditary peculiarities of *lata* will be discussed in a later chapter. It need only be pointed out here that the fluctuations in the percentage of *lata* in the offspring are explained by the behaviour of the extra chromosome, and that the percentage of 8-chromosome germ cells which mature is probably influenced by the environmental conditions during the meiotic divisions in the megaspore mother cells, or by the physiological condition of the mother plant at this time.

Oe. mut. semilata, Gates.¹ (Figs. 38, 39, 40, 41.)

¹ Since this was written, Prof. de Vries has kindly informed me that his *semilata* was different from mine, and since it bred true it probably

This mutant stands midway between *lata* and *Lamarckiana*. Its leaves are more pointed and rather less crinkled than those of *lata*, the stem is erect and taller than *lata*, though shorter than *Lamarckiana*. The buds are less stout and more squarish than *lata*, and it produces a considerable quantity of pollen.

In cultures of de Vries's race of *Lamarckiana*, *semilata*



FIG. 39.—*Oe. mut. semilata* rosette, from Lancashire race of *Oe. Lamarckiana*.

has only appeared in families of *lata* pollinated by *Lamarckiana*. Like *lata* it has 15 chromosomes, but the nature of the minor differences between *lata* and *semilata* is at present obscure. This will be discussed in the next had 16 chromosomes. It may therefore have resembled more closely the form here described as *Oe. latescens* (p. 117). However, the *semilata* of de Vries was bred from his cultures but once, and has since been lost, so we have considered it desirable to retain the name *semilata* in the sense in which I have used it, especially as this name exactly expresses the relationship of this form to *lata*. It will, therefore, be understood that the *semilata* of de Vries's *Mutationstheorie* is another mutant which probably had 16 chromosomes.

chapter. The male sterility of *lata*, and the small number of seeds it produces, was at first supposed to be due to the presence of the odd chromosome; but in *semilata*, where, contrary to expectation, an extra chromosome was also found, the sterility has been largely, though not wholly overcome.

De Vries has only obtained *semilata* three times, and always from *lata* \times *Lamarckiana*. When derived from other sources, *lata* and *semilata* form a variable series

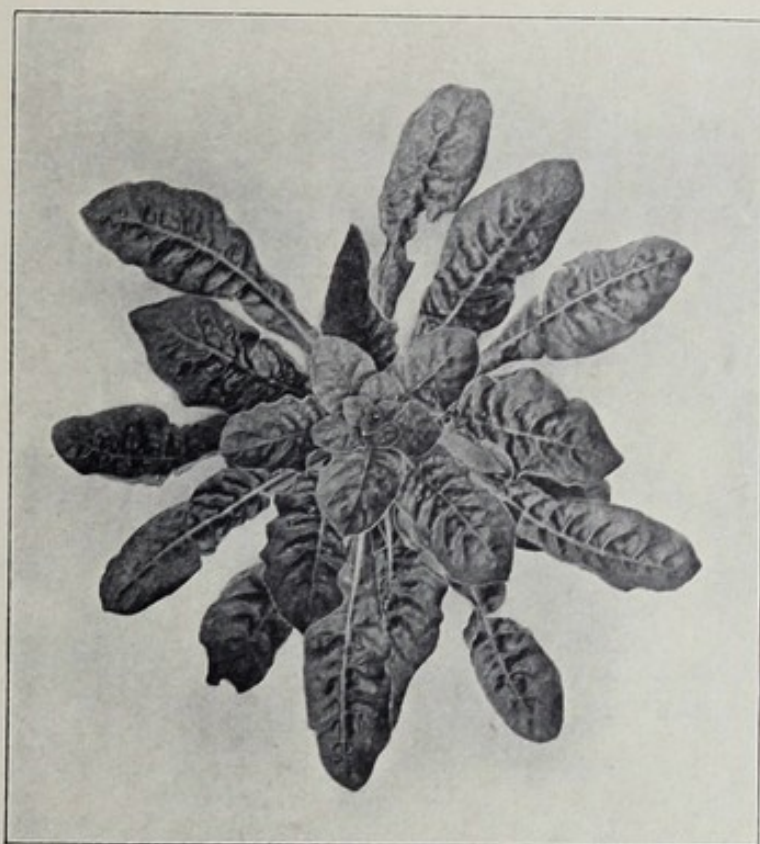


FIG. 40.—*Oe. mut. semilata* from Swedish race.

grading into each other so that it is impossible to draw a sharp line between them.

"*Semilata*" is classed by de Vries as a constant species on the basis of the following experiment. In 1897 the self-fertilised seeds of a *semilata* plant yielded 358 individuals, of which 3 were *nanella*, 3 *lata*, and the remainder were *semilata*. (See footnote, p. 111.)

In a culture of 75 plants from *lata* \times *Lamarckiana* were

obtained 63 *Lamarckiana*, 4 *lata*, 2 *lata nanella* (?), 2 *semilata*, 1 *laevifolia*, and 3 aberrant rosettes, 2 of which were probably *semilata*. One of these four *semilatas* selfed produced 40 very variable rosettes, about 11 of which were *semilata*, the remainder forming a continuous series running to



FIG. 41.—*Oe. mut. semilata grandiflora*, side branches from a mature plant.

Lamarckiana. Three which afterwards bloomed were *semilata*. One of these self-pollinated gave three offspring, two of which were *lata* found by Miss N. Thomas to have 15 chromosomes and the third a slightly modified *Lamarckiana* having 14 chromosomes. The modifications consisted only in having nearly smooth leaves, some of

which were cordate. The source of such variations is probably in the chromatin distribution during the meiotic divisions. Another *semilata* plant of the previous generation produced three plants, all of which were *Lamarckiana*. It is, therefore, evident that *semilata* is inconstant in the same way as is *lata*, and this inconstancy is no doubt due to the presence and behaviour of the extra chromosome.

MacDougal (253) first showed that a *lata*-like plant occurring in cultures from near Liverpool was capable of producing pollen. In 1909 my culture of 107 plants from a packet of seeds from Birkenhead contained eight *latas* of this pollen-producing type having more squarish buds than typical *lata*, in addition to one of the typical plants. These should therefore be classed as *semilata* except that the rosette leaves, which are variable in shape, are larger than in either type from the *Lamarckiana* of de Vries.

Cultures of *lata* and *semilata* forms, from seeds sent by Heribert-Nilsson from his Swedish race of *Lamarckiana*, show still further variability. His "komb. 6 \times *Lamarckiana*" yielded me 120 plants, 110 of which corresponded to de Vries's *rubrinervis*, though differing from it in various particulars. Of the remaining 10 plants, one was a *semilata* (see Fig. 40) having pinkish midribs, another a *lata* also with pinkish midribs, the colour of course derived from the *rubrinervis*-like parent, for ordinary *lata* never shows red pigment in any part. Another culture, containing 79 plants from open-pollinated seeds of a *lata*-like plant of Heribert-Nilsson, consisted chiefly of a race resembling *Oe. grandiflora*. But in addition there were 1 *nanella*, 1 *semilata*, 2 *lata* to *semilata*, 5 *lata*, and 1 *lata*-like plant having slender, weak stems, broad-pointed, crinkled, nearly cordate leaves, and rather small flowers. The chromosomes of all the plants in this *lata-semilata* series were counted by Gates and Thomas and we found (153) 15 in every case.

In addition to these cases, two other clear instances

have been obtained which are of still greater theoretical interest, for they show the contrast between mutations and the ordinary phenomena of heredity. The first of these is derived from 2 *lata* and 2 *semilata* mutations which occurred in the F_2 of *Oe. grandiflora* \times *rubricalyx*, and its reciprocal. These mutations, among others, occurred in a total offspring of 2,794 plants from these crosses, in 1912. One F_2 family from *grandiflora* \times *rubricalyx*, numbering 82 plants, contained a mutant *semilata grandiflora*. All the other plants in the culture possessed foliage and buds showing various degrees of intermediacy between the grandparental species. But the mutant individual differed from all the others in having its *grandiflora*-like foliage modified to show the peculiarities of *semilata* (Fig. 41). Another mutant of the same kind appeared in an F_2 family of *rubricalyx* \times *grandiflora* numbering 80 plants.

In a third F_2 family of the same cross, numbering 60 plants, occurred two *lata rubricalyx* mutants having the foliage and habit of *lata* combined with red pigmentation inherited from the *rubricalyx* grandparent. One of the mutants died before reaching maturity, but the other flowered abundantly, producing considerable quantities of pollen. As might be anticipated, it was found by Miss N. Thomas and the writer to possess 15 chromosomes. In addition to the ordinary inheritance phenomena in this family of hybrids, in which we may assume that a regular distribution of the germinal materials took place in meiosis, there was superimposed this meiotic irregularity leading to the appearance of the *lata* habit and foliage. Probably the two *lata* plants which occurred in this culture were both derived from a single 8—6-chromosome distribution in one pollen mother-cell, for two pollen grains having eight chromosomes each would result from such a heterotypic distribution.

Such definite results as these make it clear that mutation

and inheritance are processes to be sharply contrasted with each other. The latter is concerned with the regular redistribution or blending of characters, such as occurs in hybrids; the former is concerned with germinal changes which lead to a new condition of equilibrium in the organism. There has not been the creation of a new unit-character, but the polygon of forces representing the organism has moved over to a new position of stability.

The condition of stability in the case of a mutant like *lata* or *semilata* often does not last beyond the first generation. Thus the offspring from self-pollination of the *lata rubricalyx* mutant above described, as well as the offspring from crosses, all reverted to the 14 chromosome condition, and not one of them showed the peculiar features of *lata*. The reason for this absence of *lata* plants from the next generation will be shown in Chapter VI, but it may be mentioned here that the cytological studies of the pollen development in this plant, by Gates and Thomas, showed that owing to further meiotic irregularities the great majority of the pollen grains which matured ultimately received only seven chromosomes in their nuclei. It is, therefore, not surprising that no *lata* plants appeared in the offspring of this individual. The nature of these offspring will be considered in the chapter on hybridisation.

Oe. latescens mut. nov. (Fig. 42.)

Tall plant with a ring of basal shoots, leaves nearest *Lamarckiana*, but larger, with more obtuse points and larger crinkles, and narrowed gradually at the base of the blade to a very short petiole, upper leaves very distantly and obscurely repand-denticulate. Buds stouter than in *Lamarckiana*, sharply quadrangular, yellowish with reddish marginal streaks, pubescence as in *Lamarckiana*.

This very characteristic and handsome plant (No. 229, III. 3) with larger flowers than *Lamarckiana*, occurred in 1912 in a culture of *lata*-like plants obtained from N.

Heribert-Nilsson in Sweden. The culture contained 79 plants, nine of which had *lata*-like foliage and 15 chromosomes. This plant very probably had 16 chromosomes, though they have not been counted and the offspring have not been grown.



FIG. 42.—*Oe. mut. latescens*.

Oe. mut. gigas, de Vries. (Figs. 43–55.)

Rosette-leaves broadly lanceolate with obtuse or rounded tip to nearly orbicular, more crinkled than in *Lamarckiana*, petioles shorter. The stem-leaves also are larger, broader, thicker, more obtuse, and more crinkled than in *Lamarckiana*. An exact comparison of the pubescence has not been made, but the leaves appear more pubescent and the individual hairs are probably larger. The plants develop

more slowly and are hence more strongly biennial than the other derivatives of *Lamarckiana*, and the flowers are more susceptible to frost. The stem is much stouter than in *Lamarckiana* (according to de Vries, often 10 mm. in diameter, instead of 5-6 mm.) though it is not taller. This appears to be because the upper internodes are both

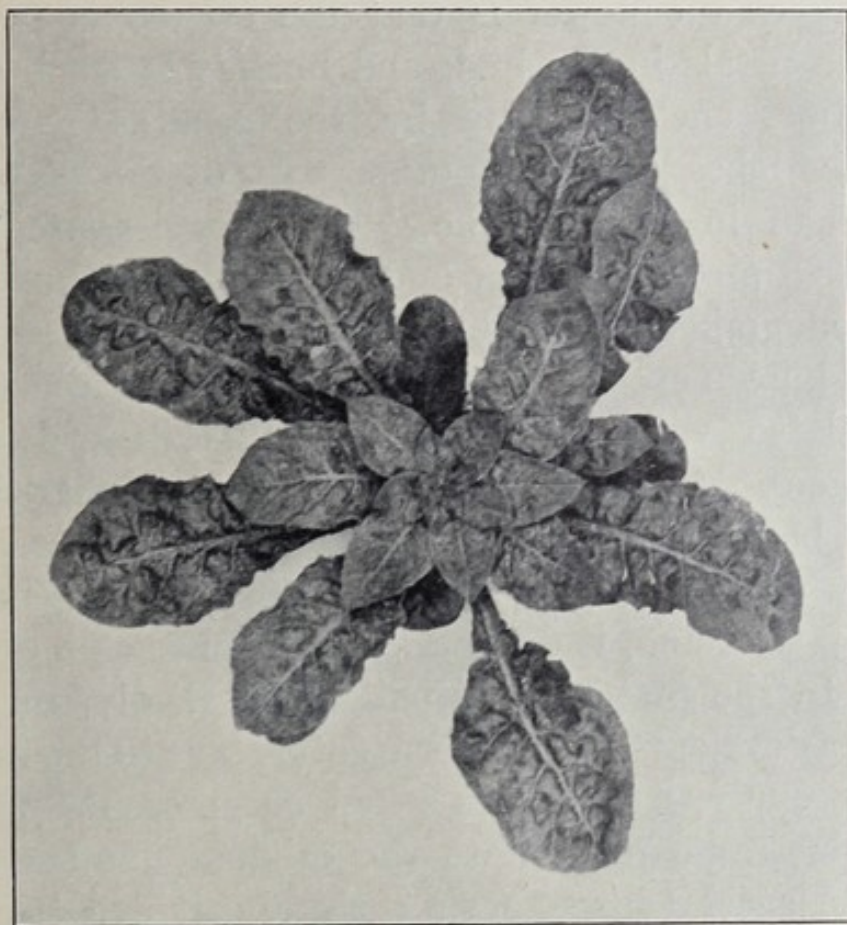


FIG. 43. *Oe. mut. gigas* rosette, Palermo race.

shorter and less numerous than in *Lamarckiana*. Comparative measurements of two typical individuals, both having a ring of basal branches, were as follows, the *gigas* belonging to the Italian race:

	<i>Lamarckiana</i>	<i>gigas</i> .
Total height	96 cm.	87 cm.
Distance of first capsule from ground . .	56 cm.	67 cm.
Length of stem from capsules 1 to 4 . .	47 mm.	50 mm.
" " " 1 to 10 . .	120 mm.	90-113mm.

The petals of *gigas* are about 50 mm. in length and 60 mm. broad, truncate or slightly emarginate; bud cone 40–45 mm. in length and 14–15·5 mm. in diameter at the base; hypanthium 40–43 mm. long, about 4·5 mm. in diameter; ovary 14 mm. long, somewhat flattened, about 6 × 5 mm. in diameter; sepal tips 5·5–8 mm. long, coloration of sepals as in *Lamarckiana*. Another peculiarity of the flower is that the stigma is enclosed within the petals in the bud, and not, as in some of the other forms, enclosed only by the sepals. The style and stigma-lobes, like every other part of the plant, are stouter than in *Lamarckiana*. The capsules are short, about 20–28 mm. in length, and the seeds few but large. The pollen grains are 4-lobed, instead of 3-lobed as in all other known species of *Oenothera*. These differences are correlated with the presence of 28 instead of 14 chromosomes. A further analysis of the peculiarities of *gigas* will be made in a subsequent chapter.

From whatever point of view we consider *gigas* in relation to *Lamarckiana*, it deserves to be ranked as a distinct species. In the first place, it differs markedly, in every stage of its development, from the cotyledons to the mature plant; secondly, it possesses a new chromosome number bearing the same relation to the original number as in many wild species now known; thirdly, it even satisfies Huxley's criterion of a distinct species, for it exhibits a large degree of sterility when crossed with its neighbours. This criterion has, however, very largely broken down; as witness the *Bovidæ* among animals, which are all fertile *inter se*; and among plants the species of *Oenothera* such as *biennis*, *Lamarckiana*, *grandiflora*, *muricata* and *Hookeri*, many of the hybrids of which show undiminished fertility. No one can reasonably pretend that these all belong to the same "species." Many other cases might be cited.

In its occurrence *gigas* is the rarest of all the mutants, unless we except *rubricalyx* which has appeared but

once, and *brevistylis* and *cruciata* the origin of which has rarely occurred in breeding experiments. The history of the first *gigas* mutation was carefully recorded by Professor de Vries, and nearly all the existing cultures are descended from this plant. It appeared in 1895, in a lot of 32 rosettes which had been selected by him from 14,000 plants constituting the fourth pure generation of his *Lamarckiana* family. The numbers of *Lamarckiana* plants furnishing seeds for the three previous generations were respectively 9, 6, and 10. These were carefully scrutinised before selecting them as seed-parents, and the presence of a specimen of *gigas* among them would have been detected.

Two other *gigas*-like plants appeared in de Vries's garden, one in 1898 as a mutant from mut. *sublinearis*, the other in 1899 from *lata* \times *hirtella*. Neither of these plants matured, and it is probable that they were polyploid mutants but different from *gigas*. A mutant resembling *gigas* also appeared once in MacDougal's cultures of *Lamarckiana* (1907), and three times in Schouten's studies from commercial seed. In addition, we have described a tetraploid ($4x$) race identical with that of de Vries, which appeared independently in the botanic garden at Palermo, Italy (146), where it was recognised as distinct and cultivated under the name *Oe. cognata*, Hort. They have since lost the strain, but we have seeds from which it is being propagated. (See Figs. 43, 44.)

Seeds of the strain above described were obtained from Palermo in 1909, which, when planted in 1911, yielded 56 rosettes at the Missouri Botanical Garden, St. Louis. The young rosettes appeared to belong to an unknown type with very long petioles and oval blades, but having passed through this stage (which may have resulted from some peculiarity of the environment), the mature rosettes were identical with those of the Amsterdam *gigas*. They showed a considerable range of variation,

though not so great as in the Amsterdam race, and included also three *gigas nanella* rosettes. The remaining seeds were sown at the John Innes Horticultural Institution, Merton, in 1912, and produced 12 plants, all of which bloomed and were identical with *gigas* of de Vries



Fig. 44.—*Oe. mut. gigas*, Palermo race.

in every stage of their ontogeny (see Figs. 43, 44). Nine of these belonged to the typical broad-leaved *gigas*, one was more slender and probably corresponded to *gigas oblonga*, having nearly smooth leaves, oblong, with a nearly smooth margin. Another differed from the type in having smaller leaves which were more deeply

crinkled, and narrow stripes of red on the buds, though the rosette was typical. The last plant was distinctly smaller in all its parts, having petals as long though broader than in *Lamarckiana*. It was found to have 75 per cent. 4-lobed pollen grains, 23 per cent. with three lobes and 2 per cent. with more than four lobes. Its chromosomes have been found to be 27, while typical plants were examined and found to have 28 chromosomes.



FIG. 45.—*Oe. mut. gigas* from Swedish race of *Oe. Lamarckiana* (cf. Fig. 43).

It appears that in all the giant races of *Oenothera* the flowers tend to remain attached longer than in other forms. In one individual of this culture the absciss layer between hypanthium and ovary was completely lacking, so that the faded flowers remained permanently attached to the plant, even weeks after blooming. This feature was exhibited to a less extent in two other plants.

Another and different race of *gigas* has appeared in

Heribert-Nilsson's cultures of the Swedish *Lamarckiana* (see Figs. 45-47). It has been found by Miss N. Thomas to have 27 or 28 chromosomes.¹

Stomps (352) has estimated the frequency or mutation-coefficient of *gigas* as nine in a million or 0.0009 per cent., but the basis of the estimate is rather speculative. It



FIG. 46.—*Oe. mut. gigas* from Swedish race of *Oe. Lamarckiana* (cf. Fig. 44).

moreover appears probable that the environmental conditions play some part in determining the frequency with which such a change as that involving tetraploidy will take place. This view is based on the fact that suspended mitoses with concomitant doubling of the

¹ I have since, from studies of the meiotic divisions, been able to determine the number as precisely 28.

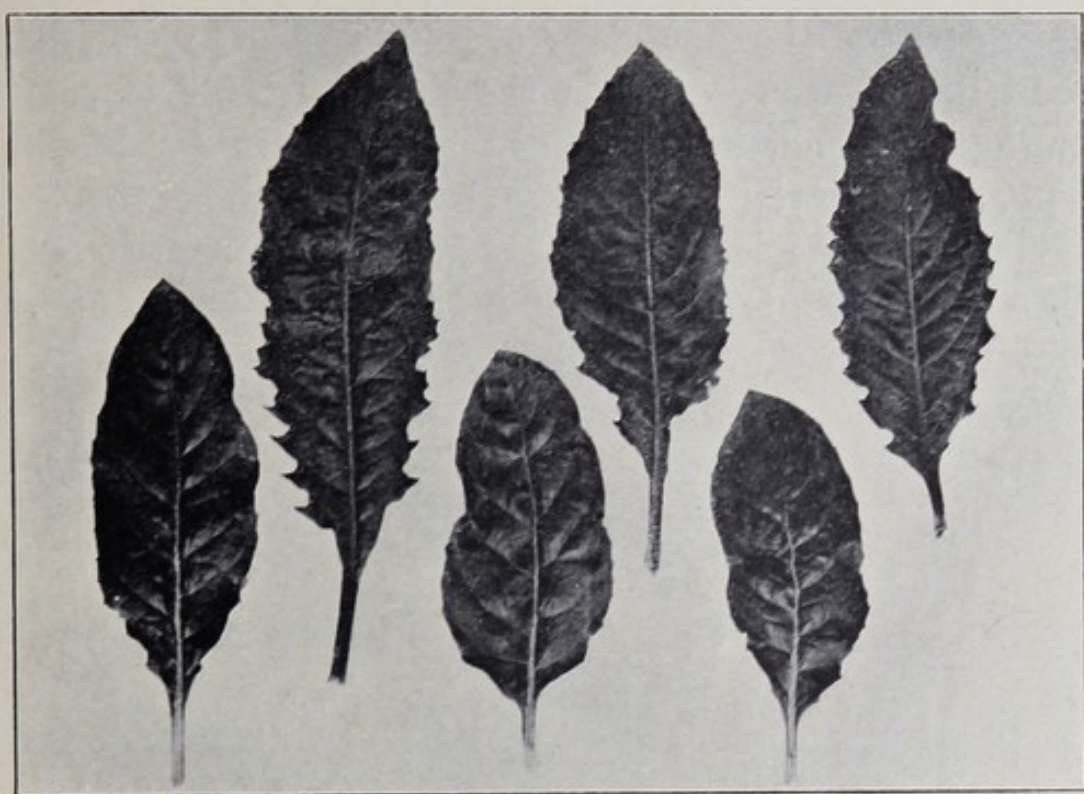


FIG. 47.—Upper row, three stem-leaves from Swedish *gigas*.
Lower row, three stem-leaves from Palermo *gigas*.



FIG. 48.—Leaves from mature rosettes of *Oe. mut. gigas*,
showing range of variation in shape.

chromosome number can be induced both in plant and animal tissues by a variety of experimental agencies.

In its offspring, *gigas* is the most variable of all the mutants, though it apparently never reverts to *Lamarckiana*. This latter fact may be regarded as evidence against the occurrence of true parthenogenesis in *gigas*. De Vries grew a family of 450 individuals from his original mutation, and they were all *gigas* except one dwarf plant, *gigas nanella* (Fig. 54). In 1909 we grew a family of 434 plants from *gigas*, constituting the sixth generation

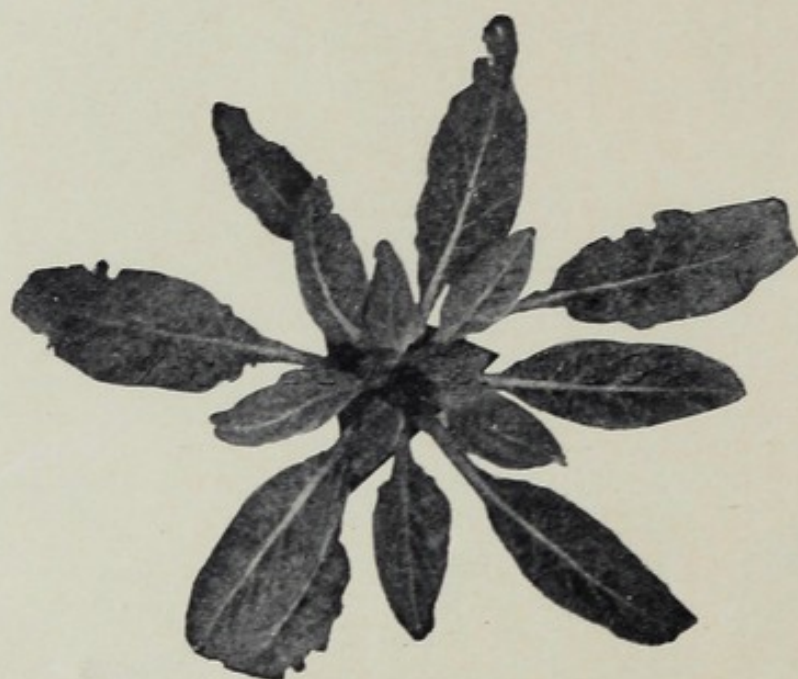


FIG. 49.—*Oe. mut. gigas*, a rather narrow-leaved rosette.

from the original mutant of de Vries. They exhibited remarkable variation in foliage, as shown by Figs. 48–51. In each rosette the leaves were all of one type, but in the whole series they ranged from very broad and almost orbicular to very narrow and almost linear. One narrow-leaved plant from a subsequent sowing from the same seeds, grown in 1912, reached the adult condition and is shown in Figs. 52 and 53. Its flowers are much smaller than normal, and its pollen sterile. Of the above-mentioned family, all except four remained in the rosette

stage. From the four which bloomed pure seeds were obtained, and from these 48 plants were raised in 1910.

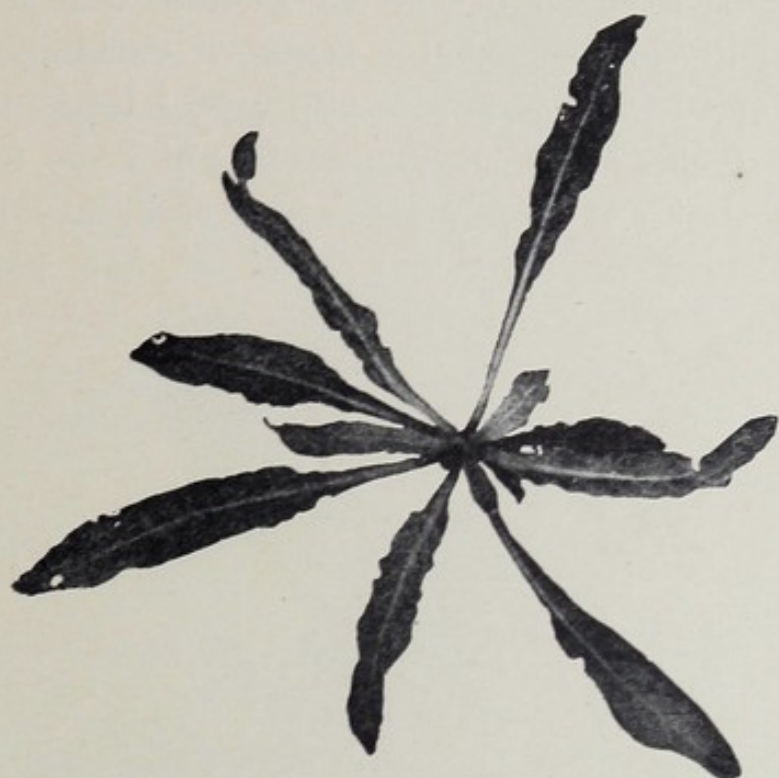


FIG. 50.—*Oe. mut. gigas*, a very narrow-leaved rosette.



FIG. 51.—*Oe. mut. gigas*, a linear-leaved rosette.

These numbers were not large enough to test the inheritance of the parental differences in foliage. Though the

offspring tended to resemble their parent, occasional rosettes departed from this rule. It appears probable that the distribution of the $4x$ meiotic chromosomes is concerned in this remarkable range of variability.

In the cultures of *gigas* also appeared a large percentage of dwarfs (*gigas nanella*). These do not have the foliage of *nanella* but are merely miniature *gigas* usually of the broad-leaved type (Fig. 54). Out of 339 plants, one



FIG. 52.—*Oe. mut. gigas*, narrow-leaved rosette.

lot contained 4.28 per cent., another 8.76 per cent., while a third lot of only 15 plants contained 10.9 per cent. *gigas nanella*. It is therefore evident that giantism and dwarfism in *Oenothera* are not the two extremes of a single series, but are due to changes of quite diverse kinds. Giantism in *Oenothera* is a result of cell giantism, apparently always accompanied by tetraploidy, while dwarfism (see *nanella*, p. 134) appears to be due to shortening of internodes accompanied by decrease in the

size of cells as well. In *gigas nanella* or miniature *gigas* plants the tetraploid chromosome-number is probably retained, and there is probably a very marked decrease in the size of the cells, accompanied by corresponding diminution in the volume of nuclei and chromosomes. This will

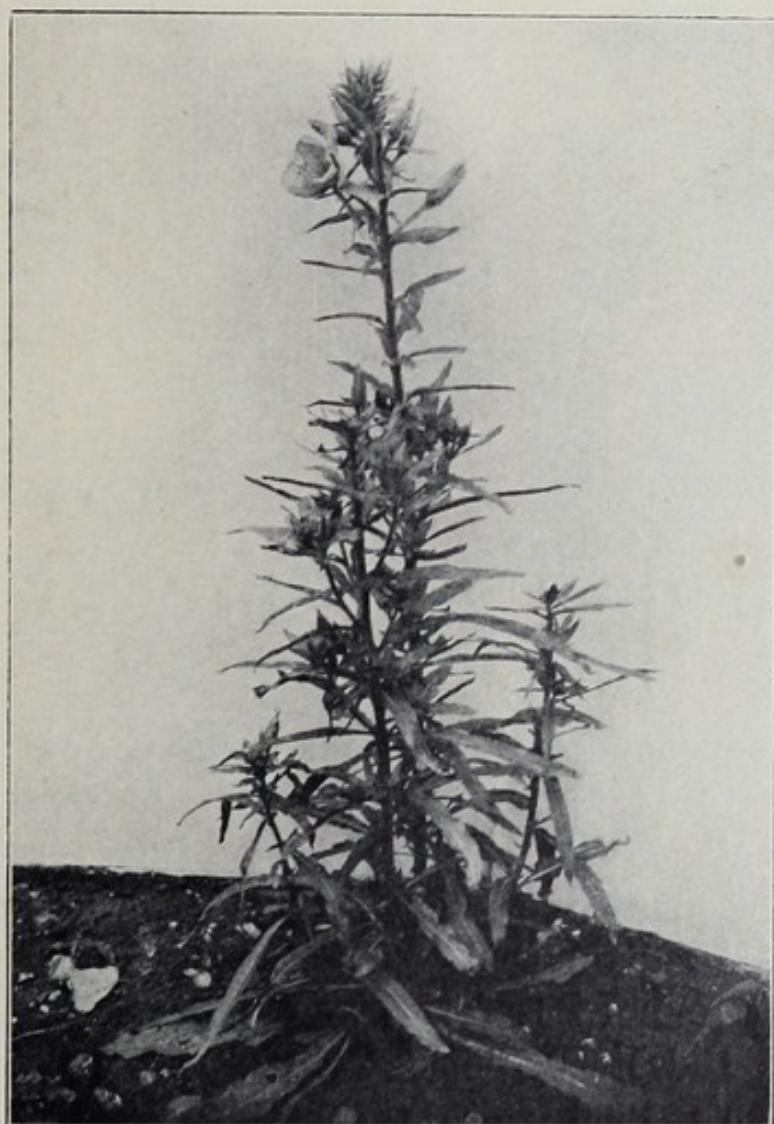


FIG. 53.—Adult stage of the plant shown in Fig. 52.

be an interesting subject for future investigation, but the facts already known make it clear that giantism and dwarfism in *Oenothera* are due to very distinct and diverse germinal changes, and that dwarfism superimposed upon giantism by no means causes return to the original type. Crosses between *gigas* and *nanella*, which

have so far been made without great success, would probably contribute to an understanding of this subject.

In 1906 Schouten (333) grew at Amsterdam about 1,200 *gigas* from seeds of de Vries. Some of their flowers

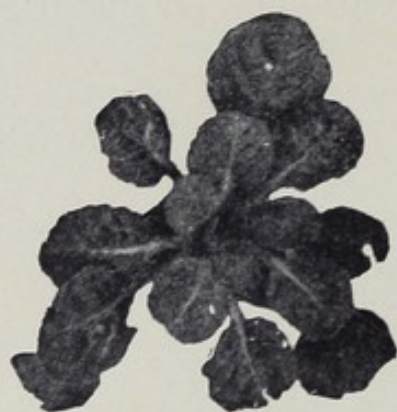


FIG. 54.
Oe. mut. gigas nanella.

were as much as 10 cm. in diameter, and the plants showed the usual wide range of variability in foliage, the culture containing also 2 per cent. *gigas nanella*. Six foliage types were distinguished, in addition to the type form. Individuals belonging to these types were selfed, but their offspring were in no case uniform, each group being, according to Schouten, as variable

as the whole culture. The seven families contained about 1,000 plants as follows:—

945 <i>gigas</i>	97.93%
18 <i>gigas nanella</i>	1.87
1 <i>gigas lata</i> ?	0.10
1 <i>laevifolia</i> ?	0.10
		} = 2.07%

The frequency of the *gigas nanella* varied from 0.74 per cent. to 14.8 per cent. The family containing the last percentage Schouten thinks came from a plant which was produced by the union of a *gigas* germ cell with a *gigas nanella* germ cell. The *gigas lata* resembled *lata* in having rounded leaf tips and buds, and in its male sterility. Did it, perhaps, have 29 chromosomes?

Schouten's 1906 culture contained also two plants called *gigas argentea*, in which the leaves, especially of the rosette, were covered with silvery pubescence. One of these was male-sterile and was pollinated from typical *gigas*. It yielded 37 offspring, all of which except one were typical *gigas* without the *argentea* character. Schouten therefore considers this feature as a non-inherited extreme variant, though it is conceivable that the character may have been inherited but recessive.

The original Swedish giant mutation appeared in 1907, in a culture of about 30 plants of the Swedish *Lamarckiana* (see p. 123) grown by Heribert-Nilsson at Lund (182). From seeds sent by him, we grew in 1912 a family of 36 plants (see Figs. 45-47) which were uniform except for two or three individuals, one of which agreed almost with the typical *gigas* of de Vries. The typical plants differ from the Amsterdam and Palermo races of *gigas* mainly in the following particulars: (1) when half developed the rosettes were indistinguishable from those of Palermo, but their later leaves are larger, with more jagged teeth at the base of the blade. (2) The stem-leaves have conspicuous red midribs, and the midribs and petioles are also pink on their ventral surface. (3) The stem-leaves are longer, less crinkled, often nearly smooth, and their margin is more conspicuously repand-dentate, often with jagged teeth near the base. (4) The basal branches are more spreading, the stem-branches more numerous and often with secondary branches, the whole plant being larger and more bushy. (5) The flowers are considerably larger (petals 60×75 mm., ovary 18 mm.), and the long hairs on the buds are longer, more numerous, and from larger papillæ. (6) The capsules are expanded at the base to a broad attachment, they are also much longer (36-39 mm.) and contain many seeds, the plants showing much less sterility than the *gigas* of de Vries, both in anthers and ovaries. (7) The development was slightly slower, five plants remaining rosettes.

Heribert-Nilsson (184) gives an extended account of



FIG. 55.—*Oe. mut. gigas*, buds.
Cf. Figs. 29, 36, and 38
(same scale).

his cultures, both of de Vries's *gigas* and the Swedish giant. He also obtained from his giant race ("Komb. 7") individuals resembling the Amsterdam form. He attributes the appearance of these to the loss of a germinal factor controlling the development of red and various other peculiarities of the organism. In this view we agree with him, since the chromosome number is the same in both forms, and for other reasons. He also describes many other aberrant types in the descendants from his cultures, but his discussion of them is for the most part abortive since he fails to take into account the cytological facts. A purely hypothetical theory which disregards these facts, and frequently runs counter to them, ceases to be of value. It is obvious that much of the variation he describes is due to combination-mutations parallel to the *Lamarckiana* series; his "Komb. 8," which he calls an intermediate between *Lamarckiana* and *gigas*, is very probably a triploid mutant; and a number of the other forms when cytologically studied will no doubt be found to be concerned with new meiotic distributions of the chromosomes.

Oe. mut. semigigas, Stomps.

This is one of the latest of the mutants to be discovered. It is a triploid or $3x$ mutant, having 21 chromosomes and standing intermediate between *gigas* and *Lamarckiana*. The first recognition of this fact was published simultaneously in 1912 by Stomps (351) and Miss Lutz (241), the latter having apparently observed such a plant in 1908, while de Vries seems to have first studied its characters in 1910, though it was recognised some years earlier. Two plants from cultures at Woods Hole, Mass., in 1905 and 1906, having characters resembling this form, were found (1909) to have respectively 20 and 21 chromosomes. The mother of these plants was *Oe. lata*, but the seeds were, unfortunately, afterwards found to have been open-pollinated, so that the father was un-

certain. The father was considered to be *gigas*, but there is a possibility that these plants may also have been triploid mutants.

Miss Lutz (241) has observed eight such *semigigas* individuals, two of them appearing in 1908 in offspring of *lata* \times *Lamarckiana*, five in the offspring of three pure *Lamarckiana* plants in 1910, and one from *lata* self-pollinated. In addition, one mutant having 22 chromosomes was found in a culture of *lata* selfed, and another having 20 to 22 chromosomes from a separate source. In none of these cases does the full number of offspring appear to be given.

Similar triploid mutants have since been obtained from several crosses which will be described later. De Vries has compared the reciprocal hybrids between *gigas* and *Lamarckiana*, with the mutant *semigigas*, and finds them alike, as might be expected.

The exact manner of origin of *semigigas* is a matter of much interest. Its existence has been assumed by de Vries (423), Stomps (351) and Miss Lutz (241) to prove that *gigas* originated through the union of two diploid germ cells. But this conclusion by no means follows. The matter will be discussed in Chapter VI, but it may be pointed out here that there are at least three possibilities regarding the origin of $3x$ mutations, (1) from the union of a diploid egg with a haploid male cell, (2) from the union of a haploid egg with a diploid male cell, and (3) from the union of both male cells with a haploid egg in fertilisation.

The nature of the inheritance of *semigigas* is at present imperfectly known. Having a triploid chromosome number, which is, moreover, an odd number, it is not probable that all the offspring will be like the parent. Cytological studies of pollen development in 21-chromosome plants (hybrids or mutants) by myself (125) and by Geerts (159) have shown that in some cases the chromosomes are regularly distributed in the reduction divisions while in

others certain of the chromosomes degenerate in the cytoplasm, leaving a smaller number of chromosomes to enter the nuclei. One would therefore expect to find in the offspring of *semigigas* some reversions to *Lamarckiana* with 14 chromosomes, some plants with numbers intermediate between 14 and 21, and occasional individuals having 22 or more chromosomes. Miss Lutz (241) has already observed great variation in the offspring of certain triploid mutants, which is fully in accord with cytological expectation. The relation here between chromosome number and external characters can only be determined by chromosome-counts of many individuals, combined with careful study of their external features.

Oe. mut. nanella, de Vries.

The young seedling of *nanella* is very early recognisable (even in the first leaf following the cotyledons) by its broader blades with broader base and much shorter petiole, giving the young rosette a much more compact appearance. One whorl of the rosette leaves, however, has long petioles, and this is regarded by de Vries as representing an atavistic stage in the ontogeny. The leaves of the mature rosette are about 7-8 cm. in length, so that the diameter of the rosette is very much less than in *Lamarckiana*. The stems are slender, brittle, and very short, reaching only 15 to 30 cm. in height, very little or not at all branched. The internodes are numerous and very short; the leaves crowded, with brittle petioles; the bracts obtuse with broad base, sessile. The flowers are sometimes almost as large as in *Lamarckiana*, petals usually about 25 × 40 mm., but the buds are often bent where the hypanthium joins the bud cone. The foliage of *nanella* is subject to much variation, and in Amsterdam cultures the plants appear to be particularly susceptible to attacks of bacteria, as shown by Zeijlstra.

Nanella has 14 chromosomes, like its parent *Lamarckiana*, but the cells and their nuclei are much smaller. The

same is probably true of the chromosomes. Detailed studies of cell-size have not been made, but a condition of cell-dwarfism will probably explain many of the changes which have taken place, though the shortness of the internodes is probably the main feature determining the height. The dwarf varieties of many cultivated species have no doubt originated in a similar manner. Wild dwarf species appear to be less common, presumably because they are eliminated in many cases by natural selection.

The precise manner of origin of such dwarf races—we mean the place in the life-cycle where the germinal change occurs—is a question of very much interest. So far as known, we believe that all dwarf races are recessive to their tall ancestors and appear to have originated by a single retrogressive character-change. They also, like *Oe. nanella*, apparently always breed true. In Mendelian terms, they are homozygous and have originated through the loss of a unit-factor, but it will be seen that this view of the matter is misleading. In the case of *Oe. nanella*, its peculiarities are completely recessive and obscured in crosses with *rubrinervis*, so that this tall race, having been crossed with *nanella*, can carry dwarfness without giving any external sign of it whatever.

There is perhaps no clearer proof of the impossibility of explaining the mutation phenomena in terms simply of recombinations of Mendelian units, than by attempting to apply this conception to the case of *nanella*. On the Mendelian interpretation *nanella*, since it breeds true, must have come from the union of two germ cells both of which had lost the dominant factor for tallness. This seems reasonable so far as it goes. But the difficulties soon begin. (1) On this hypothesis certain individuals of *Lamarckiana* must be heterozygous for tallness, having come from the union of a normal germ cell possessing the dominant character, with a mutated germ cell in which

that character had been dropped out. Such individuals should produce in their offspring about 25 per cent. of dwarfs. But no such case is known, and *nanella* appears always sporadically in a small percentage (about 0·2 per cent. to 3 per cent.) of the offspring of *Lamarckiana*, though it has appeared nearly 400 times in all, in the cultures of de Vries alone. (2) Another fact which cannot be accounted for by the simple presence and absence hypothesis of Mendelism, is that when *Lamarckiana* and *nanella*, both of which breed true and are homozygous in the Mendelian sense, are crossed, they give rise to both *Lamarckiana* and *nanella* in F_1 , and both types remain constant in later generations. This behaviour is by no means unique with *nanella*, but when several of the mutants, e.g., *rubrinervis* or *lata*, are crossed with their parent, the F_2 contains both the mutant and *Lamarckiana*.

The peculiarity of this behaviour is further emphasised by the fact that, when crossed with *rubrinervis*, *nanella* behaves in a different way. De Vries showed some years ago that from such a cross the F_1 contains *Lamarckiana* and *rubrinervis* while in F_2 the *Lamarckiana* and a portion of the *rubrinervis* breed true and the remaining *rubrinervis* split off dwarfs. In 1909 we made the cross *rubrinervis* \times *nanella* and the F_1 contained 77 plants, about 25 of which were *Lamarckiana* (there was some uncertainty in the exact numbers for many remained rosettes), and 52 *rubrinervis*. Certain of the latter, selfed, yielded in F_2 42 plants, of which 32 were *rubrinervis* and 10 *nanella*. This 3 : 1 ratio may be significant. The dwarfs so obtained differed from pure bred *nanella* in being considerably larger with many basal branches.

The important point is that whereas *Lamarckiana* \times *nanella* yields both parent types in F_1 and both breed true, in mut. *rubrinervis* \times *nanella* the dwarf character behaves as a recessive, reappearing for the first time in

F₂. The Mendelian presence-absence hypothesis completely fails to explain why splitting should occur in F₁ in one case and in F₂ in the other. The hypothesis of de Vries (425), that characters can exist in three conditions, active, inactive, or labile, is the only one which makes any attempt to meet such cases, the existence of which is in itself a denial of the notion that Mendelian behaviour can be universal. This fundamental conception of de Vries, the significance of which no Mendelian seems to have grasped, will be discussed later (see p. 225). De Vries has similarly found that in *nanella* × *biennis* (though not in the reciprocal) both tall and dwarfs appear in F₁. This he attributes to the presence, in the pollen grains of *biennis*, of a labile pangen for height, as will be explained later.

Oe. gigas nanella, or the miniature *gigas*, furnishes two cases, however (see p. 130), which may possibly be explainable through the *heterozygous* union of a mutated with a non-mutated germ cell. Thus two lots of pure *gigas* seeds yielded respectively 8.76 per cent. and 10.9 per cent. *gigas nanella*. Similarly, Schouten obtained among 1,196 *gigas* plants 24 dwarfs, or 2.01 per cent., while the next generation of about 1,000 plants, which were chiefly the offspring of *gigas* individuals of the previous year, yielded 1.87 per cent. dwarfs, one culture containing as many as 14.81 per cent. The high percentages might be explained as originating from individuals heterozygous for tallness, in which also the tall form showed greater viability than the dwarf. The departures from 25 per cent. are so wide, however, that there is really very little basis for such a suggestion.

The complete absence, hitherto, of such heterozygous individuals in the offspring of *Lamarckiana* makes it impossible to accept the view that *nanella* arises only from the union of two germ cells both lacking the factor

for tallness. The following table shows the frequency of *nanella* as a mutant in the cultures of de Vries :—

TABLE VIII.
Mutations of *nanella* from *Lamarckiana*.

	Total.	<i>Nanella</i> .	Per cent.
<i>Lamarckiana</i> family, 1889–1899	53,000	158	0.3
A branch of same, 1895 ..	10,000	111	1.1
<i>Lævisfolia</i> family, 1889	400	12	3.0
<i>Lamarckiana</i> × <i>nanella</i>	1,063	5	0.47
<i>lata</i> × <i>nanella</i>	1,693	12	0.71
"	390	6	1.54
<i>lata</i> × <i>brevistylis</i>	1,026	3	0.29
<i>O. scintillans</i> , 1897–8	1,654	15	0.9
A biennial cult. 1897	1,529	9	0.6
Cult. of plants with variegated leaves, 1899	1,972	9	0.5
<i>Lamarckiana</i> × <i>biennis</i> , 1900 ..	80	1	1.0
<i>lata</i> × <i>biennis</i> , 1899	299	2	0.7
<i>Lamarckiana</i> × <i>brevistylis</i> , 1898..	293	5	1.7
<i>Lamarckiana</i> × <i>gigas</i> , 1899 ..	100	2	2.0
<i>Lamarckiana</i> × <i>scintillans</i> , 1899	112	1	1.0
<i>lata</i> × <i>Lamarckiana</i> , 1900 ..	2,000	3	0.2
<i>lata</i> × <i>Lamarckiana</i> , 1895–1900..	2,387	26	1.1
<i>lata</i> × <i>brevistylis</i> , 1896–99 ..	425	6	1.4
	78,423	386	0.493

The later, and probably more carefully examined families, gave about 1 per cent. as the mutation-coefficient or percentage of mutations for *nanella*.

In 1895 de Vries self-pollinated 20 *nanella* which yielded 2,463 offspring (F_2), all *nanella*, as well as the F_3 (547 plants) and F_4 (100 plants) and two following generations. In 1896 he selfed 38 *nanella* and obtained 18,649 offspring, all dwarfs, including 3 *oblonga nanella* and 1 *elliptica nanella*. Similarly, 9 *nanellas* from *scintillans* were selfed and yielded 64 offspring all like the parent. Hence *nanella* never reverts. On the other hand, combination forms with a number of the other mutations are now known from the offspring of *nanella*. They include *nanella-lata*, *nanella-oblonga*, *nanella-albida*, *nanella elliptica*, and *nanella-scintillans*. The presence of these combination forms

has been regarded by some as an indication that the whole process of mutation is merely a phenomenon of hybridity. It is, of course, obvious that each of the combination types is a hybrid in the sense that it came from the union of two unlike germ cells. But the fact that a series of mutants parallel to those of *Lamarckiana* can also be obtained from *nanella*, shows that *nanella* is lacking only the capacity for height and the various correlated features. With this exception, its germ plasm is still capable of undergoing the same series of alterations as in *Lamarckiana*. Thus the *nanella-lata* mutants no doubt have 15 chromosomes, and have originated through the same meiotic irregularity in *nanella* as in *Lamarckiana* or *Oe. biennis*. The fact that *nanella-lata* appears also in *Lamarckiana* \times *nanella* and in *lata* \times *nanella*, is fully in accord with these views.

Oe. mut. oblonga, de Vries.

The young seedlings have narrow leaves with long petioles. In the mature rosette the leaves are oblong or narrowly ovate-lanceolate, with rounded tips and unmarginated petioles, the transition from blade to petiole being abrupt. The leaves are rather thick and fleshy and the broad, pale veins have a reddish tinge on their ventral surface. The plants are shorter than *Lamarckiana*, seldom reaching a metre in height, and the fruits are only a third the length of those of *Lamarckiana*, containing usually few seeds, the flowers also somewhat smaller (petals about 3 cm. long). The stem-leaves are crowded, strongly crinkled, dark green, hanging down, oblong-elliptical with acutish or obtuse apex.

In cultures of *Lamarckiana* numbering 14,000, 8,000 and 1,800 plants, de Vries obtained respectively 1.3 per cent., 1.7 per cent. and 1.6 per cent. *oblonga*, and in a total of about 70,000 seedlings 700 *oblongas* or about 1 per cent. mutants. This is hence one of the more common forms to appear. It occurs also in the offspring of various

hybrids and mutants, and 35 individuals occurred in the cultures of MacDougal, constituting a frequency of 1.25 per cent. That *oblonga* breeds true was shown by de Vries in 1896, when he obtained as the offspring of seven *oblongas*, 1,683 plants, all of which were *oblonga*, but one having characters of *albida*. This constancy is independent of its origin from a hybrid or other source. A total of 2,554 individuals from *oblonga* self-pollinated contained 3 *albida*, 1 *elliptica* and 1 *rubrinervis*; and in another case 365 offspring of *oblonga* included 6 *rubrinervis*.

Oe. mut. albida, de Vries.

This very delicate form seems to have been brought to maturity only in the cultures of de Vries and MacDougal. It is pale green or whitish-grey, and rather brittle. The rosettes resemble *oblonga* in leaf-shape. The stem is zigzag but stout, the height not exceeding a metre, the flowers are paler and smaller than in *Lamarckiana*, more nearly erect on the stem, and opening out less widely. The fruits are small, containing few seeds. The stem-leaves are narrow, pointed, and with crinkles more numerous and pronounced than in *Lamarckiana*.

This very weak mutant was found by de Vries to be constant, five biennial plants yielding in 1897 an offspring of 86 plants, all of which were *albida*. The next generation from these numbered 36 plants, all *albida*.

Table IX on the following page shows the frequency of *albida* in the cultures of de Vries.

The frequency of *albida* as a mutation thus varies from 0.05 per cent. to 9 per cent. It is an obviously retrogressive variation, and since it breeds true it should be classed with *nanella*. *Albida* seems to have been used very little in crossing-experiments. It appeared to the number of 17 individuals in the cultures of MacDougal (253), and six of these were derived from a race of *Lamarckiana* introduced in Nantucket City from garden seeds many years before.

TABLE IX.

Mutations of *albida* from *Lamarckiana*.

Source.		Total.	albida.	% albida.
<i>Lamarckiana</i> family	1895-9	28,500	56	0.2
<i>Lamarck.</i> from crosses	1898	4,599	2	0.05
Lateral branch of <i>Lamarckiana</i> family	1895	10,000	255	2.6
<i>Oe. lata</i>	1900	2,000	42	2.1
<i>Oe. lata</i>	1896-99	751	31	4.0
<i>Oe. Lamarck.</i> biennial	1896	164	15	9.0
<i>Lamarck.</i> × <i>nanella</i>	1897	1,341	1	0.1
<i>lata</i> × <i>nanella</i> ..	1895-00	1,586	15	1.0
<i>lata</i> × <i>rubrinervis</i>	1900	1,844	37	2
<i>lata</i> × <i>scintillans</i> .	1900	636	2	0.3
<i>scintillans</i> × <i>nanella</i>	1898	95	3	3.0
<i>lata</i> × <i>suaveolens</i> .	1900	743	13	2.0
Total		52,259	472	0.903

Oe. mut. elliptica, de Vries.

The seedling leaves are recognisable by their long petioles and very narrow blades (0.5-0.7 cm. × 8-10 cm.). The plants are weak and frequently remain in the rosette stage, but when they form a stem it is profusely branched. The petals are elliptical, the fruits small with few seeds.

Elliptica has appeared more than 50 times, having a frequency of about one in a thousand. Its offspring are inconstant, mostly reverting to *Lamarckiana*, but containing a proportion of *elliptica* which varies from 0 to 15 per cent. This is like the behaviour of *lata*, and suggests that the germinal change may have been of a similar nature though not necessarily involving a visible nuclear change.

In cultures of the Birkenhead *Oenotheras* we obtained in the offspring of a *lata* or *semilata* self-pollinated, seven plants having *elliptica* foliage, but the small flowers of *Oe. biennis*. Similar plants will be referred to again elsewhere (see p. 289).

Oe. mut. scintillans, de Vries.

The smooth, shining, dark green, narrow leaves are the most characteristic feature of this mutant, making its aspect quite different from that of *Lamarckiana*. The earlier rosette leaves are oblong-obovate, obtuse or acutish, tapering to a white margined petiole. As the rosette develops, the leaves become relatively narrower and lanceolate. The inflorescence is much elongated above the flowers in bloom; the petals about 25 mm. in length, the stigma slightly above the anthers. The ovary is 6 to 7 mm. in length, the capsules short and thick, half the normal length, the seeds small.

This form is not only inconstant but is one of the rarest to appear, having been observed in the cultures of de Vries only 14 times in about 37,000 plants. Its frequency is therefore about 0.038 per cent. *Scintillans* also appeared four times in the cultures of MacDougal.

The hereditary behaviour of *scintillans* is of much interest, since when self-pollinated it regularly produces an offspring composed of *Lamarckiana*, *oblonga*, and *scintillans* in varying proportions, together with occasional mutants such as *lata* and *nanella*. It has been derived both from *lata* and *Lamarckiana*. The percentage of *scintillans* in the offspring varies from 15 per cent. to 84 per cent., and these differences in *scintillans*-producing capacity seem to be inherited. For example, one such family of *scintillans* offspring contained 68 per cent. *Lamarckiana*, 15 per cent. *scintillans*, 15 per cent. *oblonga* and 2 per cent. *lata*. Similarly, MacDougal (253) obtained, in 78 offspring of *scintillans*, 46 *Lamarckiana*, 15 *scintillans*, 16 *oblonga*, and one other mutant. It is probable that the reason for this peculiar behaviour will only be understood when cytological studies have been combined with further breeding experiments. Occasionally combination-forms also occur, such as *scintillans nanella* and *scintillans elliptica*, but these are rare.

Oe. mut. sublinearis, de Vries.

This form is most like *elliptica*, from which it differs chiefly in its much narrower leaves. The seedling leaves are of equal breadth throughout the greater part of their length, whitish, little crinkled, scarcely narrowed at the base, nearly grass-like. The stems are less than a metre high, weak, densely foliated with narrow, nearly linear leaves. The flowers agree with those of *elliptica*, having elliptical petals, and the capsules are short and not slender as in *elliptica*.

On account of their delicacy, these plants usually perish in the rosette stage, only 4 individuals having been reared beyond this stage and only one of these having furnished seeds. The offspring were even more polymorphic than in the case of *scintillans*. They were as follows:

19 <i>Lamarckiana</i>	1 <i>albida</i>
3 <i>sublinearis</i>	1 <i>gigas</i>
1 <i>lata</i>	1 <i>oblonga</i>
1 <i>nanella</i>	3 <i>subovata</i>

The large proportion of mutations is probably connected with the small harvest of seeds, since there is other evidence for believing that the mutants are often more viable than *Lamarckiana*.

Oe. mut. leptocarpa, de Vries.

This mutant is only distinguishable from *Lamarckiana* in the adult stage. It flowers later, the first flower node appearing higher on the stem. The stem is also rather flaccid, the buds greener with less yellow, the bracts broader, more triangular and more flattened, standing nearly erect and covered with small pits. The capsules are long and thin.

This form appears to breed true, but is somewhat variable and tends to transgress the limits between it and *Lamarckiana*.

In addition to the mutants already described, several others have appeared which have been given names and

a certain amount of study by de Vries. These are *spathulata*, *fatua*, *subovata*, and, more recently, *ovata* and *obovata*. These forms and the various other aberrant individuals which have appeared in the cultures of de Vries, MacDougall, the author, and others from time to time, serve to show that this type of variability in *Lamarckiana* is practically unlimited. They show also that there is no sharp line visible between the very marked and wide mutations, and narrower ones which require greater care for their observation. Some of the latter should no doubt be classed as partially-inherited fluctuations rather than mutations, and the precise position of the line between the two categories, mutations and fluctuations, will probably remain obscure, though the extremes of the two series are shown, both by their hereditary behaviour and the cytological work, to be so clearly distinct. It is quite useless, therefore, to argue as certain writers have done, that because the precise line between mutations and fluctuations is difficult to determine, the two categories should be combined into one.

Perhaps the most striking fact to be derived from the recent breeding experiments, and especially from the cytological work, is that mutation is a process *sui generis*, and not merely a manifestation of some type of hereditary behaviour.

Some mutations are also teratological in their nature, and it is impossible again to draw a sharp line between teratological malformations and mutations of other kinds. It is again probably impossible to make a sharp distinction between the narrower mutations such as *leptocarpa*, and smaller inherited differences, for example, in lengths of fruits. Both de Vries and Heribert-Nilsson have found that the offspring of different *Lamarckiana* individuals may differ in the average length of their fruits. This again is connected with the degree of sterility. It will require much further study to determine whether such

differences as these have originated through the same type of variability as the ordinary mutants, but there are reasons for believing that this is not the case.

Another fact which must be evident from a comparison of the various mutants in their characters, origin, and inheritance, is the great diversity in the types of germinal change through which they have originated. We may almost say that each one comes in a category by itself. Thus *gigas*, *lata*, *nanella*, *rubricalyx*, and *brevistylis* obviously represent very different types of change from their parent. This is in striking contrast with many series of Mendelian characters, such as the colour series in sweet peas or in *Antirrhinum*, where the changes are rung on the pigmentation of certain portions of the corolla. The *Oenothera* mutations, on the other hand, usually affect every part of the plant, including foliage, flowers, habit, etc., and the disturbance which has been produced in the germ plasm must therefore be considered to be much more fundamental in character. A further analysis of these changes will be made in Chapter VI.

CHAPTER V

MUTATIONS IN OTHER OENOTHERAS

1.—*Mutations in other races of Oe. Lamarckiana*

WE may now summarise the facts regarding mutation in races of *Oe. Lamarckiana* other than that of de Vries, and in such species as *Oe. biennis* and *Oe. grandiflora*, for mutations are by no means confined to the one species.

De Vries's race of *Oe. Lamarckiana* is known to have been derived from seeds introduced into commerce in 1860 by Messrs. Carter & Co. (see p. 74). But the origin of the Swedish race of *Lamarckiana* which Heribert-Nilsson (184) has studied (see p. 80) and which differs from that of de Vries, is unknown. This race evidently resembles closely some of the forms which seed themselves in English gardens from year to year. It yields a striking series of mutations which are parallel to those of de Vries but differ from them in nearly every case. The giant mutant has already been described in comparison with the *gigas* of de Vries (see p. 131).

Under the mistaken notion that all the mutants represent merely new combinations of Mendelian unit-characters, Heribert-Nilsson calls them "combinations." In following out this idea and attempting to apply it in detail, his reasoning often becomes curious, but the whole conception is so obviously contrary to the cytological facts that any detailed criticism of it is unnecessary here. His "comb. 1" is *lata*. We have grown this race from open-pollinated seeds kindly sent by Heribert-Nilsson. It

agrees, as he says, with the *lata* of de Vries. Our culture (No. 229) contained 79 plants, most of which belonged to a type the buds of which resembled those of *grandiflora*, while the leaves were nearly smooth and cordate. There were also one *nanella*, one very close to *rubrinervis*, and one resembling *oblonga*. The remaining 11 belonged to the *lata*-like series. They included one *semilata*, two *lata* to *semilata*, five *lata*, and one (No. I., 10) belonging to a new type, like a small, weak *lata* having broad-pointed, crinkled leaves nearly cordate at base, and rather small flowers. All these nine plants were found by Gates and Thomas (153) to have 15 chromosomes.¹ The other two plants remained rosettes and belonged to the same type as No. I., 10. The latter when selfed in 1912 yielded six plants, five of which were exactly alike (see Fig. 56), and belonged to the new type, while the sixth resembled *Lamarckiana*. One of the five plants was found by Miss N. Thomas to have 15 chromosomes, and since these five plants were precisely alike there is no doubt that they all possessed the extra chromosome.

This new 15-chromosome type may be briefly described. The rosettes (Figs. 56, 57) have long, rather narrow, spatulate leaves with broad points, the blades tapering gradually to the long petioles. The leaves are deeply crinkled, the stems slender and tall with a loose, elongated inflorescence. The stem-leaves resemble those of the rosette and are easily recognisable by the fact that, owing to unequal growth in the blade, one margin is usually turned up or down along the whole edge. These plants differ from *lata* (cf. Fig. 37, p. 107) (1) in the much narrower leaves with long petioles, (2) in having one edge of the leaf characteristically folded over, (3) in being as tall as *Lamarckiana* with long internodes, (4) in having more squarish

¹ The offspring from self-fertilising two of the *semilata* were grown in 1913. One yielded a single plant (Fig. 40, p. 113), which was *semilata*. The other produced nine of the ordinary type and three *semilata*, the latter no doubt having 15 chromosomes.

buds which produce pollen. They agree with *lata* in the obtuse tips and deep crinkling of the leaves. For convenience of reference we will call this mutant type *Oe. incurvata*. A specimen of a flowering shoot is preserved in the British Museum (Natural History).

One of the *semilata* plants (No. I., 6) in culture $\frac{229}{12}$ when selfed produced, in 1913, 12 plants, of which nine resembled *Lamarckiana* and three were *semilata*. This type is clearly



FIG. 56.—*Oe. incurvata* mut. nov. from Swedish race.

shown in Fig. 40, p. 113, which represents a plant from another culture from this source having the same characters.

The "comb. 2" of Heribert-Nilsson resembles *albida*, "comb. 3" is like *rubrinervis*, "comb. 4" was a rosette, "comb. 5" was a peculiar plant having the branching habit of *rubrinervis*, certain leaf-characters of *scintillans*, and buds and capsules like *lata*. It not improbably has a modified chromosome-number. "Comb. 6" most nearly

resembles the *rubrinervis* of de Vries. From seeds of Heribert-Nilsson we grew 120 plants of comb. 6 \times *Lamarckiana*. There were one *lata* and one *semilata* (both having 15 chromosomes), about seven belonging to the *Lamarckiana* type, while the remainder were classed in the *rubrinervis* type (comb. 6). The latter differ from the *rubrinervis* of de Vries in having nearly smooth leaves and somewhat more red pigment in the buds, the sepals having the extreme

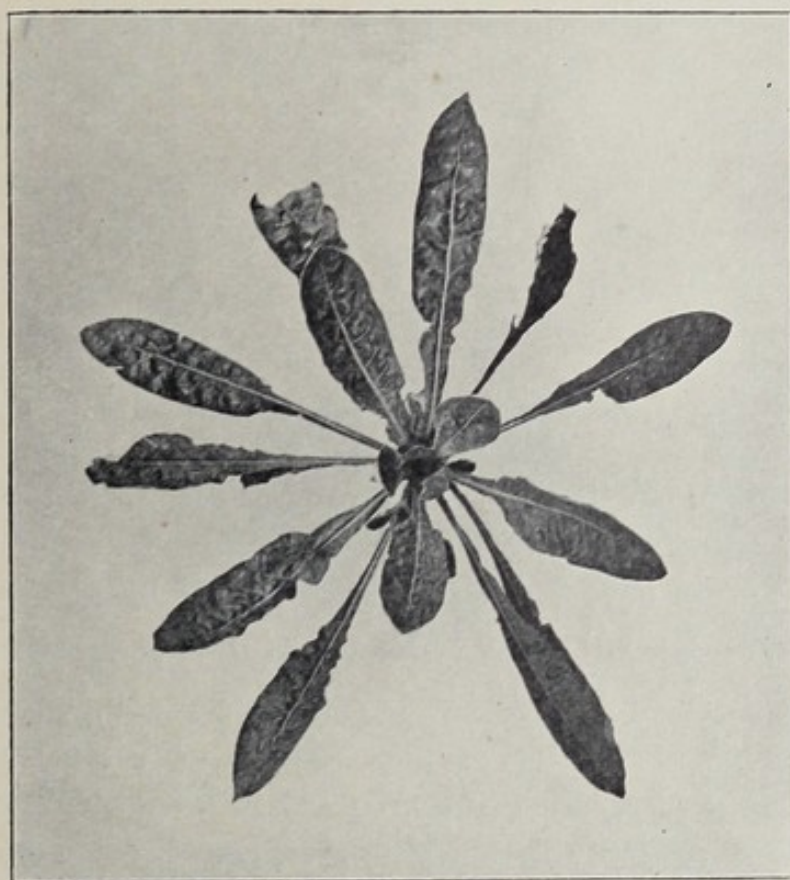


FIG. 57.—*Oe. incurvata*, second generation.

amount present in *rubrinervis* (type 7) together with a small amount on the hypanthium. The quantity of anthocyanin, however, in no way approaches that present in *rubricalyx*. Three of these plants, moreover, had buds like *grandiflora* in shape and pubescence, while in four others the buds were like typical *rubrinervis*.

The "comb. 7" of Heribert-Nilsson is the giant type already described, while "comb. 8" is almost certainly

a triploid mutant. In general, it may be said that Heribert-Nilsson's race of *Lamarckiana* shows greater variability than that of de Vries, while the *Oenotheras* from Birkenhead gave indications in our cultures of an even greater variety of forms. This would seem to show that continued inbreeding in *Oe. Lamarckiana*, by narrowing the network of descent as well as by eliminating many hybrids, tends to lessen the amount of variability exhibited. One may of course hold this view without subscribing to the doctrine (so obviously contradicted by the facts) that *Oe. Lamarckiana* is merely a Mendelian heterozygote throwing off recessive forms and new combinations of unit characters. The view here expressed also involves the blending and modification of many characters which are not inherited as independent units.

2.—*Mutations in Oe. grandiflora, Solander*

Oe. grandiflora from Tensaw, Alabama, where it was originally discovered, has been shown by our cultures and those of Davis (77, 79) to possess a considerable range of variability. In 1910 we grew 55 plants from this source, and they included two aberrant rosettes (see Fig. 58, *a* and *b*) which did not mature. In 1911 pure seeds from three of these plants yielded a total offspring of 480. These were grown under crowded conditions only a few inches apart, so that they produced very spindling stems, and their characters were not fully developed. But they exhibited considerable variation in width of leaf and in amount of crinkling. In 1912 a fresh sowing of seeds from Alabama yielded 221 plants, which were quite uniform with the exception of two individuals. One of the latter was a dwarf, having an unbranched stem only two feet high. The other aberrant differed in its foliage, which was somewhat crinkled and curled and darker green than in normal *grandiflora*. It is thus evident that *Oe. grandiflora*, when

derived directly from the wild condition, is capable of producing dwarfs and other aberrant forms.

In seeds from the same locality, Davis obtained four distinct types of *grandiflora*, and from one of these types

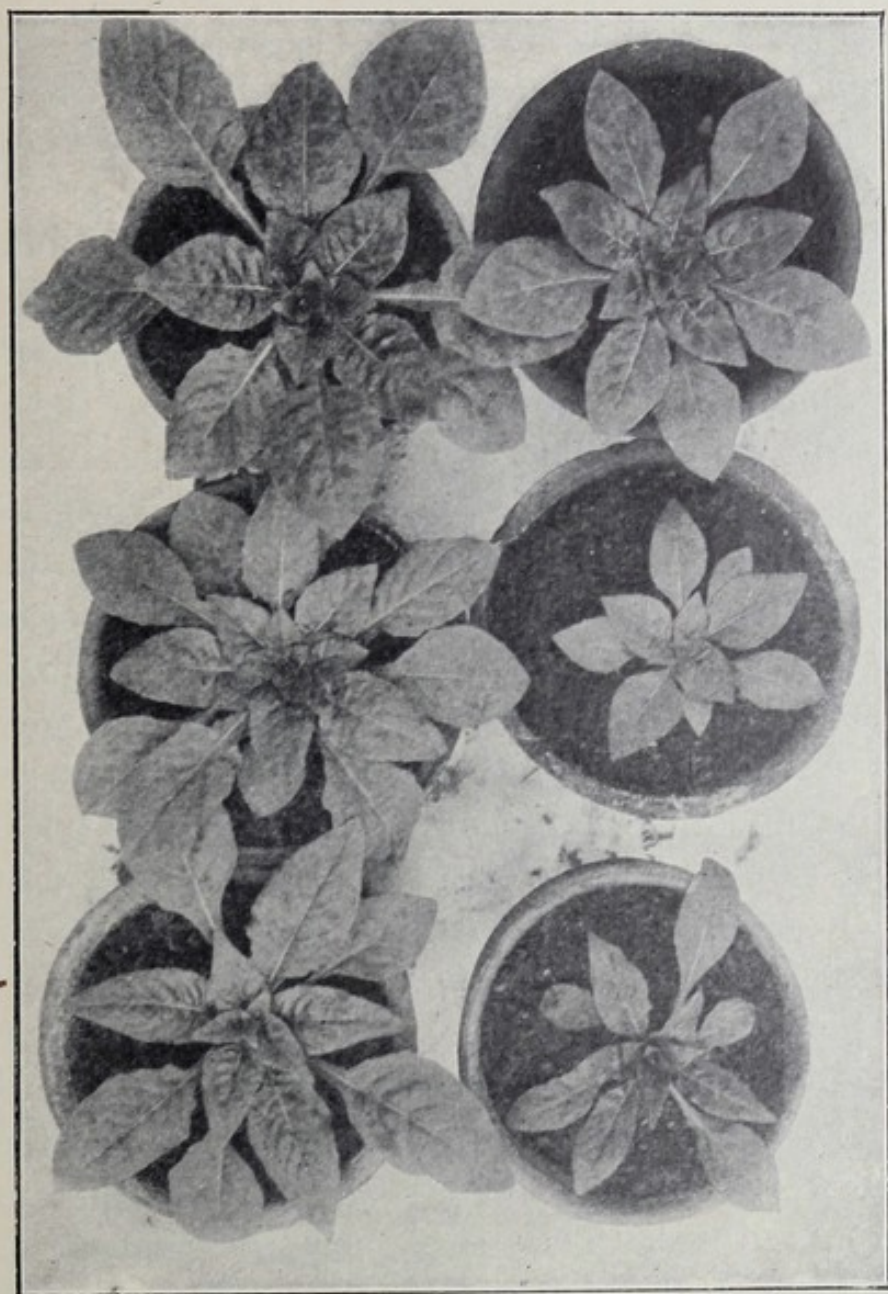


FIG. 58.— *Oe. grandiflora*, young rosettes ;
a and b aberrant.

which proved stable he afterwards differentiated three strains. These types differed chiefly in foliage and in the colour pattern of their sepals. His culture, moreover, contained, in addition to 127 *Oe. grandiflora*, 42 *Oe. Tracyi*,

which resembles a small-flowered *grandiflora*. The presence of this species probably accounts for the greater variability of his plants than the author's, for de Vries and Bartlett have since visited the type locality and found that the two species are freely intercrossing there.

In this connection it is desirable to describe the results of certain cultures made with a race received from the Nantes Botanic Garden under the name *Oe. suaveolens*, Desf. From these seeds we grew in 1911 a progeny of 192 plants, and from another sowing in the following year 29 plants more. They were very variable, but belonged chiefly to two types which most nearly resembled *Lamarckiana* and *rubrinervis* in foliage, though the leaves were nearly smooth. Many of them exactly resembled in foliage some of my F_2 hybrids of *grandiflora* \times *rubricalyx*, and there is little doubt that these plants were descended from garden crosses between forms of *Lamarckiana* and *grandiflora*. They had also probably been crossed at some time with a race of *Oe. biennis*, for the family contained, in addition to a dwarf and several other aberrants, several plants with short styles and somewhat smaller flowers. In the earlier flowers on these plants the stigma was below the anthers, hence intermediate between *biennis* and *brevistylis*; in the later flowers the stigma reached to the base of the anthers. One of these plants yielded a total offspring of 96 individuals, nearly all of which possessed a short style, though it varied much in length and in a few plants was above the anthers. The petals also fluctuated in size between *biennis* and *Lamarckiana*. Among other variations, this family contained a plant having the peculiarities of *lata*, showing that the unequal distribution of chromosomes occurs also in these hybrids. Another short-styled plant in the above family gave also 33 offspring, nearly all of which showed this peculiarity. In these cultures also occurred a number of plants, probably

diseased, having sickle-shaped leaves with the mesophyll developed chiefly on one side of the midrib.

In experiments with the Birkenhead *Oenotheras*, several races belonging to *Oe. grandiflora* were differentiated, and one of the races was found to produce dwarfs regularly in the proportion of 7·6 tall to 1 dwarf. The latter were shown to breed true. This behaviour will be referred to again (see p. 227).

3. *Mutations in Oe. biennis*, Linn.

In 1912, we grew a race of *Oe. biennis* obtained from the Madrid Botanical Garden under the name "*Oe. longiflora*," which produced a series of forms parallel in part to the mutants derived from *Lamarckiana* (140). The culture numbered 131 plants, and the race had no doubt undergone crossing at some time with a large-flowered form. The plants were distributed as follows:—

(1) " <i>Lamarckiana</i> " type	23 plants
(2) " <i>rubrinervis</i> " or red-veined type		
(Fig. 59)	91 plants
(3) <i>biennis lata</i> , with pink midribs (Fig. 60)		1 plant
(4) " <i>Lamarckiana</i> " type, but with finely		
crinkled leaves	1 plant
(5) " <i>lævifolia</i> " type	6 plants
		<hr/> 122

Types (1) and (2) differ, as in the race of *Oe. Lamarckiana* from the Isle of Wight (see p. 79), only in having red or white midribs, the difference being probably inherited as a Mendelian character. Type (3) has the characteristic foliage and sterile pollen of *lata* and the small flowers of *biennis*, as well as 15 chromosomes (see also p. 179). It is, therefore, a precise parallel to *Lamarckiana lata*. Type (4) is not exactly like any known mutant of *Lamarckiana*. Type (5) resembles *lævifolia* in having long, narrow, pointed, furrow-shaped and less crinkled leaves, but its flowers varied greatly in size and had an extensive



FIG. 59.—*Oe. biennis*, race from Madrid Botanic Garden, red-veined type.



FIG. 60.—*Oe. biennis* mut. *lata*, from Madrid race (cf. Fig. 59).

colour-pattern (7) on the sepals with a little red on the hypanthium.

The offspring of these plants were grown in 1913, and were of much interest. Type (1) bred true, producing 90 rosettes which were exactly like the parent plant. The mature rosettes closely resembled *Lamarckiana*, though when half-developed they were less crinkled. Type (2) yielded only seven offspring, four of which had red midribs, three white midribs. The latter had buds smooth and rounded like *grandiflora*, one with large flowers and two with small. This perhaps indicates the ancestors of the cross. Type (3) was crossed with pollen from type (1) and furnished nine plants, two with pink midribs (type 2), five type (1), and two *biennis lata* type (3). The last, no doubt, had 15 chromosomes, though they have not been examined in these individuals. Type (4) yielded 14 plants all like their parent in the fine crinkling of their leaves. Type (5) gave 150 plants which exhibited great variability. The rosettes varied from crinkled to smooth, red midribs to white, leaves narrow to broad, with one resembling *oblonga*. The flowers, however, in the 38 plants which bloomed, showed the most interesting features. The buds were exactly alike in all, except that the petals varied greatly in size. The length of petal was practically constant for each plant, but in different plants the sizes were as follows :—

TABLE X.
Length of Petals in *Oe. biennis laevifolia*.

Length of petals.	Number of plants.	Length of petals.	Number of plants.
12 mm.	1	21 mm.	1
14 "	1	22 "	1
15 "	2	24 "	4
16 "	2	25 "	1
17 "	1	26 "	1
18 "	3	28 "	1
19 "	3	38 "	1
20 "	2	43 "	1

The size of petal, therefore, varied from as small as in *Oe. muricata*, to rather larger than in *Lamarckiana*. The nature of the inheritance of this feature should afford a study of much interest. The plant used as seed-parent for this culture had flowers about the size of those in *biennis*. This suggests a condition similar to the one obtained by East in *Nicotiana* (97).

That wild races of *Oe. biennis* will produce mutants is shown by the fact that a study of the pollen development in material collected at Woods Hole, Mass., in 1905 (124) disclosed several cases in which eight and six chromosomes respectively were distributed to the nuclei in the reduction division. Davis afterwards (76), from material also collected in the same locality, found two cases of the same irregularity. These are potential mutations, and would no doubt give rise to *lata* mutants as in the cultivated race above described. The possibility of crossing in the Woods Hole race appears to be very remote. Hence it must be concluded that wild American races of *Oe. biennis* can produce mutations.

A pure strain of *Oe. biennis*, L., from Wykaan-Zee and another of *Oe. biennis cruciata* from Santpoort, Holland, were crossed reciprocally by Stomps (351) in 1909. In both cases the F_1 had the broad petals of *biennis*, while the F_2 split into the two types. In addition, in *Oe. biennis* \times *Oe. b. cruciata* F_2 appeared one dwarf, *Oe. biennis nanella*; and in the reciprocal F_2 one *biennis semigigas* mutant having 21 chromosomes. It will require more extensive cultures of the pure races to determine whether the mutations occurred as a consequence of the disturbance of equilibrium in the germ plasm caused by crossing. But that hybridisation is not the *only* means by which such germinal changes can be induced, is shown by the fact that de Vries obtained a dwarf mutant, *Oe. biennis cruciata nanella*, in a culture of 500 plants of *biennis cruciata*

which had bred true for two generations. The mutant gave two offspring, both dwarfs.

Since the foregoing paragraph was written, Stomps (354) has published an account of several mutations in the pure race of *Oe. biennis* above-mentioned. In 1913 he grew 430 plants of the third generation and 490 of the fourth generation descended from a single rosette of *Oe. biennis* dug up at Wykaan-Zee in 1905. These had been purely self-pollinated in each generation. The 920 individuals grown in 1913 contained six mutants as follows: In the F_3 culture there was one *biennis nanella*, one *biennis semigigas* with 21 chromosomes, and one *sulphurea*. The F_4 family included three *sulphurea* mutants. Hence the type of *Oe. biennis*, which has continued constant as naturalised in Holland for three centuries, produces occasional mutants (0.65 per cent.), including the very interesting variety *sulphurea* of de Vries. This variety was first recognised by Hermann in *Hort. Lugd.-Bat.* under the name *Lysimachia corniculata non papposa, Virginiana major, flore sulphureo*, in 1687 (see p. 66). Linnæus also recognised it in the *Hort. Cliff.* 1737. By this time it was no doubt established in Holland along with the parent form which has retained ever since the capacity of producing it occasionally. Such facts as these furnish incontrovertible evidence for the mutation theory. Whether *Oe. biennis* was producing mutations before it was taken to Europe is not certain, but this was probably the case, since other American races, referred to above, possess this capacity in their native habitats.

MacDougal (253) found that *Oe. cruciata* from the Adirondacks had a wild variety, which also appeared in cultures. And de Vries (425) has obtained dwarf mutants several times in hybrid races as follows: (1) The fourth generation from *Hookeri* \times *biennis* contained 64 *Hookeri* and six *rubienis*, one of the latter being a dwarf. (2) *Hookeri* \times *biennis* in another cross gave similar results

in F_3 , with one dwarf in 75 plants. The pollen of the *biennis* parent is considered to have been responsible for both these mutations. (3) *Oe. cruciata*, Nutt., \times *Oe. biennis cruciata*, in an F_2 numbering 60 plants, contained one dwarf. (4) In the same cross another dwarf appeared in an F_2 numbering 45 plants.

A race of *Oe. biennis* collected by de Vries in Chicago, and afterwards at Courtney on the Missouri River, was found in the latter locality to have produced a single aberrant among a large number of normal plants. This mutant differed from the rest in having nearly linear leaves, smaller flowers, and thinner fruits. Seeds were collected from this and from surrounding plants, and they yielded respectively 140 and 110 offspring, one of the former and four of the latter belonging to the new type. These were found to differ among themselves, one kind having smooth and the other wrinkled leaves. Pure seeds from each showed that they bred true, the offspring numbering respectively 197 and 293. The smooth-leaved mutant was called *salicastrum*, and the other was found to correspond to a form called by MacDougal *salicifolia*. Such observations as these and the cases previously cited remove the cogency from the argument that mutations are in some way a result of cultivation.

4.—Mutations in *Oe. muricata*, Linn.

Mutations have also been observed from this species, though they are much more infrequent than in *biennis*. A taller, stouter mutant with larger leaves and flowers (perhaps triploid) appeared in a culture of 36 plants from a pure race in Zandpoort, Holland, in 1905 (425), and a similar plant afterwards occurred in *Oe. cruciata* \times *muricata*. Another type appeared in *Oe. muricata* \times (*biennis* \times *muricata*), a hybrid race having the features of pure *muricata*. This mutant had small, very narrow

leaves (6.5 cm. wide), small flowers and reddish buds. De Vries's figure of it (425, Fig. 109, p. 303) shows it to have been, apparently, an exact parallel to a narrow-leaved mutant (see Fig. 61), which appeared in a culture



FIG. 61.—Mutant occurring in (*Oe. mut. rubricalyx* \times *grandiflora*) \times *grandiflora*.

of (*Oe. mut. rubricalyx* \times *grandiflora*) \times *grandiflora* in 1912 (154). The family numbered 134 plants, and this individual was strikingly different from all the others. The characters of the main body of hybrids corresponded with expectation, while the peculiarities of this plant were wholly unexpected and unpredictable. This is, of course, one of the marks of a mutation in contradistinction to a hybrid.

5.—Mutations in hybrids

A number of obvious instances of mutations in hybrids have already been mentioned. In fact they frequently, though not invariably, appear in races which have undergone crossing. Indeed, one effect of crossing appears to be to induce a tendency to the more frequent production of germinal variations, by disturbing the balance of conditions within the organism. In concluding this chapter, we shall refer to only one more case of mutations in hybrids. Several other instances of a

somewhat different kind will be considered in Chapters VII and VIII.

Numbers of triploid mutants have been obtained by de Vries (425, p. 324 ff.) in crosses between *Lamarckiana*, *nanella*, *rubrinervis*, *lata*, or *oblonga* as seed parent, and such species as *cruciata*, *muricata*, or *Millersi* as pollen parent. In all these crosses the hybrids are, for the most part, slender plants with yellowish foliage. But occasionally much larger, stouter plants appear, which are easily recognisable by their dark green foliage. These plants, after the usage of Darwin in his experiments on *Ipomœa purpurea*, were called Hero, and have since been found by Stomps (352) to be triploid mutants having 21 chromosomes. The experiments may be summarised in the following table (XI) :—

TABLE XI.
Triploid Mutations in Crosses.

Cross.	Number of offspring.	Hero.
<i>Oe. Lamarckiana</i> × <i>cruciata</i>	6,760	15
<i>Lamk. derivatives</i> × <i>cruciata</i>	900	10
<i>Lamarckiana</i> × (<i>muricata</i> × <i>cruciata</i>) ..	150	2
<i>Lamarckiana</i> × <i>muricata</i>	4,850	4
<i>Lamk. derivatives</i> × <i>muricata</i>	1,360	4
<i>Lamk. derivatives</i> × <i>Millersi</i>	1,658	9
(<i>Lamarckiana</i> × <i>biennis</i> Chicago) <i>velutina</i> × <i>Millersi</i>	140	1
	15,818	45 = 0.3%

Hence in these crosses triploid mutants occur with a frequency of about 3 in 1,000.

In contrast with other species of *Oenothera*, *Oe. Hookeri* appears to be more constant in cultures. In a family of 133 plants we found great uniformity, though there was some variation in width of leaf and amount of pubescence. Among 369 plants of var. *irrigua* were found three individuals with crinkled leaves, and one rosette having broad leaves with very blunt tips. But this species hitherto has

not exhibited a series of mutations parallel to those of *Lamarckiana* and *biennis*. Examination of the pollen shows very few bad grains, probably not more than 10 per cent., while in *Lamarckiana* and probably also in *biennis* the percentage is nearer 50 per cent. The greater frequency of good grains indicates that the meiotic processes less frequently go awry: *Oe. Hookeri* has not



FIG. 62.—Sectorial chimera in a race of *Oe. Lamarckiana*.

yet been examined cytologically, but it may be that the heterotypic chromosomes are more closely paired than is known to be the case in *Oe. Lamarckiana* and *Oe. biennis*, and that it is therefore less easy for the meiotic mechanism to be thrown out of balance.

Many other types of mutations frequently occur in *Oenothera* cultures. As instances of these, mention may be made first of a sectorial chimera (Fig. 62) which appeared



FIG. 63.—Virecence in *Oe. multiflora*.

in 1909 in a culture of 55 *Oe. Lamarckiana* plants derived from Lancashire (133). One side of this rosette was white, being devoid of chloroplasts. On the other side of the rosette some of the leaves were entirely green and some green on one side of the midrib and white on the other. This mutation probably occurred in the growing point of the young embryo, through the loss of chloroplasts from

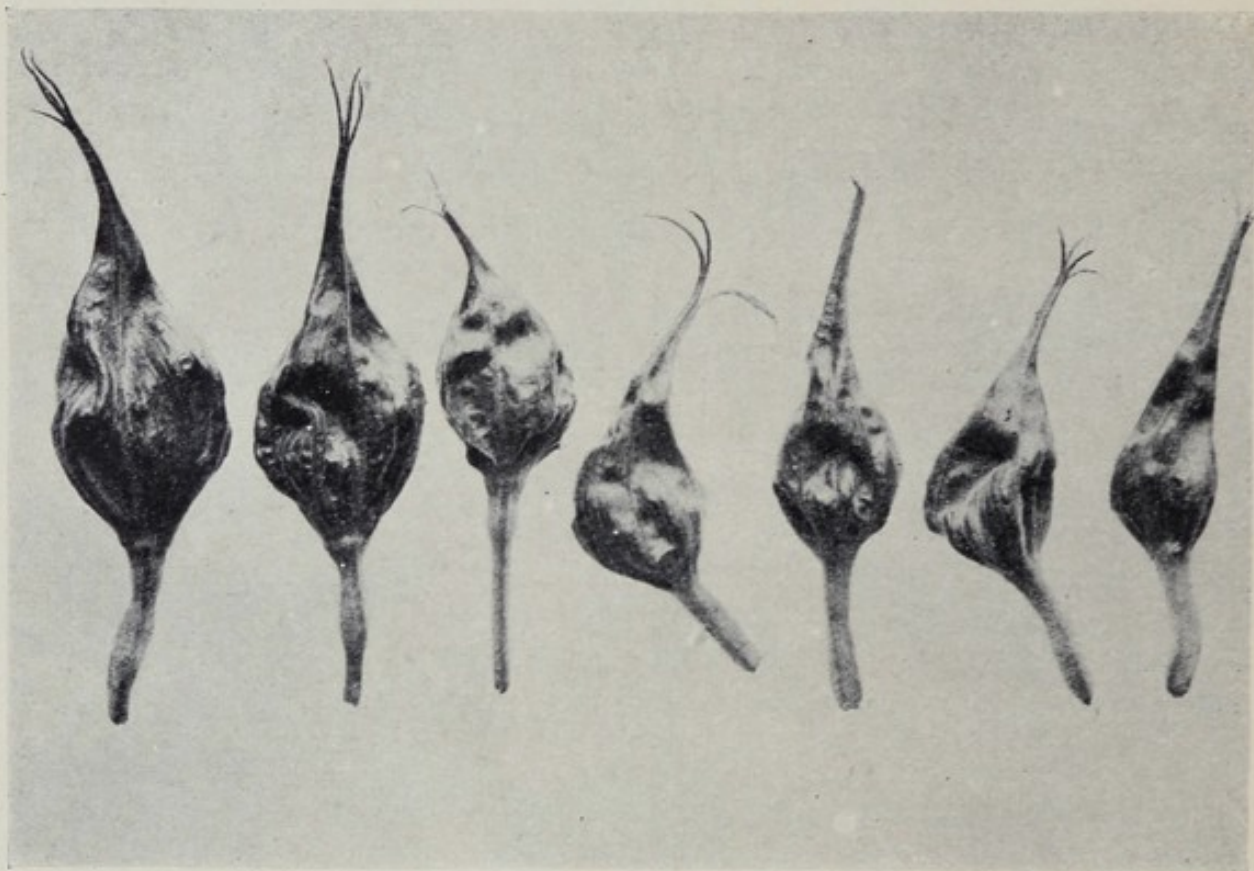


FIG. 64.—Virescent buds, showing baggy calyx and absence of hypanthium.

some of the cells in an unknown manner. In 1912, a periclinal chimera, partly devoid of chloroplasts, developed to maturity from the *Lamarckiana* race from Lancashire. Another interesting variation occurred (133) in a race from Lancashire, which we have called *Oe. multiflora*. Among 376 offspring of one individual, forming a nearly constant race, 15, or about 4 per cent., were virescent (Fig. 63). The virescence did not appear in the earliest flowers, and may have been due to the hot climate of

St. Louis, where the plants were growing. But they appeared only in this race (except a single case in a race called *Oe. Chilensis*), and as they appeared also in two generations the capacity for producing them was inherited. In a later generation of this race, grown in the English climate, they failed to appear, indicating that the high temperature probably acted as a stimulus to call them forth. The



FIG. 65.—Virescent flowers, showing various abnormalities.

peculiarities of the virescent buds are shown in Fig. 64, and of the opened flowers in Fig. 65. The sepals are green and baggy, the hypanthium completely fails to develop, though a woody stalk frequently develops below the ovary, the petals are rudimentary, and the style slender and pubescent, tapering to a point. Frequently such a flower develops into a short side-branch, with a group of narrow leaf-like organs in the centre of the flower, and sometimes even internodes are formed.

CHAPTER VI

THE CYTOLOGICAL BASIS OF THE MUTATION PHENOMENA

It is evident that every mutation is the result of a change in the constitution of a particular cell or cells. One may expect this change to be in the great majority of mutations either ultramicroscopic or chemical in character, and hence invisible to the observer of the cell. Indeed, the only instances yet known in which a visible alteration in the structure of the cell has taken place are those which involve a change in the size of the cell as a whole or in the chromosomes of the nucleus.

In dwarf mutations, one of the most fundamental changes involved is a general reduction in the size of the cell, although this takes place unequally in different tissues. The chromosome-number, so far as is known, remains unchanged. Conversely, constitutional giantism, among plants at any rate, involves a marked increase in cell volume. This increase is usually accompanied by a doubling, or a partial doubling, in the number of chromosomes. In certain instances, however, cell giantism appears without any change in the number of chromosomes. This has been shown by Gregory (164) and Keeble (210) to be the case in certain giant races of *Primula*, though tetraploidy occurs here as well (88, 165).

Another type of change in chromosome-number takes place in the *lata-semilata* series of mutants in *Oenothera*. This consists in an increase of one in the chromosome-number, through a chromosome entering the wrong

nucleus at the time of the meiotic distribution of chromosomes. This type of mutations will probably be found in other plants having cytological peculiarities similar to those of *Oenothera*. It is a notable fact, which will be discussed later, that in the offspring of crosses in several other genera, giants and dwarfs appear.

It may be pointed out that although only a portion of the mutants from *Oe. Lamarckiana* exhibit visible changes in their nuclear structure, yet these cases have thrown much light upon the nature of the mutation process. By exhibiting the character of the visible changes which have occurred, they give an important clue to the nature of the alteration involved in each case. The determination of the chromosome-number is also obviously important in those cases where it remains unchanged. The fundamental number of chromosomes in *Oenothera*—14—has become in *lata* and *semilata* 15, in *semigigas* 21, and in *gigas* 28. Various intermediate numbers are derivable by crossing, by double mutations, and by further chromosome changes in the offspring of mutants. Several of these new numbers have already been recognised. Thus plants have been described having 16, 20, 22, 23, 24, 27, 29, and 30 chromosomes.

The first discovery in this field, made by the writer (116) in 1906, indicated about 14 chromosomes in one plant and 20 in another. The latter number was afterwards confirmed, but the former count, which was in *lata*, has since been shown by the work of Miss Lutz (241), the writer (141), and Miss N. Thomas (153) to be 15. On the basis of this observed difference in number we concluded (116) in 1907 that "some process of differentiation, the most probable seat of which is the germ plasm, has led to the production of distinct types of germ cell [in *Oe. Lamarckiana*] differing in chromosome morphology and in hereditary value." This view remains essentially correct in the light of the later work, but, as will be seen

from Chapter IX, it now requires considerable amplification.

1.—*The Process of Cell Division*

To make clear the nature of the continuity between a cell and its descendants, the following brief account is given of mitosis as it occurs in the cells of the nucellus (ovule) of *Oe. mut. lata*. The various stages are represented in Fig. 66. In the so-called "resting" condition of the nucleus its stainable substance forms a network or reticu-

FIG. 66.—SOMATIC MITOSIS IN THE NUCELLUS OF *Oe. lata*.

- a. Resting nucleus, containing a uniform moniliform network.
- b. Cell showing the earliest prophase stage of the nucleus. Certain threads of the network are becoming thicker and more markedly moniliform.
- c. The distinction between the thicker and the more delicate threads is becoming more apparent.
- d. First appearance of chromosomes, as long and coiled bodies.
- e, f. The chromosomes are shorter and thicker, but portions of the fine network still remain.
- g. Only the chromosomes (15) and the nucleoli are visible, embedded in the transparent nuclear gel.
- h. Showing chromosomes more evenly distributed in the nucleus.
- i. A nucleus in two foci, showing the 15 chromosomes which are shorter and thicker.
- j. A nucleus in two foci showing the 15 chromosomes all split lengthwise.
- k. The split in the chromosomes has closed up, the nuclear membrane has disappeared and in its place the spindle is beginning.
- l. The spindle just before metaphase.
- m. Polar view of metaphase showing the 15 chromosomes.
- n. Same as last; *a* is the odd chromosome.
- o. Early anaphase, showing the two daughter groups of chromosomes in polar view.
- p. Later anaphase in profile view; the spindle fibres are now parallel.
- q, r. The chromosomes have reached the poles and granular thickenings are appearing in the median region of the spindle.
- s. The chromosomes have formed a compact group at the poles.
- t. A membrane has developed around the daughter nuclei and the chromosomes are constricted into dumb-bells.
- u. Telophase nucleus showing the chromosomes.
- v. Later telophase; the nucleus has grown in size and the constriction in the chromosomes has disappeared.
- w. Showing two daughter cells; the chromosomes have begun to anastomose with each other.
- x. Further growth of the nucleus and anastomosis of its chromosomes.
- y. A network is being formed, but the centres of the chromosomes still remain condensed.
- z. Complete resting condition as in *a*.—From the *Annals of Botany*.

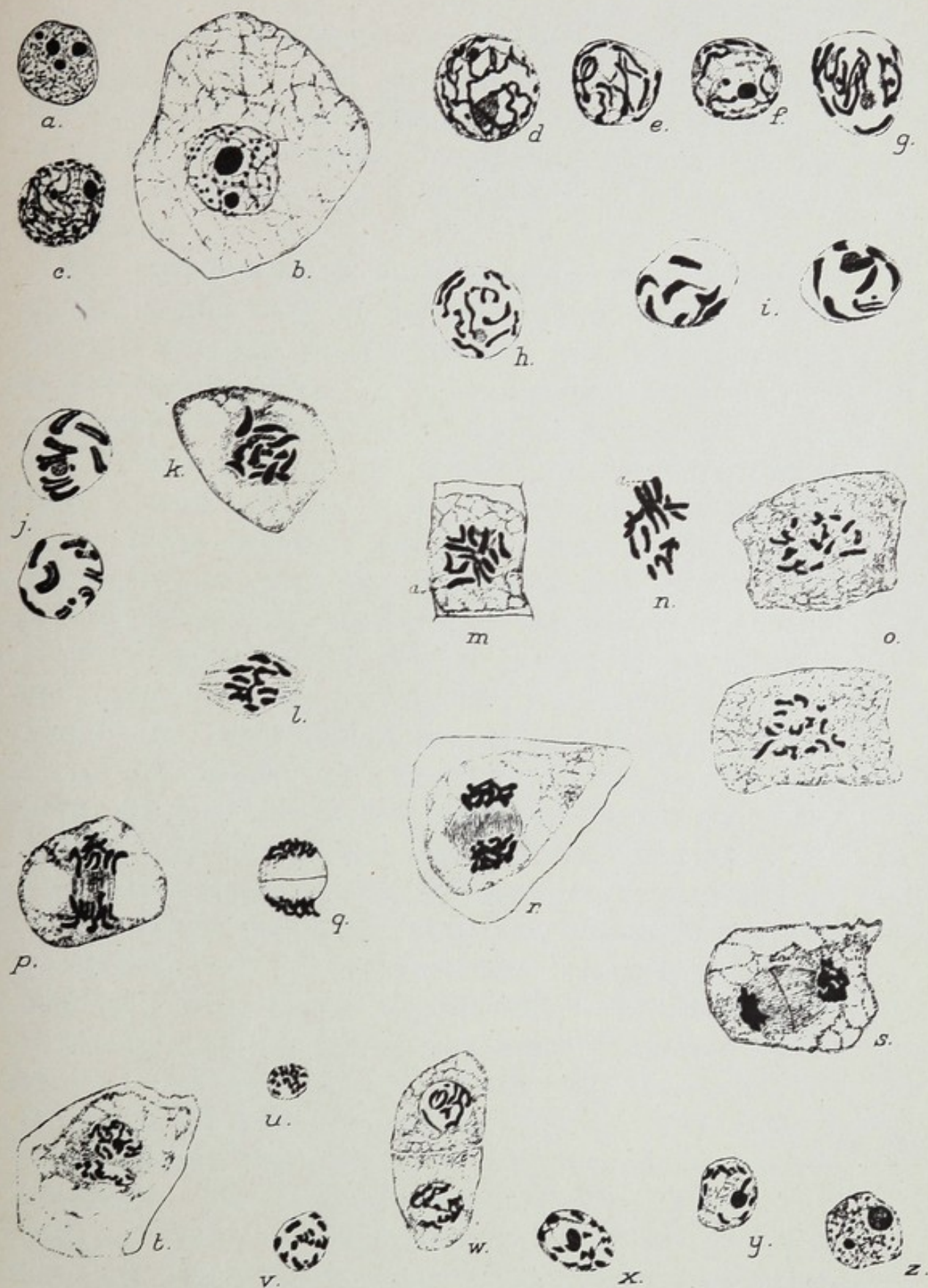


Fig.66.

Mitosis in the nucellus of *Oe. lata*.
From the *Annals of Botany*.



lum in which the threads are more or less moniliform, like chains of delicate beads. The spaces between these threads are filled with a transparent, colourless gel or jelly, in which are also suspended one or more globular nucleoli, and the whole structure is enclosed by a definite nuclear membrane.

The first indication of approaching division appears in the enlargement of certain nuclear threads at the expense of others (*b*, *c*). Precisely how this takes place is not entirely clear. The threads may be thought of as interstices or spaces in the nuclear gel, and it appears that in some cases several of these are swept together to form a coarser thread, or the material may perhaps flow from certain spaces to others. In this way the chromosomes (15) are first formed as long and twisted thick threads lying mostly just within the nuclear membrane (*d-f*). There is thus a distinct peripheral movement of chromatin substance during the prophases of division. Finally, the remnants of fine threads disappear, being apparently taken into the chromosomes (*g*, *h*). The latter are now curved rods suspended in the gel. They shorten and thicken (*i*) and then split lengthwise (*j*). The nucleoli meantime remain apparently unchanged.

Towards the end of these processes, portions of the cytoplasm around the nuclear membrane become modified into wefts of delicate fibrillæ (*k*), the split in the chromosomes closes up, and the nuclear membrane disappears. The chromosomes now become arranged on the spindle (*l*) formed by the delicate cytoplasmic fibrillæ, and are finally drawn into one plane (*m*) at right angles to the long axis of the spindle. This is the metaphase of mitosis. The chromosomes at this time are frequently though not always in pairs (*n*), and the pairing can sometimes be seen earlier, in the prophase. The paired arrangement seems to arise during prophase, and there is no distinct evidence that the chromosomes are paired when they first appear.

In metaphase the chromosomes split lengthwise and in anaphase move towards the poles of the spindle (*o-r*). At the poles they form a close group, while indications of the new cell-wall appear as thickenings of the spindle fibres (*s*). A nuclear membrane is then formed around each daughter nucleus, enclosing the chromosomes, and the latter begin to be separated by transparent substance appearing between them (*t*). At this time the chromosomes are distinctly dumb-bell shaped, owing to a median constriction (*u*) which is, however, only of temporary duration. The daughter nuclei now grow in size (*v*), the chromosomes lose their constriction and begin to anastomose with each other (*w*). Fresh nucleoli are developed in the nucleus meantime (*x*), and by continuation of the process of loosening up of the chromosomes (*y*) a network is finally formed as before (*z*), and the nucleus then grows to its original size, when it is ready to divide again. The chromosomes are thus split lengthwise in each mitosis, and so passed on to the daughter cell, where they grow to their previous size. The nucleoli and all other parts of the nucleus on the other hand originate *de novo* with each mitosis, and the cytoplasm undergoes merely a mass division.

2.—*The Meiotic Processes*

Before discussing some of the details of the work with chromosomes, we may first examine the meiotic processes as they occur in *Oenothera*, for it is evidently during meiosis that many of the germinal changes occur. That the method of chromosome reduction in *Oenothera* involves the telosynaptic or end-to-end pairing of the chromosomes is agreed by all investigators of the subject. We first described this process in detail as it occurs in the pollen mother cells, in 1908 (119), and that description, with selected figures, and the amplifications of subsequent



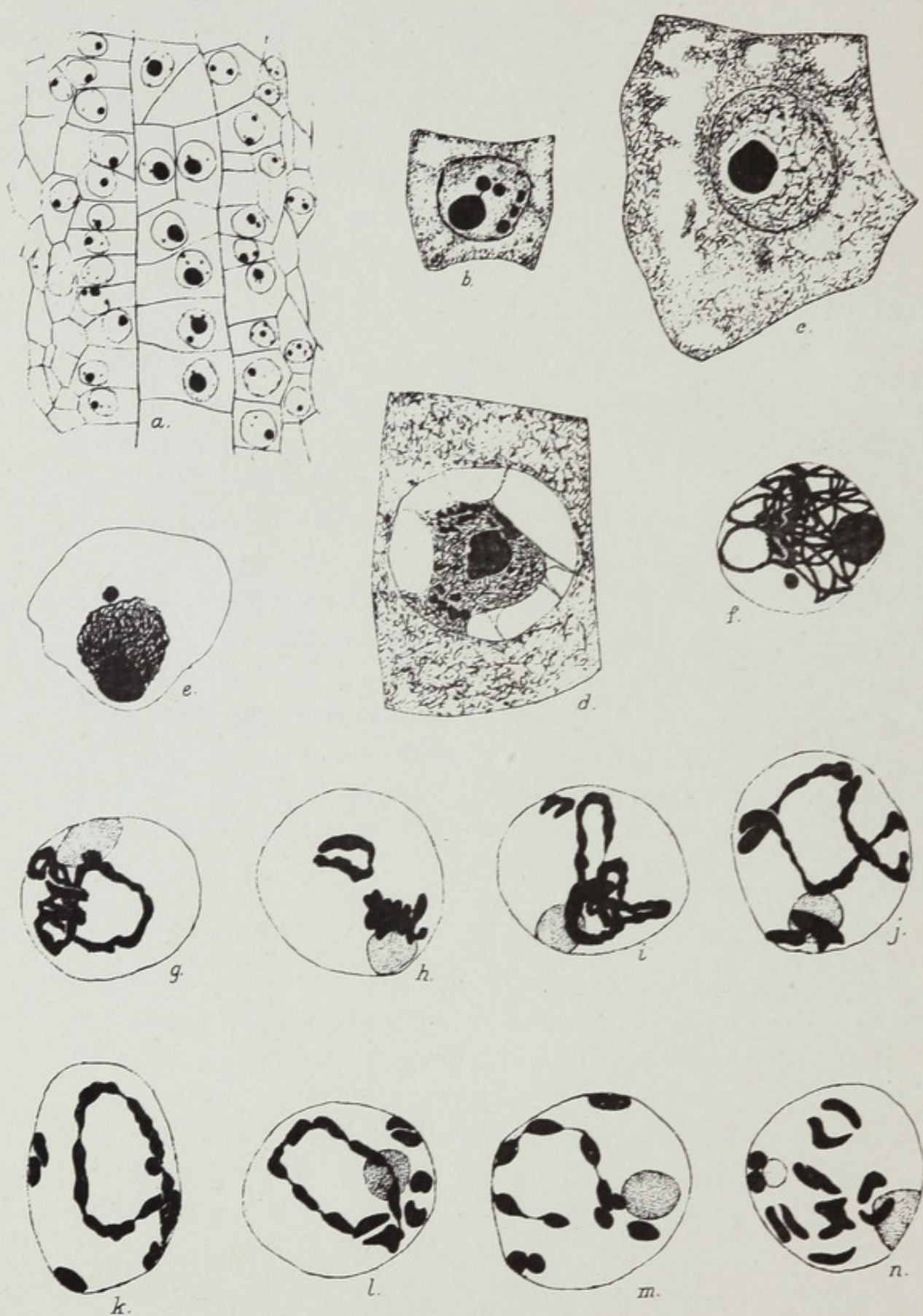


Fig.67.

Meiosis (early stages) in the pollen mother cells of *Oe. rubrinervis*.

From the Botanical Gazette

study, will form the basis of the present condensed account. Selected stages are shown in Fig. 67.

The archesporial cells are at first undifferentiated from the other cells of the anther, and all are quite small (Fig. 67, *b*), the nucleus containing usually one larger nucleolus and a variable number of small, dark-staining bodies for the most part peripherally arranged. Then the anther becomes differentiated into a central axis of sporogenous tissue surrounded by a single layer of tapetal cells in the form of a cylinder, around which are a variable number of wall layers enclosed by an outer epidermal layer (*a*, lower magnification). The axis of sporogenous tissue is composed of cells which enlarge enormously in size. This enlargement is accompanied by a corresponding growth in the size of the nucleus and the nucleolus, so that the nucleus is now as large as the whole cell in the

FIG. 67.—STAGES OF MEIOSIS IN *Oe. rubrinervis*.

- a.* Longitudinal section of anther, showing central row of sporogenous cells with larger nuclei and very large nucleoli.
- b.* Meristematic cell of young anther.
- c.* Later spore mother cell, showing growth in size and fusion of smaller nucleoli previous to synapsis.
- d.* Beginning of synapsis; the nucleus suddenly expands, a few threads remaining attached to the nuclear membrane.
- e.* Completion of synapsis; the nuclear network re-arranges itself into a more or less continuous thread, which contracts into a compact ball.
- f.* After synapsis the thread spreads out and becomes shorter and thicker.
- g.* Thread much shorter and thicker, entering upon the second contraction.
- h.* Second contraction, a pair of chromosomes precociously cut off from the thread.
- i.* Spireme uncoiling from second contraction.
- j.* Spireme segmented in three places, each segment showing constrictions which will form the chromosomes.
- k.* Constriction of spireme farther advanced; chromosomes elongated, connected by bands of linin.
- l.* Spireme segmented, showing chain of 8 chromosomes and 3 pairs. The chromosomes are much shorter and denser.
- m.* The 14 chromosomes contracted into their globular or pear-shaped definitive form, with longer linin connections. Several are in pairs.
- n.* The 14 chromosomes are nearly all closely paired. This condition is exceptional in *Oenothera*.—From the *Botanical Gazette*.

archesporial stage. During this period one or two divisions of the sporogenous cells may take place, forming the pollen mother cells (Fig. 67 *c*). In the latter the processes of meiosis or chromosome reduction take place. The tapetal cells in the meantime also grow considerably in size, and in preparation for their glandular function of nourishing the young pollen grains their cytoplasm becomes dense and granular in appearance.

The pollen mother cells now enter the condition of synapsis, which is shown in its beginning in Fig. *d* and completed in Fig. *e*. At the beginning of the process there is a tendency for the chromatic material of the nucleus to accumulate in its periphery; and in *Oenothera* the nucleus frequently, if not always, undergoes at this time a rather sudden and marked increase in size (*cf.* Figs. *c* and *d*). The volume of the nucleus is more than doubled at this time, in some cases increasing by 138 per cent. Portions of the reticulum of the nucleus often remain attached to the nuclear membrane, but after this expansion has taken place the network is gradually rearranged into an apparently continuous thread or spireme, and the latter is contracted into the so-called synaptic knot (*e*) at one side of the nucleus. The nucleolus remains, and the rest of the nucleus, which appears empty, is occupied by a transparent gel.

It should be mentioned that at the time of synapsis the pollen mother cells separate from the tapetum and partly from each other, but they usually remain in contact at their ends. Rather large cytoplasmic connections occur between mother cells, sometimes a single one but usually several along each wall. They are doubtless formed by openings left at the time the cell wall is laid down, and through each passes a strand of cytoplasm (see Fig. 68, *b*).

The existence of these openings from one mother cell to another makes possible a curious phenomenon of





Fig.68.

Cytomixis and meiotic spindles in *Oe. gigas*.
From the *Annals of Botany*.

nuclear extrusion which sometimes occurs during synapsis. In many plants the synaptic nucleus moves to one side of the cell, and in *Oenothera* if the nucleus at this time comes in direct contact with an opening in the wall, chromatin may be extruded from the nucleus through the cell wall into the adjacent mother cell. Here it forms one or more viscous masses around which a clear area develops, limited by a more or less definite membrane (Fig. 68, *a*). We have called such structures pseudo-nuclei, and the process of extrusion cytomyxis (136). It usually occurs simultaneously and in the same direction throughout all the mother-cells of a loculus, so that each nucleus discharges chromatin into the cytoplasm of another mother-cell while receiving into its cytoplasm chromatin from a third. It seems that in some cases the nucleus after extrusion passes back to the centre of the cell, while the extruded material is gradually absorbed into the cytoplasm (Fig. 68, *b*). The meaning of this process is at present quite unknown. It was first described by Koernicke (219) in *Crocus*. A similar process, in which the nucleoli also took part, was described by Miss Digby (87) in *Galtonia*, and it will no doubt be found in other plants having cytoplasmic connections between their mother-cells. A very important point is whether nuclei in which

FIG. 68.—STAGES OF MEIOSIS IN *Oe. gigas*.

- a.* A row of pollen mother cells showing cytomyxis. Each synaptic nucleus comes to the edge of the cell and pours chromatic material into the next mother cell through openings in the cell wall, thus forming a pseudo-nucleus in the next cell.
- b.* A case in which this extrusion of chromatic material has taken place and the nuclei have moved back to the centre of the cell.
- c, d.* Heterotypic metaphases, showing the scattered and loosely-paired arrangement of the chromosomes.
- e.* Heterotypic anaphase; the lower pole of the spindle shows the full number of 14 chromosomes.
- f.* Later anaphase; several chromosomes have a median constriction.
- g.* Homotypic prophase, showing 14 bivalent or split chromosomes on the multipolar spindle.
- h.* Homotypic anaphase, showing the halves of the chromosomes moving to separate poles of the spindle.—From the *Annals of Botany*.

extrusion has occurred afterwards complete the meiotic processes.

The condition of synapsis, which is unique in the life cycle, is followed by the gradual progressive loosening, shortening and thickening of the spireme (Fig. 67, *f*), until, from resembling a ball of yarn, it becomes a short, heavy, tortuous thread in the nuclear cavity (Fig. *g*). The spireme, in the stage shown by Fig. *f*, is often moniliform in appearance owing to its containing alternate light and dark areas, and in certain stages there are indications that it is double owing to a longitudinal split.

After the thick thread (pachynema) is formed it undergoes a marked second contraction (Fig. 67, *h*) and then at once loosens up and is transversely segmented into the full somatic number of chromosomes. Stages in the constriction of the thread to form the segments are shown in Figs. *i*, *j*, *k* and *l*. Frequently, as in Figs. *h* and *i*, one or more pairs of chromosomes are cut off from the spireme precociously. With this exception the spireme is undoubtedly continuous in *Oenothera* during the greater part of its nuclear evolutions, and it is formed by the chromosomes joining hands, so to speak, and becoming arranged end to end.

This end-to-end or telosynaptic pairing is, we think, undoubtedly the method of synapsis in *Oenothera* and various other plants and animals. But we consider it probable that in some organisms the parasynaptic method occurs, involving the side-by-side pairing of long, delicate threads to form the bivalent chromosomes. This view, first expressed in 1908, has been considerably strengthened by the publications of the last few years and is now being adopted by several cytologists.

The chromosomes, when finally formed by the segmentation of the spireme in *Oenothera*, continue to shorten and thicken, but delicate linin connections remain between

them for some time (Fig. 67, *l*, *m*). Finally the nuclear membrane breaks down and the chromosomes become loosely arranged in the middle region of the heterotypic spindle, which has developed meantime in the cytoplasm (*cf.* Fig. 68, *c*). This stage is peculiar in *Oenothera* and a few other plants, the peculiarity being that, whereas in most plants the chromosomes are in regular alignment in pairs across the equator of the spindle at the heterotypic metaphase, in *Oenothera* the pairs are much less close and they are irregularly arranged. This applies, however, only to the heterotypic mitosis and leads to occasional inequalities in the distribution of the heterotypic chromosomes. For while the two members of each pair usually go to opposite poles of the spindle, occasionally both members of a pair will enter the same daughter nucleus. Thus in *Oenothera* the respective nuclei in this, the reduction division, get eight and six chromosomes instead of seven and seven, in possibly about 1 per cent. of cases.

While the chromosomes are moving towards the poles of the heterotypic spindle they usually split lengthwise, but the two halves remain closely in contact during the interkinesis between the two meiotic divisions and in the prophase of the second or homotypic division. After the appearance of the two homotypic spindles in each pollen mother cell, the halves of the chromosomes separate. There is no growth of the chromosomes during the brief period of interkinesis. What happens, or what interchange takes place among the chromatin particles during the unique condition of synapsis and the subsequent evolutions of the spireme, is unknown, but the general visible result of the heterotypic mitosis is the segregation of the somatic chromosomes which were very loosely arranged in pairs, while the homotypic mitosis merely separates the halves into which the heterotypic chromosomes split. The homotypic division therefore differs from an ordinary mitosis in that it is partly telescoped into the previous mitosis. Fig. 68, *c*

to *h* shows stages of the heterotypic and homotypic mitoses in *gigas*.

Since the chromosomes are now known to be paired in the metaphase of somatic mitosis in many plants and animals (including *Oenothera*), it cannot be assumed, as was formerly done, that the function of synapsis is to bring about this pairing of maternal and paternal elements. The condition of synapsis is unique and is known to be practically co-extensive with sex itself, so it doubtless has some fundamental significance in preparation for the chromosome reduction, but that significance is at present obscure. It appears from recent work that the transparent, colourless part of the nucleus (the so-called "karyolymph"), which was usually considered to be liquid, is really a gel, and it may be that this substance has an unsuspected importance in connection with the synaptic condition. In any case, one cannot regard the chromatin as any more "living" than the invisible gel.

A few words may be devoted to the history of the tapetal cells. During synapsis the pollen mother-cells begin to separate from the tapetum, and at this time the tapetal nuclei simultaneously undergo a mitotic division so that all the cells become binucleate. Later, while the mother-cells are undergoing the heterotypic mitosis, the tapetal nuclei divide again mitotically. Bonnet (36) has made the interesting suggestion that these two mitoses of the tapetal nuclei correspond with the reduction divisions of the pollen mother cells. There are certain difficulties in this view; (1) the absence of synapsis in the tapetal nuclei, (2) the fact that both mitoses are of the ordinary somatic type. They are also completed some time before the reduction divisions, and are followed by further divisions of the tapetal nuclei.

A peculiarity of the nucleoli in the tapetal nuclei is that they frequently become elongated into a rod and then

constricted into two bodies. This is presumably prior to a mitotic division, but it suggests amitosis.

The second division in the tapetum is of interest because the two spindles are very much crowded in the small tapetal cells, and often two of their poles may come so close together that two groups of chromosomes in the telophase form a single nucleus, thus making only three nuclei, having different chromosome contents, in the cell. Other irregularities may also occur. The relatively large nuclei often come into contact and their nuclear membranes become flattened against each other, giving the false appearance of having originated by amitosis. But the first two divisions appear always to be mitotic.

Later, the tapetal cells are found to contain a group of seven or eight or more small nuclei, and these may perhaps arise by amitosis or fragmentation. This multinucleate condition is found in the tapetum at the end of the meiotic divisions and before the pollen tetrads have broken out of the mother cell. Still later, while the pollen grains are undergoing their growth, the tapetal nuclei fuse again into one or two large nuclei, but the cells have now a very different aspect. Their cytoplasm, which was dense and granular in appearance, has become highly vacuolate with a coarse reticulum of wide meshes. The nuclei also at this time have an "empty" appearance, having lost most of their chromatic material. This seems to be given off from the nucleus and reappears in the cytoplasm in the form of threads or chromidia. Such mitochondria were first described by Meves (262) in the tapetal cells of the white water lily. The contents of the cells become more and more sparse until finally they break down altogether, having served their purpose as glandular cells to feed the young pollen grains.

To return to meiosis, it will be seen that so complicated and delicate a process offers many opportunities for irregularities to occur, and a great variety of such departures

from the normal have been described in various plants, chiefly hybrids, and particularly in *Oenothera*. These are all to be regarded as germinal changes, though the great majority of the germ cells in which they occur fail to complete their development. The frequency of the *lata* mutations in *Oenothera* is undoubtedly due to the weak attraction between the heterotypic chromosomes, which results in very loose pairs being formed. The degree of this pairing varies greatly in different organisms, and it is so close in some of the *Lepidoptera* that the two members of each pair fuse into a single body.

The meiotic processes in megaspore formation are very similar to those in the pollen mother cell, and are in fact identical so far as the nuclei are concerned. The following figures are chiefly from *Oe. lata*. Instead of a tetrad of pollen grains, a row of four megaspores is formed, only one of which develops—the usual condition in Angiosperms. The functional megaspore forms the embryo sac. Modilewski (266) showed some years ago that instead of three there are only two successive nuclear divisions in the embryo sac of *Oenothera*. As a consequence, the mature sac contains only four nuclei—the egg, two synergids, and a polar nucleus, but no antipodals. In fertilisation one male cell unites with the egg, the other with the polar nucleus to form the endosperm. The latter is evanescent and soon disappears, the seed being “exalbuminous.” Geerts (158) has published an account of embryo sac development in *Oe. Lamarckiana*, in which he concludes, because of the absence of antipodals, that the first nuclear division in the sac has been omitted. He finds a cleavage in the cytoplasm across the middle of the sac, and describes double fertilisation. Important discoveries undoubtedly await a more detailed study of the female gametophyte in the various forms, as this is the key to the origin of the triploid and tetraploid conditions.

Fig. 69, *a* to *g*, shows a few of the conditions observable

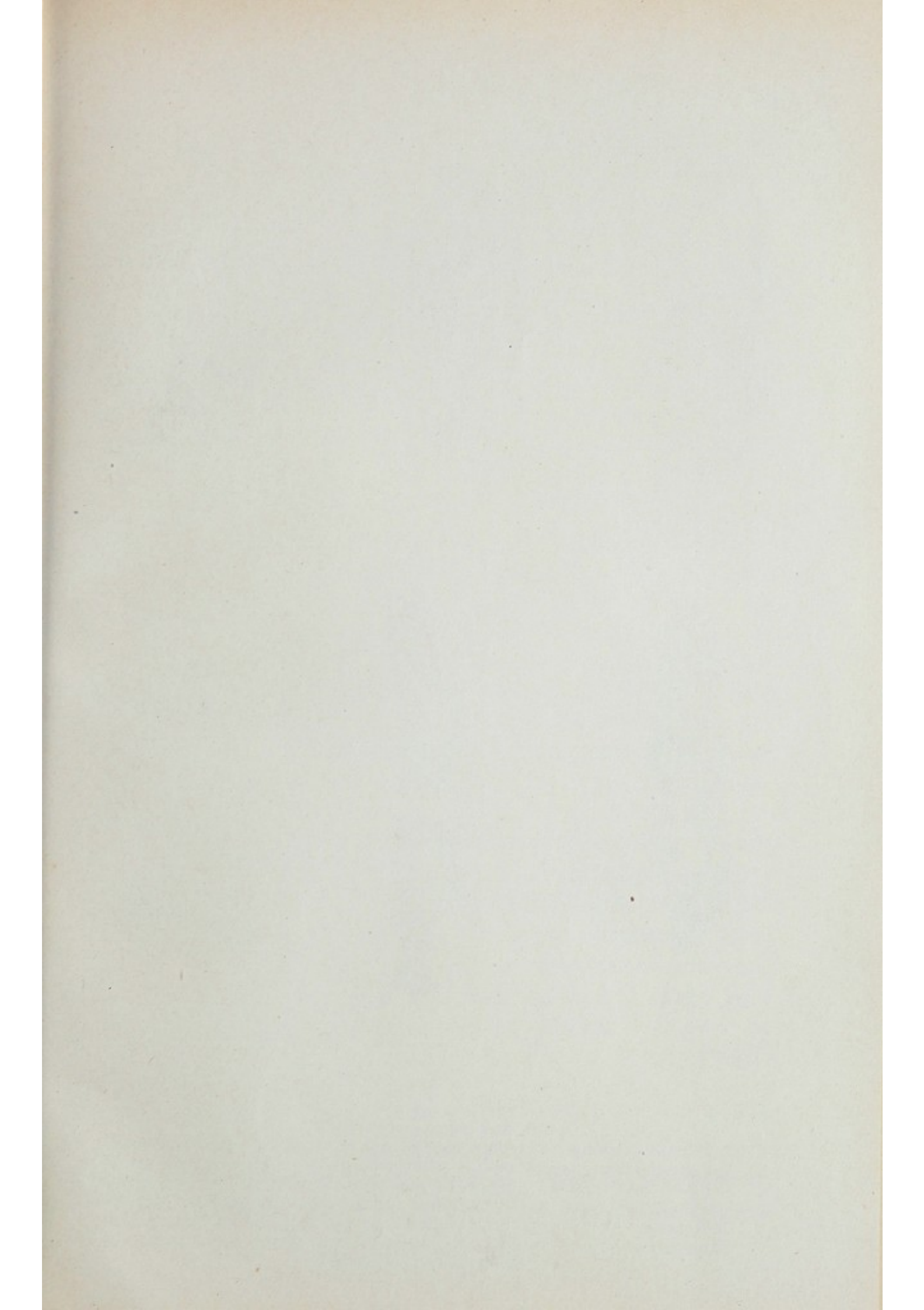




Fig. 69.

Ovules and megaspores in *Oe. lata*.

(a) Ovule showing megaspore mother cell in synapsis. (b) Ovule with pre-synaptic megaspore mother cell surrounded by degenerating (dark) cells of the nucellus. (c) Ovule with row of megaspores, and many degenerating cells in the nucellus. (d) Megaspore mother cell in diakinesis. (e-f) Megaspore mother cells which are abnormally small; same magnification as (d). (g) Row of megaspores degenerating in the homotypic telophase.

in the ovules and megaspores of *lata*. Fig. 69, *a* is a longitudinal section of an ovule, showing the megaspore mother cell in synapsis. Frequently, in the nucellus of *lata*, various cells surrounding the megaspores are found to be breaking down. This is seen in Fig. 69, *b*, in which the megaspore mother cell is in the presynaptic condition, and in Fig. 69, *c*, in which the row of megaspores has been formed. A megaspore mother cell is shown highly magnified in Fig. 69, *d*, the nucleus being in diakinesis with traces of the spindle appearing in the cytoplasm. Several counts at this stage showed 15 chromosomes. Sometimes the megaspore mother cell fails to grow in size, although its nucleus may undergo division. This is shown in Fig. 69, *e*, *f*, which are on the same scale of magnification as Fig. 69, *d*. Some factor, which we may call "lack of nutrition," prevents the germ cell and nucleus growing to their usual size. Normally there is an enormous increase in chromatin at this time. Fig. 69, *g*, shows again a megaspore row in which the lower pair of megaspores is already degenerating in the homotypic telophase while the upper pair persists. These represent a few of the types of failure which may occur in the development of the megaspores.

This very brief account must suffice. It is only necessary to add that not only may the same irregularities occur in the megaspores as in the pollen development, but others as well. The relation of these various departures from the normal to the production of new chromosome numbers, will be considered next, but first Table XII (page 180) shows the actual numbers which are now known in *Oenothera*.

3.—*Chromosome Duplication*

In 1908, we first observed actual cases of a 6 + 8 distribution of the chromosomes in the heterotypic mitosis of the pollen mother-cell, in *rubrinervis*. We afterwards

TABLE XII.
Chromosome Numbers in *Oenothera*.

Type.	Author.	Chromosome number.
<i>Oe. longiflora</i>	Beer, 1906	14
<i>Oe. Lamarckiana</i> , Ser. ..	Geerts, 1907; Gates, 1907; Lutz, 1907; Davis, 1911	14
<i>Oe. grandiflora</i> , Solander..	Davis, 1909	14
<i>Oe. biennis</i> , L.	Gates, 1909; Davis, 1910	14
<i>Oe. muricata</i> , L.	Stomps, 1912	14
<i>Oe. cruciata</i> , Nutt.	Stomps, 1912	14
<i>Oe. Millersii</i> , de Vries ..	Stomps, 1912	14
<i>Oe. mut. rubrinervis</i> , de Vries	Gates, 1908	14
<i>Oe. mut. rubricalyx</i> , Gates	Gates and Thomas, 1914	14
<i>Oe. mut. nanella</i> , de Vries	Gates, 1908; Lutz, 1908	14
<i>Oe. mut. gigas</i> , de Vries	Lutz, 1907; Gates, 1908, 1911, 1913; Davis, 1911	28
<i>Oe. mut. gigas</i> , from Sweden	Gates and Thomas ..	28
<i>Oe. mut. lata</i> × <i>mut. gigas</i> (?)	Gates, 1909	20
<i>Oe. mut. semigigas</i> , Stomps	Stomps, 1912; Lutz, 1912	21
<i>Oe. laevifolia</i> , de Vries ..	Gates, 1909	14
<i>Oe. brevistylis</i> , de Vries ..	Gates	14
<i>Oe. mut. lata</i> , de Vries (see Fig. 37, p. 107)	Lutz, 1912 ¹ ; Gates, 1912; Gates and Thomas, 1914 ²	15
<i>Oe. mut. semilata</i> , Gates (see Figs. 38-40, pp. 108-113)	Gates and Thomas, 1914 ²	15
<i>Oe. mut. incurvata</i> , Gates ($\frac{8}{13}$) (see Figs. 56, 57, pp. 148-9)	N. Thomas, 1914	15
<i>Oe. biennis mut. lata</i> , Gates (see Fig. 60, p. 155)	Gates and Thomas, 1914	15
<i>Oe. lata rubricalyx</i>	Gates and Thomas, 1914	15
<i>Oe. biennis semigigas</i> , Stomps	Stomps, 1912	21
Smaller-flowered offspring of <i>gigas</i> ($\frac{22}{12}$ I.4)	Gates and Thomas (one plant)	27
Narrow-leaved offspring of <i>gigas</i> ($\frac{18}{12}$) (see Fig. 53, p. 129)	Gates (one plant)	27 or 28
Mutant from <i>lata</i> selfed ..	Lutz, 1912	22
<i>Oe. mut. gigas</i> × <i>lata rubricalyx</i> ($\frac{30}{13}$) (see Figs. 74-75, p. 191)	Gates and Thomas (one plant)	22
<i>Oe. mut. rubricalyx</i> × <i>gigas</i> ($\frac{19}{13}$) (see Figs. 76-77, p. 193)	Gates and Thomas (one plant)	21
Offspring of <i>lata</i> × <i>gigas</i>	Lutz, 1912	
	No. of individuals, 2	15
	" " 16	21
	" " 25	22
	" " 3	23
	" " 2	29
	" " 4	30

¹ This number was counted constantly in 28 individuals.² 21 plants were studied in all, having 15 chromosomes.

found it to occur in a wild race of *Oe. biennis* and in *Lamarckiana* derived from *lata* \times *Lamarckiana*. We have found the corresponding 13 + 15 distribution both in *gigas* de Vries (1911) and the Swedish giant; and in a plant having 20 chromosomes, which probably came from *lata* \times *gigas* (and hence from 7 + 13 or perhaps 8 + 12 chromosomes), we found usually 10 + 10, but occasionally 9 + 11 as the heterotypic distribution. Davis has also observed this phenomenon in *biennis* (76) and *Lamarckiana* (78).

It is obvious that the whole series of *lata* and *semilata* mutants having 15 chromosomes have been derived through this irregular meiotic distribution of the chromosomes. In these cases both members of one pair of chromosomes must enter the same germ cell, which therefore contains a duplicate for one pair. Such a germ cell, with eight chromosomes, meets a normal one with seven, and an individual is produced having an extra chromosome which is a triplicate for a pair already present in 14-chromosome forms.

The extra chromosome in *Oenothera* bears certain resemblances to the accessory chromosome in some Insects. It will be recalled that when a single accessory is present the embryo becomes a male, and when two are present it becomes a female. One might make a comparison by the statement that the accessory chromosome when present in duplicate determines a female in the insects, while in plants a *lata*-like mutant is produced in the presence of a triplicate for a certain pair of chromosomes. At present it appears probable that the result will be essentially the same, to whichever pair of chromosomes the extra one belongs. But it is conceivable that seven types of such mutants might occur, as each of the seven gametophytic chromosomes may constitute the extra one.

The extra chromosome bears a greater resemblance to the supernumerary chromosomes described by Wilson (448) in the Hemipteran genus *Metapodius*. In *M.*

granulosus the number of chromosomes in different individuals ranges from 22 to 27, though constant for each individual. This variation results from successive duplications of one chromosome (the small idiochromosome or Y-element in sex determination) in the same manner as in the origin of *lata*, i.e., by both members of this chromosome-pair passing into the same germ cell in meiosis. By repetition of this process the number of supernumeraries in an individual may become as high as six.

The *lata* mutants, having the extra or odd chromosome, are almost completely male-sterile and their seed-production is also greatly reduced. In *semilata*, however, with the same number of chromosomes, a considerable quantity of good pollen is produced. The nature of the difference between *lata* and *semilata* therefore remains at present obscure, and the male sterility of *lata* cannot be attributed entirely to the presence of the odd chromosome. Cultures of these plants from various sources show that they form a variable series without a sharp line of demarcation between *lata* and *semilata*. This variability may be due to the loss or acquisition of fragments of chromatin by certain chromosomes.

The very complex question of the causes of sterility cannot be considered here, but we have shown that the phenomena of degeneration in the anthers of *lata* frequently begin as early as synapsis, and sometimes even in the archesporium, though many cells complete the meiotic divisions. After the breakdown of the pollen grains, the tapetal cells collapse and may form a dark-staining mass lining the cavity of the anther. In some cases this is finally absorbed and the wall cells behind, being freed from pressure, grow in and more or less completely fill the cavity with non-glandular tissue.

We may now consider the meiotic irregularities during pollen development in *Oenothera*. The facts have been derived from work in collaboration with Miss N. Thomas



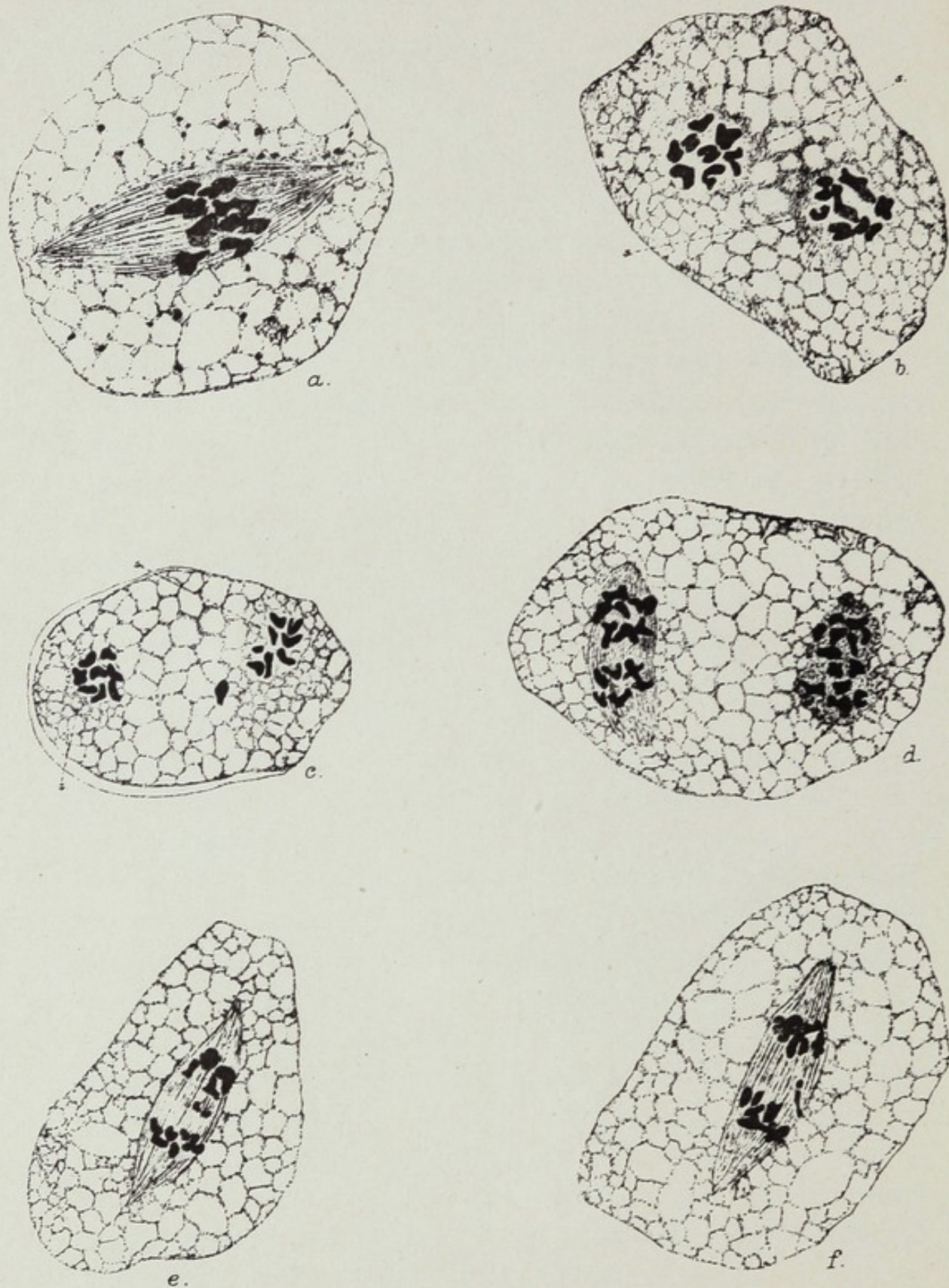


Fig. 70.

Meiotic divisions in the pollen mother cells of (a) *Oe. rubricalyx* and (b-f) *Oe. lata rubricalyx*. From the *Quart. Journ. Micr. Sci.*

(153), on *lata* and *semilata* as well as from previous work on various forms. The irregularities now known to occur in *lata* and *semilata* may be classified as follows:—(1) the distribution of the 15 chromosomes on the heterotypic spindle is usually eight whole chromosomes to one daughter nucleus and seven to the other (Figs. 70, *d*, 71, *b*, *c*). But occasionally one chromosome goes to the same nucleus with its mate, making the distribution 9 + 6; (2) sometimes one chromosome (probably the extra one) divides on the heterotypic spindle (see Figs. 70, *b*, *c*, 71, *a*, *d*, 72, *b*, *d*). In Figs. 71, *a*, and 72, *b*, this is not a regular longitudinal split, but rather an irregular pulling apart transversely, leaving a trail of chromatin behind. This behaviour sometimes extends to a second chromosome (Fig. 72, *c*), and may also occur in 14-chromosome plants descended from 15-chromosome individuals; (3) the fragmentation and later degeneration of certain chromosomes may occur on the heterotypic (Fig. 72, *c*), or homotypic spindles (Fig. 70, *e*, *f*); (4) loss of material from one or more chromosomes sometimes occurs, by the chromosome as it moves leaving a trail of chromatin on the heterotypic spindle (Figs. 71, *a*, 72, *b*, *c*); (5) certain

FIG. 70.—CHROMATIN DISTRIBUTIONS IN POLLEN MOTHER CELLS.

- a.* *Oe. rubricalyx*, profile view of heterotypic spindle in pollen mother cell showing 14 chromosomes. *b-f*, *Oe. lata rubricalyx*.
- b.* Polar view of the two groups of chromosomes in homotypic metaphase. In each group 7 whole chromosomes and one $\frac{1}{2}$ chromosome (*s*), showing that the extra chromosome split in the first meiotic division.
- c.* The same, showing $7\frac{1}{2}$ chromosomes in the left-hand group, and in the right-hand group 6 whole chromosomes, a $\frac{1}{2}$ chromosome (*s*) and a small fragment. The 15th chromosome is in the cytoplasm between the two nuclei.
- d.* A homotypic anaphase in the same plant. The spindle on the left contains 8 chromosomes and that on the right 7 chromosomes, in each group.
- e. f.* Same as last, both spindles from one pollen mother cell. The left-hand spindle contains 6 chromosomes approaching either pole, and two fragments degenerating at the equator; the right-hand spindle has two groups of 8 chromosomes each and two more degenerating fragments. These fragments together make up the extra chromosome, which split in the heterotypic division.—From *Quart. Journ. Micr. Sci.*, after Miss N. Thomas. × 1930.

chromosomes are not infrequently left behind to degenerate on the heterotypic and homotypic spindles (Figs. 70, *c, e, f*, 72, *d*); (6) small extra nuclei are frequently formed by lagging chromosomes, both in the heterotypic and homotypic mitoses; (7) in certain cases portions of chromosomes are included in the germ nuclei; at least up to the homotypic metaphase. In such cases the individuality of certain chromosomes is probably not strictly maintained, and this may be a source of variation in the *lata-semilata* series of forms.

It will be understood that these irregularities all occur much more frequently in plants with an odd number of chromosomes than in those with an even number, and they appear to be rather more frequent in *lata-semilata* than in the triploid mutants with 21 chromosomes. Two or more types of irregular behaviour may also be exhibited in the same pollen mother cell.

It has been pointed out (p. 110), that *lata* and *semilata* yield as offspring both 14- and 15-chromosome plants. Curiously enough, no 16-chromosome plants have yet been observed, but further search will doubtless reveal them (see p. 118).

4. Triploidy

The *gigas* and *semigigas* mutants from *Oe. Lamarckiana* and *biennis* constitute a distinct series from the *lata* and *semilata* forms above considered. The latter have orig-

FIG. 71.—*Oe. biennis lata*, POLLEN MOTHER CELLS.

- a.* Heterotypic spindle, showing 14 chromosomes. The 15th is on the next section. Several of the chromosomes are leaving a trail of chromatin behind as they move towards the poles.
- b.* Homotypic metaphase, showing the usual distribution, 8 chromosomes on the left-hand spindle and 7 on the right.
- c.* Same stage, showing the 7-8 distribution.
- d.* In this cell the lower group contains 8 whole chromosomes and a $\frac{1}{2}$ chromosome; the upper group contains 6 whole and a $\frac{1}{2}$ chromosome. Hence in the heterotypic mitosis one chromosome split and another was distributed to the wrong nucleus.—From *Quart. Journ. Micr. Sci.*, after Miss N. Thomas. $\times 1930$.

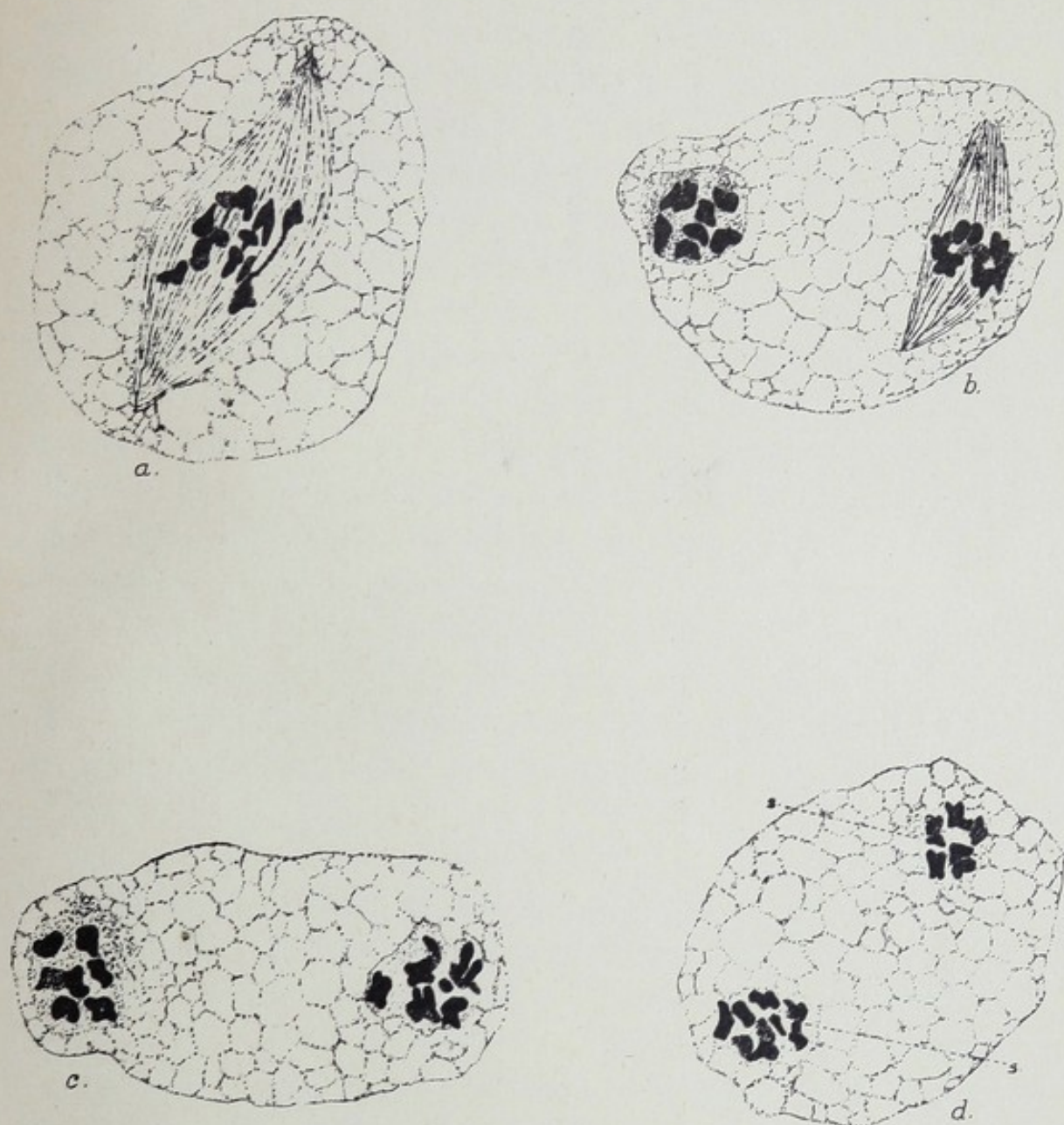


Fig. 71.

Meiotic divisions in the pollen mother cells of *Oe. biennis lata*.
 From the *Quart. Journ. Micr. Sci.*



inated through the duplication of one chromosome, and that duplication has come about, not by a split in a chromosome, but by one chromosome passing bodily into the wrong nucleus. The manner of origin of the *gigas* and *semigigas* mutants is not yet so clearly proved, but it must come about either from a split in the whole series of chromosomes or from what is tantamount to the omission of the chromosome reduction from one or both sides of the house. When the tetraploid chromosome number in *gigas* was first discovered by Miss Lutz (237) in root tips and the author (120) in the pollen mother cells, the existence of triploid mutants was unknown. In their absence, and for other reasons, we concluded that the doubling in the chromosomes which led to the origin of *gigas* probably occurred in the fertilised egg, through a suspended mitosis in one of its early divisions. This view was strongly supported by Strasburger (361). Triploid mutants have since been discovered by Stomps (352) and Miss Lutz (241), and this opens up possibilities which before seemed excluded, though the matter is by no means settled.

As pointed out elsewhere (p. 161), in a series of crosses by de Vries in which *Lamarckiana* or one of its derivatives was the mother, and *muricata*, *cruciata*, or *Millersi* the father, triploid mutants appeared with a frequency of about 3 in 1,000. This is no doubt correctly considered to represent the frequency with which diploid megaspores occur in *Lamarckiana*, but there are no corresponding data for determining the frequency of diploid pollen grains, nor is there at present any proof that they occur. Another possible source of $3x$ mutants is by the union of both male cells with the haploid egg. Němec (282) believes that he has actually observed this in *Gagea lutea*, although it must be said that the evidence is not very conclusive.

There is at present no evidence that triploidy in *Oeno-*

thera originates in any way except by the union of a diploid egg with a haploid male cell. But there are difficulties even with this manner of origin, for it has generally been considered by Strasburger and other botanists that a diploid egg will develop apogamously without fertilisation, and this is known to happen in many plants. It will be seen that a large amount of work with the embryo-sac will be required before these questions in *Oenothera* are fully cleared up. As indicating, however, that the conditions in *Oenothera* may be different from those in other plants, it may be mentioned that castration experiments have furnished no evidence for a tendency towards apogamy in the tetraploid *gigas*, although this species has diploid eggs.

The same is true of the other *Oenotheras*, with the possible exception of one instance in which three small seeds were obtained from *lata* (127), apparently without fertilisation. Again, Miss Lutz (241) has obtained *lata* plants with 15 chromosomes in the offspring of *lata* \times *gigas*. It is possible that such plants come from the apogamous development of an unreduced egg, although it is also conceivable that they originated from the union of a *lata* egg having seven or eight chromosomes with a *gigas* pollen grain the nucleus of which, as the result of meiotic irregularities, contained only seven or eight chromosomes.

FIG. 72.—MUTANTS RESEMBLING *Oe. lata*, POLLEN MOTHER CELLS.

- a. Normal heterotypic spindle, showing 15 chromosomes in their usual scattered arrangement.
- b. Heterotypic anaphase showing 9 chromosomes moving to one pole and 5 to the other. The fifteenth chromosome has been pulled into two parts, leaving a trail of chromatin between them.
- c. This spindle has been cut, but it shows two chromosomes pulling apart and losing some of their chromatic substance. The chromosomes are much smaller than normal.
- d. Homotypic metaphase showing in the upper group $7\frac{1}{2}$ chromosomes, in the lower group $6\frac{1}{2}$, and between the groups several fragments which together constitute the 15th chromosome, which was left behind on the heterotypic spindle.—From *Quart. Journ. Micr. Sci.*, after Miss N. Thomas. \times 1930.

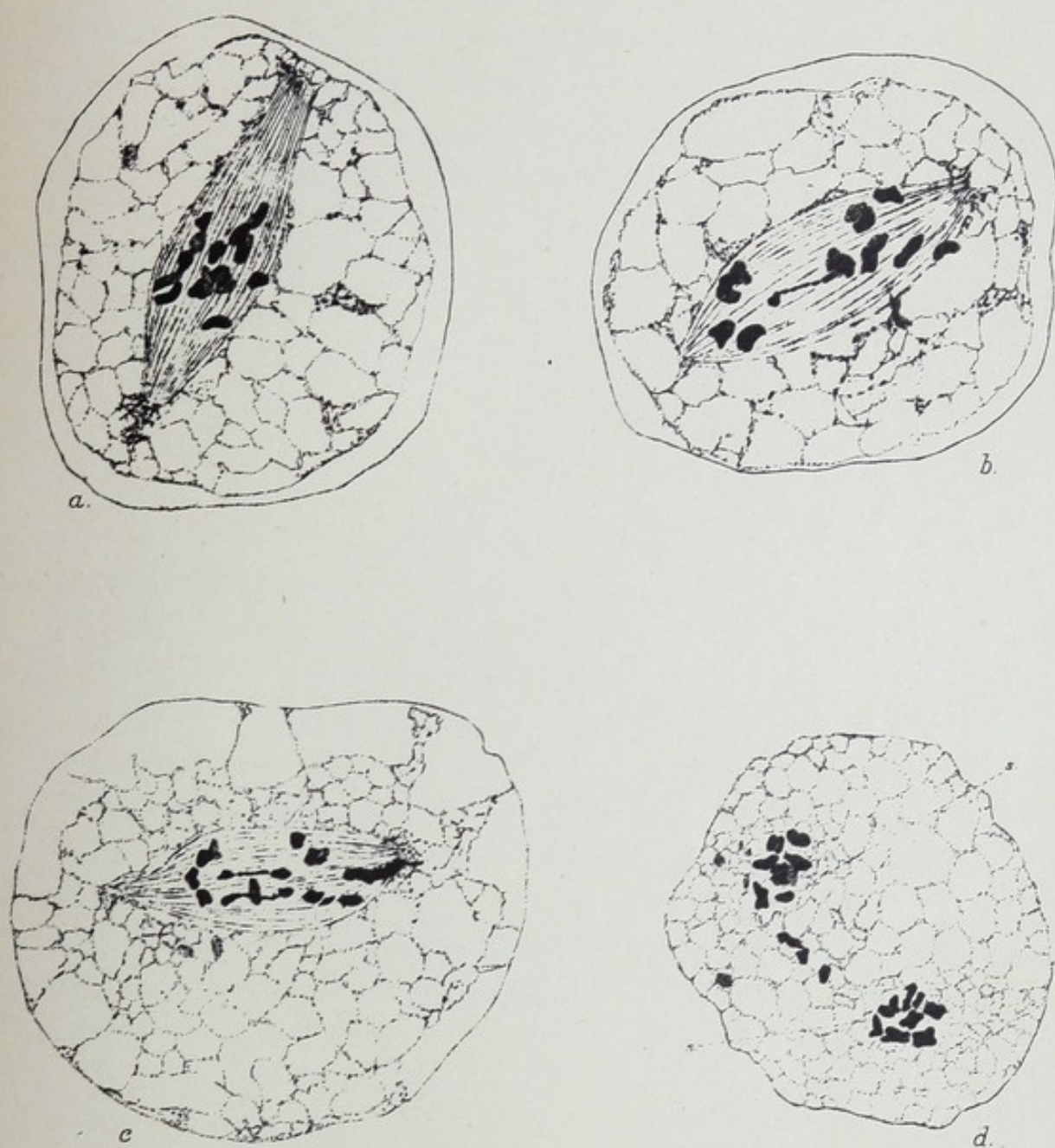


Fig. 72.

Meiotic divisions in *lata*-like mutants from Sweden.
From the *Quart. Journ. Micr. Sci.*



It will be pointed out later that there is evidence for the occasional occurrence of such pollen grains in *gigas*. The above-mentioned cross (see Table XII, p. 180) was also found to contain *gigas*-like plants having 29 and 30 chromosomes. It seems very probable that these individuals came from the union of diploid eggs of *lata* having 15 chromosomes with *gigas* pollen grains having respectively 14 and 15 chromosomes. The bulk of the offspring from this cross, having 21, 22 and 23 chromosomes, obviously arise (a) from 7 *lata* + 14 *gigas* chromosomes, (b) from 8 + 14, occasionally 7 + 15, and (c) from 8 + 15. Miss Lutz has also obtained a mutant having 22 chromosomes, in the offspring of *lata* self-pollinated. This probably arose through the union of a 15-chromosome egg with a 7-chromosome male cell, although in all these cases the possibility of two haploid male cells taking part in fertilisation is not excluded. Hence there seems fairly strong evidence, although it is at present indirect, that diploid eggs occur both in *lata* and *Lamarckiana*, and that they can be fertilised.

The plant having 20 chromosomes, in the F_1 of *lata* \times *gigas*, very probably came from the union of an egg having seven chromosomes with a male cell having 13; and the plant with 22 chromosomes, derived from *gigas* \times *lata rubricalyx* (see p. 191), doubtless came from $14\text{♀} + 8\text{♂}$ chromosomes.

It remains to describe the chromosome distributions during meiosis in these triploid plants. We have devoted considerable study to this subject, but only the more general features, which are themselves of very great theoretical importance, can be considered here. In the first place it may be said that there is probably no essential difference as regards the behaviour of the chromosomes in triploid mutants or hybrids. Indeed, if triploid mutants originate, as we think most probable, through the union of a diploid egg with a haploid male cell, they are essen-

tially hybrids. In the second place, there is a curious tendency in some cases for the chromosomes to segregate into two equal groups in the heterotypic division. Thus in the 20-chromosome plant above-mentioned (125), 10 + 10 was the distribution regularly observed, though occasionally 9 + 11, but other irregularities were found rarely if at all at this stage.

Again, in the 21-chromosome plant in which we studied the meiotic phenomena in 1909 (125), this distribution was almost invariably 10 + 11 (Fig. 73, *b*) and only occasionally 9 + 12. This means that in both these cases all the chromosomes almost invariably reached the daughter nuclei in the heterotypic mitosis, although in the homotypic lagging chromosomes were occasionally found outside the tetrad nuclei (Fig. 73, *c*). In his study of *lata* × *gigas* Geerts (159) found more numerous irregularities, only seven of the chromosomes regularly reaching each of the daughter nuclei, while the remaining seven were unpaired and irregularly distributed or left behind to fragment in the cytoplasm. Our material was collected in the height of the flowering period, while Geerts collected his later in the season, and there is no doubt that this accounts for the much greater frequency of irregularities in his study than in mine. We may probably conclude from this that seeds derived from pollination of flowers early in the season will produce a less variable offspring than those from pollinations

FIG. 73.—POLLEN MOTHER CELLS, *a-c*, *lata* × *gigas*.

- a.* A homotypic spindle showing 11 bivalent chromosomes.
- b.* Homotypic metaphase, showing 10 + 11 chromosomes.
- c.* Homotypic telophase; two of the nuclei contain 10 chromosomes each, and one chromosome is left behind on the spindle.
- d.* Homotypic metaphase in *gigas* × *lata rubricalyx*, showing 10 + 12 chromosomes.
- e.* Showing 13 + 15 chromosomes in the Swedish *gigas*.
- f.* Homotypic telophase in the Swedish *gigas*, showing one nucleus with about 28 chromosomes.
- g.* Somatic cell of a plant descended from *gigas*, having 27 chromosomes.

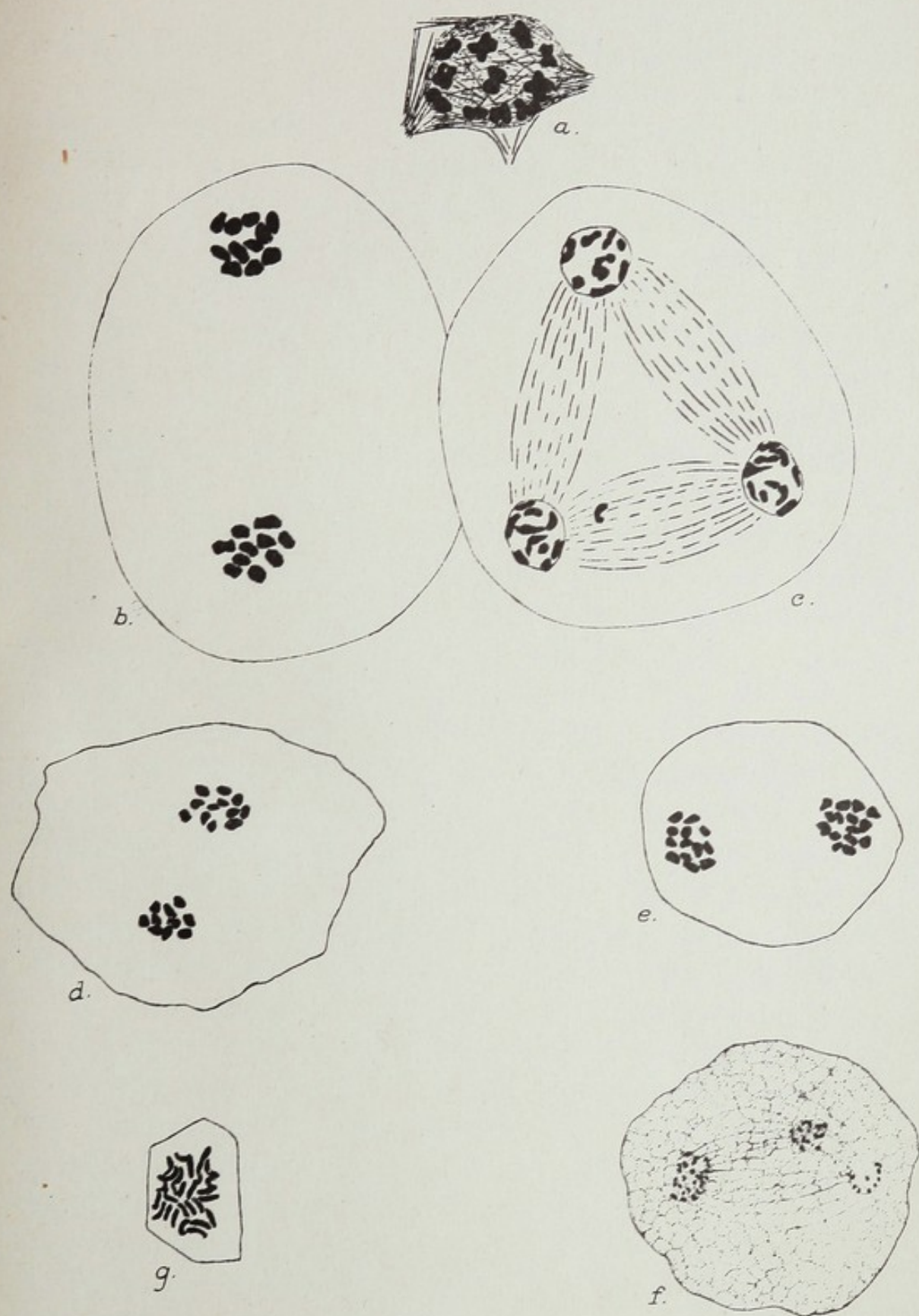


Fig. 73.

Meiotic divisions (a-c) in *Oe. lata* x *gigas*, (d) in *gigas* x *lata rubricalyx*, and (e-g) in certain *gigas* races. The figures are unequally magnified.

Figs. a-c are from the *Botanical Gazette*.



towards the end of the season, when the plants are losing in strength and the environment is also less favourable. Thus, early in the season the offspring produced by *lata* \times *gigas* may be expected to have for the most part 20, 21, and 22 chromosomes, while seeds from late pollinations should be found to produce mostly plants with chromosome numbers as low as 14 or 15.

It may be said that while there were indications of pairing of chromosomes on the heterotypic spindle in our material, they were not clear enough to be conclusive, although there was probably a weak tendency to pairing at this time. But since one of the chief peculiarities of all the *Oenotheras* is the very weak pairing at this stage, it is quite impossible to declare definitely that there were seven pairs of chromosomes and seven unpaired chromosomes. In cases where, as in the Lepidopteran genus *Pygæra* recently described by Federley (102), the homologous maternal and paternal members of the chromosome pairs are closely attached to each other or fused into a single larger body in the heterotypic metaphase, it is relatively easy, as Federley has shown, in crosses between species with different chromosome numbers to trace the maternal or paternal origin of the unpaired chromosomes. But the loose pairing in *Oenothera* makes this impossible.

Of even greater interest are the meiotic distributions in the 22-chromosome plant derived from *Oe. gigas* \times *lata rubricalyx* (see Figs. 74, 75), for here the arrangement in the heterotypic telephase is distinctly not into two equal groups of 11 each, but usually (and apparently with much regularity) into 10 and 12. The counts were made in interkinesis or in polar views of the homotypic metaphase from preparations of Miss N. Thomas. Four cases were observed in which the 10 + 12 distribution had taken place and both daughter groups could be clearly counted. Usually, however, only one group in a given mother cell can be counted, and of such cases 18 groups were found having

clearly 10 chromosomes and 12 groups having 12 chromosomes each. The greater number of 10's may have been produced by chromosomes being left out of the heterotypic telophase. In only a single case was a clear count of a group of 11 chromosomes made, although six doubtful cases were observed. In one clear case 13 chromosomes were found in the daughter nucleus, and in another (not in the same cell) nine, the corresponding groups not being countable. Not infrequently one or two chromosomes were left behind on the heterotypic or homotypic spindles, and in the latter case they frequently appeared to be degenerating.

A series of other irregularities were observed, similar to those already mentioned (p. 183). Thus one daughter nucleus in interkinesis contained only $6\frac{1}{2}$ chromosomes, and one homotypic metaphase possessed $9\frac{1}{2}$ chromosomes, showing that certain chromosomes sometimes split on the heterotypic spindle just as in *lata* forms. Chromosomes are more frequently left behind on the homotypic than the heterotypic spindle, and several cases were counted in which only nine chromosomes had entered the homotypic telophase. Hence we conclude that a considerable number of the pollen grains will contain only nine chromosomes, although the majority will probably contain 10, 11, or 12.

As already pointed out, the 22 chromosomes of this individual were probably derived, eight of them from *lata* and 14 from *gigas*, and there is no obvious reason why the heterotypic segregation should be usually $10 + 12$. Comparison of this behaviour with that of other 22-chromosome plants will be necessary before it will be possible to interpret this result further, but in any case it would seem that the cytoplasm controls in a general way the distribution which will take place, and there is no evidence at all that the distribution bears any definite relation to the source of the chromosomes, *i.e.*, whether from *lata* or *gigas*. Of course this result might be anticipated, since the extra

chromosome of *lata* is merely a duplicate of one of the others, probably without any change in its properties, and similarly the *gigas* chromosomes appear to be merely a double set of the *Lamarckiana* bodies. The relation between the chromosome number and the morphology of the pollen grains in this plant will be considered on p. 214.



FIG. 74.—Rosette of *gigas* \times *lata rubricalyx*
(22 chromosomes).

The plant of which the chromosome behaviour is described in the last two paragraphs, was the only one which developed from our cross *gigas* \times *lata rubricalyx*. The rosette is shown in Fig. 74, and the upper part of the flowering plant in Fig. 75. They show a striking resemblance to *gigas* (cf. Figs. 43–45, pp. 119–123), though there are conspicuous differences, particularly in the full-grown

plant. The rosette resembled the Swedish giant more than the de Vriesian type, having basal jags on the leaves. Since the *lata rubricalyx* parent contained *grandiflora* as one of its ancestors, we are inclined to believe that the Swedish race of *Lamarckiana* has been derived through crossing of the original *Lamarckiana* with *grandiflora*,



FIG. 75.—*Oe. gigas* × *lata rubricalyx*.

especially as other facts point to the same conclusion. The stem of the above plant was densely clothed with leaves; the buds large, having sepals with red colour pattern 7 and red blotches on the hypanthium; the leaves with pink midribs and serrated margins. The flower dimensions were as follows: petals, 49 mm. long × 71 mm. broad, dark yellow; ovary, 14–19 mm. long; hypanthium, 52–57 mm. long, 4–4.5 mm. in diameter; bud cone,

45 mm. long, 12–13 mm. in diameter at base; sepal tips, 4–5 mm. long. The capsules were remarkably square, and not contracted at the top. The plant thus resembled *gigas* more than *rubricalyx* in all features except pigmentation, which was intermediate. For the pollen grains, see p. 213.

In Figs. 76 and 77 are shown photographs of a plant



FIG. 76.—Rosette of *rubricalyx* \times *gigas*
(21 chromosomes).

from *rubricalyx* \times *gigas*, having 21 chromosomes. The rosette and the flowering shoot resembled *gigas* (cf. Figs. 74 and 75); the buds were red as in *rubricalyx*, but pale. This plant was afterwards potted in the greenhouse and then cut back. Several shoots which subsequently developed resembled in foliage the parent plant, but one branch

was much nearer *Lamarckiana* and another intermediate. In the latter branches a loss of chromosomes had probably taken place.

It is clear that triploidy leads to the production of many new chromosome-numbers, through the irregularities it introduces into the meiotic phenomena. All these irregu-

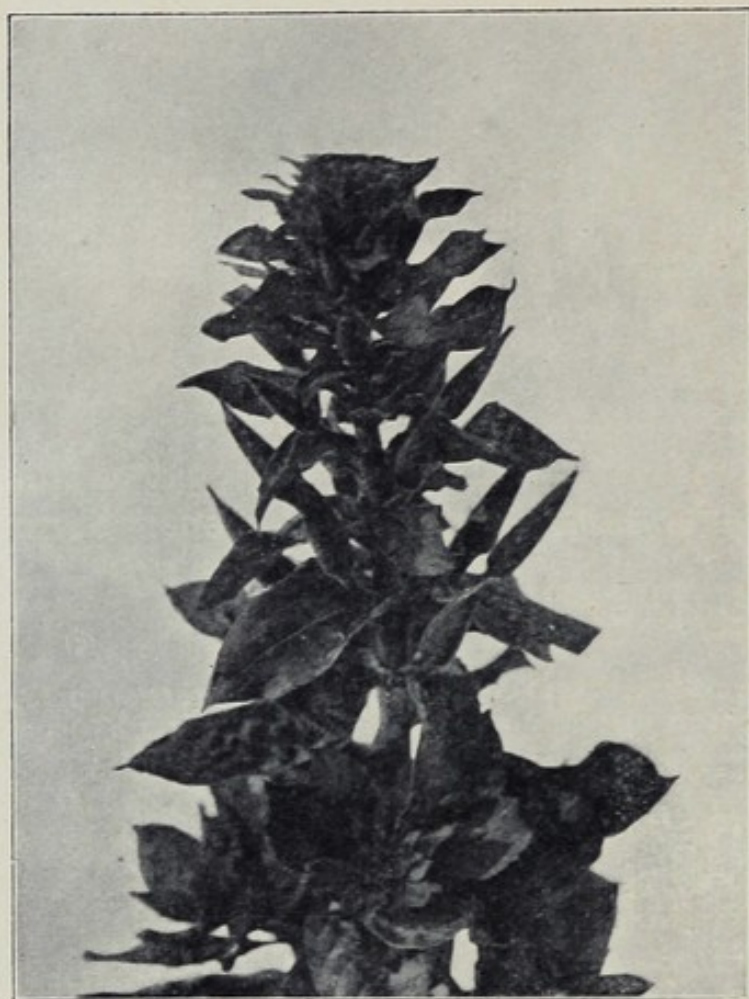


FIG. 77.—*Oe. rubricalyx* \times *gigas*.

larities are germinal changes *par excellence*, but only a portion of them is capable of giving rise to viable germ cells. It is at present unknown whether the number alone determines the viability, or whether particular chromosome combinations will, owing to incompatibility, fail to produce an embryo after fertilisation. It is conceivable that the formation of incompatible combinations without change of number in the 14-chromosome *Oenotheras*

(allowed by the loose pairing in meiosis), may be a cause of the large amount of sterility observed in them. One may hope that more detailed studies of the triploid forms will lead to a determination, within limits, of the degree of differentiation which actually exists between the chromosomes in *Oenothera*, and of the relation that chromosome identity as well as chromosome number bears to the cytoplasm in the development of the external characters.

The history of meiosis in these forms furnishes the strongest kind of proof that (for some unknown reason) the identity of the individual chromosomes is, with rare exceptions, strictly maintained. It is also evident that whatever may happen in synapsis in the way of interchange of materials or "influences," does not interfere with the maintenance of that identity, for the chromosomes reappear in the same number as in the somatic divisions and are distributed as whole and independent bodies immediately afterwards. The few exceptions to this, as already described, merely serve to emphasise the almost universal character of the rule.

5. *Tetraploidy*

Turning now to tetraploidy, it is usually although not invariably associated in plants with cell giantism. Thus it appears that if the chromosomes segment transversely, a doubled number of chromosomes appears, each having half the size, while the volume of the nucleus and cell remains essentially unchanged. This seems to have taken place in the genus *Rumex*. In such cases one must think of the chromosomes as having merely segmented or fragmented into a larger number of bodies without any growth, and since there is much evidence that, other things being equal, the volume of the nucleus is a function of the number of chromosomes, the size of such nuclei will remain unchanged. On the other hand, as Boveri emphasised some

years ago, when a chromosome splits lengthwise the daughter chromosomes are each capable of growth to their original volume or thickness. Hence it follows from the relationship between chromatin and "karyolymph" above stated, that if the daughter chromosomes remain in the same nucleus, that nucleus will grow to twice its former volume. This law of Boveri has been shown to hold in many cases, and the size of the cell increases along with that of the nucleus.

It does not appear, however, that all cases of tetraploidy will come under one of these two simple categories, *i.e.*, a transverse or a longitudinal split of the chromosomes. Thus in *Dahlia*, the figures of Ishikawa (197) indicate that in the tetraploid races the cells are somewhat larger although the individual chromosomes are distinctly smaller. That giantism may also appear owing to a sudden increase in the size of the cells in the new race, but without any change in the chromosome number, was shown by Gregory¹ (164) and afterwards by Keeble (210) in the giant *Star Primulas*. In this case there is an increase in the size of the chromosomes but not in their number, and it is possible that here also the increase in the volume of chromatin is the primary change.

Giantism, therefore, does not necessarily mean tetraploidy, nor does tetraploidy necessarily involve giantism, but nevertheless the condition of cell giantism is usually accompanied by tetraploidy. In such cases it is indeed easier to analyse the nature of the change than in those cases where cell giantism is unaccompanied by a change in the chromosome number.

In Table XIII is brought together a list of the known cases of tetraploidy in plants and animals. The list is probably incomplete, and is constantly being added to by fresh discoveries, but casual inspection of the list

¹ Gregory (165) has since found tetraploid mutants in *Primula sinensis*.

shows that chromosome doubling has taken place with sufficient frequency in the various phyla to be of very considerable evolutionary interest and significance.

TABLE XIII.
Tetraploid Species.

Name.	Reproduction.	Chromosomes.		Author.
		<i>x</i>	<i>2x</i>	
SEED PLANTS.				
<i>Potentilla rupestris</i>	—	8	16	Forenbacher, 1914
<i>P. sylvestris</i> ...	—	16	32	Forenbacher, 1914
<i>P. anserina</i> ...	—	16	32	Forenbacher, 1914
<i>P. reptans</i> ...	—	16	32	Forenbacher, 1914
<i>Alchemilla arvensis</i>	Fertilised ...	16	32	Murbeck, 1901
<i>A. grossidens</i> ...	Fertilised ...	16	32	Strasburger, 1904
<i>A. gelida</i> ...	Fertilised ...	16	32	Strasburger, 1904
<i>A. pentaphylla</i> ...	Fertilised ...	32	64	Strasburger, 1904
<i>Eualchemilla</i> —				
<i>A. acutangula</i> ...	—	32	64	Murbeck, 1901
<i>A. speciosa</i> ...	Apogamous ...	32	64	Strasburger, 1904
<i>A. splendens</i> ...	—	32	64	Strasburger, 1904
<i>A. fallax</i> ...	Apogamous ...	32	64	Strasburger, 1904
<i>A. micans</i> ...	Apogamous ...	32	64	Strasburger, 1904
<i>Antennaria dioica</i>	Fertilised ...	12—14	24—28	Juel, 1900
<i>A. alpina</i> ...	Apogamous ...	—	45—50	Juel, 1900
<i>Hieracium venosum</i>	Fertilised ...	7	14	Rosenberg, 1907
<i>H. auricula</i> ...	Fertilised ...	9	18	Rosenberg, 1907
<i>H. umbellatum</i> ...	Fertilised ...	9	18	Juel, 1905
<i>H. excellens</i> ...	Partly apogamous and aposporous	17	34	Rosenberg, 1907
<i>H. flagellare</i> ...	Apogamous ...	21	about 42	Rosenberg, 1907
<i>Taraxacum confertum</i> ...	—	8	16	Rosenberg, 1909
<i>T. officinale</i> ...	—	12—13	26—30	Juel, 1905
<i>Drosera rotundifolia</i> ...	Fertilised ...	10	20	Rosenberg, 1903
<i>D. longifolia</i> ...	Fertilised ...	20	40	Rosenberg, 1903
			(smaller)	
<i>Crepis virens</i> ...	Fertilised ...	3	6	(Rosenberg, 1909, Digby, 1914)
<i>C. tectorum</i> ...	—	4	8	Juel, 1905
<i>C. taraxacifolia</i> ...	—	4	8	Digby, 1914
<i>C. lanceolata</i> var. <i>platyphyllum</i> ...	—	5	10	Tahara and Ishikawa, 1912
<i>C. japonica</i> ...	—	8	16	Tahara, 1910
<i>Saxifraga sponhemica</i> ...	—	15	30	Pace, 1912
<i>S. granulata</i> ...	—	30	60	Juel, 1907
<i>Dahlia coronata</i> ...	—	—	32	Ishikawa, 1911

¹ For the references see general bibliography.

TABLE XIII.—*contd.*

Name.	Reproduction.	Chromosomes.		Author.
		<i>x</i>	<i>2x</i>	
SEED PLANTS.				
<i>D. variabilis</i> (nine varieties)...	—	—	64	Ishikawa, 1911
<i>Thalictrum minus</i>	Fertilised ...	12	24	Overton, 1909
<i>T. purpurascens</i>	Apogamous ...	24	48	Overton, 1909
<i>Rosa livida</i> ¹ ...	Fertilised ...	8	16	Strasburger, 1904
<i>R. cinnamomea</i> ...	Fertilised ...	8	16	Strasburger, 1904
<i>R. canina</i> (many forms) ...	Fertilised ...	8	16	(Strasburger, 1904 Rosenberg, 1909)
<i>R. canina persicifolia</i> ...	Apogamous ...	16—17	33—34	Rosenberg, 1909
<i>R. glauca</i> (one form) ...	Apogamous ...	16—17	33—34	Rosenberg, 1909
<i>Rumex Acetosa</i> ...	Apogamous ...	8	16	Roth, 1906
<i>R. hispanicus</i> ...	Apogamous ...	8	16	Roth, 1906
<i>R. arifolius</i> ...	Apogamous ...	8	16	Roth, 1906
<i>R. nivalis</i>	Apogamous ...	8	16	Roth, 1906
<i>R. scutatus</i> ² ...	—	(12)	24	Roth, 1906
<i>R. Acetosella</i> ³ ...	Apogamous ...	(16)	32	Roth, 1906
<i>R. cordifolius</i> ⁴ ...	—	(40)	80	Roth, 1906
<i>Wikstroemia canescens</i> ...	Fertilised ...	9	18	Strasburger, 1910
<i>W. indica</i> ...	Apogamous ...	26	26—28 ⁵ gemi.	(Winkler, 1906 ; Strasburger, 1910)
<i>Houttuynia cordata</i>	Parthenogenetic	—	52—56	(Shibata and Miyake, 1908)
<i>Daphne alpina</i> ...	Fertilised ...	9	18	Osawa, 1913
<i>D. mezereum</i> ...	Fertilised ...	9	18	Strasburger, 1909
<i>D. pseudo-mezereum</i>	Fertilised ...	9	18	Osawa, 1913
<i>D. kiusiana</i> ...	Fertilised ...	9	18	Osawa, 1913
<i>D. odora</i> ...	Sterile ...	14	28	Osawa, 1913

¹ Strasburger points out that the genus *Rubus* commonly has 12 chromosomes ($2x$) while the usual number in *Rosa* is 16, and he remarks that if the *Aphanes* group of *Alchemilla*, having 32 chromosomes, have been derived from such ancestors, they should be regarded as tetraploid, and the *Eualchemillas* as octoploid in character.

² Nuclear size same as in previous species.

³ Strasburger (1910) points out that in this case the chromosomes of the tetraploid species are half the size of those in the diploid species, while the nuclei are the same size in both. From this it follows that in this case the tetraploid number probably originated through a transverse division of the chromosomes.

⁴ Nuclei larger than in the section *Acetosa*. Also the species with low chromosome numbers do not hybridise, while the species with high numbers cross readily.

⁵ The gemini are larger than in *W. canescens*, the cells, as well as the stigmas and ovules being also larger. As Strasburger has pointed out, *W. indica* appears to be di-triploid in comparison with *W. canescens*, while *Houttuynia cordata*, another member of the *Balanophoraceae*, is tetraploid in comparison with *W. indica*.

TABLE XIII.—*contd.*

Name.	Reproduction.	Chromosomes.		Author.
		<i>x</i>	<i>2x</i>	
SEED PLANTS.				
<i>Morus indica</i> ...	—	14	28	Tahara, 1910
<i>M. alba</i> var. <i>Roso</i>	—	14	28	Tahara, 1910
<i>M. alba</i> var. <i>Shiro-wase</i>	—	17	40—50	Tahara, 1910
<i>Funkia ovata</i> ...	Fertilised ...	24	48 ¹	Sykes, 1908
<i>F. Sieboldiana</i> ...	Fertilised ...	24 ²	48	{ Strasburger, 1899 Sykes, 1908; Miyake, 1905
<i>Gyrostachys gracilis</i>	—	15	30	Pace, 1914
<i>G. cernua</i>	—	30	60	Pace, 1914
<i>Oenothera Lamarckiana</i>	Fertilised ...	7	14	{ Geerts, 1907; Gates, 1907
<i>Oe. gigas</i>	Fertilised ...	14	28	{ Lutz, 1907; Gates, 1908
<i>Hordeum distichum</i>	Self-pollinating	7	14	Nakao, 1911
<i>Secale cereale</i> ...	Self-pollinating	8	16	Nakao, 1911
<i>Triticum vulgare</i> ...	Self-pollinating	8	16	{ E. Overton, 1893; Koernicke, 1896; Nakao, 1911
<i>T. dicoccoides</i> ...	Self-pollinating	8	16	Bally, 1912
<i>Aegilops ovata</i> ...	Self-pollinating	16	32	Bally, 1912
<i>Primula floribunda</i>	Fertilised ...	9	18	Digby, 1912
<i>P. verticillata</i> ...	Fertilised ...	9	18	Digby, 1912
<i>P. verticillata</i> × <i>P. floribunda</i> ... (= <i>P. verticillata</i> F ₁)	Fertilised ...	9	18	Digby, 1912
<i>P. Kewensis</i> (type) (= <i>P. floribunda verticillata</i>)	Self-sterile (no pin-flowers)	9	18	Digby, 1912
<i>P. Kewensis</i> (seedling) (from a pin-flower) ³	Fertile ...	18	36	Digby, 1912
<i>P. Kewensis farinosa</i> (by selection)	Fertile	18	36	Digby, 1912
<i>P. Kewensis farinosa</i> (from <i>P. verticillata</i> × <i>P. floribunda isabellina</i>)	Fertile	18	36	Digby, 1912

¹ This number is tetraploid as compared with many other Liliaceæ, and probably originated through a transverse division of the chromosomes.

² Six long, eighteen short.

³ This single pin-flower appeared, presumably as a bud mutation, on a plant which bore only thrum flowers. Self-sterility accounts for the failure of the original *P. Kewensis* to set seed.

TABLE XIII.—*contd.*

Name.	Reproduction.	Chromosomes.		Author.
		<i>x</i>	<i>2x</i>	
SEED PLANTS.				
<i>P. floribunda isabellina</i> × <i>P. Kewensis</i> (type) (= <i>P. floribunda isabellina</i> F ₁)	Fertile	9	18	Digby, 1912
<i>P. Kewensis</i> (type) × <i>P. floribunda isabellina</i>	Sterile	—	—	Digby, 1912
<i>P. floribunda isabellina</i> × <i>P. Kewensis</i> (seedling) (= <i>P. floribunda isabellina</i> , F ₁)	Fertile	9	18	Digby, 1912
<i>Primula sinensis</i>	Fertile	12	24	Gregory, 1914
<i>Primula sinensis</i> giant race.	Fertile	24	48	Gregory, 1914
<i>Musa sapientum</i> var. "Dole"	Sterile	8	16	Tischler, 1910
<i>M. sapientum</i> var. "Radjah Siam"	Sterile	16	32	Tischler, 1910
<i>M. sapientum</i> var. "Kladi" ...	Sterile	24	48	Tischler, 1910
<i>Viola glabella</i> , Nutt.	—	6	12	Miyaji, 1913
<i>V. phalacrocarpa</i> , Makino	—			Miyaji, 1913
<i>V. grypoceras</i> , A. Gray	—	10	20	Miyaji, 1913
<i>V. verecunda</i> A. Gray	—	10	20	Miyaji, 1913
<i>V. nipponica</i> , Maxim	—	10	20	Miyaji, 1913
<i>V. Okuboi</i> , Makino	—	12	24	Miyaji, 1913
<i>V. Okuboi</i> , var. <i>glabra</i> Makino...	—	12 ¹	24	Miyaji, 1913
<i>V. japonica</i> , Langsd	—	24 ²	48	Miyaji, 1913
<i>V. patrini</i> , D.C....	—	36(?)	72(?)	Miyaji, 1913
BRYOPHYTES.				
<i>Mnium hornum</i> ...	Normal	6	12	M. Wilson, 1911
<i>M. hornum bivalens</i>	Aposporous ...	12	—	Él. and Ém. Marchal, 1911
<i>Bryum capillare</i> ...	Normal	10	20	Él. and Ém. Marchal, 1911
<i>B. capillare bivalens</i>	Aposporous ...	20	—	Él. and Ém. Marchal, 1911
<i>Amblystegium serpens</i>	Normal	12	24	Él. and Ém. Marchal, 1911

¹ Chromosomes less than half as large as in *V. japonica*.² Chromosomes less than half the size of those in *V. grypoceras*.

TABLE XIII.—*contd.*

Name.	Reproduction.	Chromosomes.		Author.
		<i>x</i>	<i>2x</i>	
BRYOPHYTES.				
<i>A. serpens bivalens</i>	Aposporous ...	24	48 ¹	Él. and Ém. Marchal, 1911
<i>A. irriguum</i> ...	Normal ...	12	24	Ém. Marchal, 1912
<i>A. riparium</i> ...	Normal ...	24	—	Ém. Marchal, 1912
PTERIDOPHYTES.				
<i>Scolopendrium vulgare</i> ...	—	32	64	Stevens, 1898
<i>Cystopteris fragilis</i>	—	32	64	Stevens, 1898
<i>Pteris aquilina</i> ...	—	32	64	Stevens, 1898
<i>Alsophila excelsa</i>	—	about 60	—	R. P. Gregory, 1904
<i>Nephrodium molle</i>	Fertilised ...	64 or 66	128 or 132	Yamanouchi, 1908
<i>Nephrodium molle</i>	Induced apogamy	64 or 66	64 or 66	Yamanouchi, 1908
<i>Athyrium Filix-foemina</i> ...	Fertilised ...	38—40	76—80	Farmer and Digby, 1907
<i>A. F.</i> var. <i>clarissima</i> , Bolton ...	Aposporous and apogamous	84	84	Farmer and Digby, 1907
<i>A. F.</i> var. <i>clarissima</i> , Jones ...	Aposporous and apogamous	90	90	Farmer and Digby, 1907
<i>A. F.</i> var. <i>unconglomeratum</i> , Stansfield	Aposporous and apogamous	100	100	Farmer and Digby, 1907
<i>Lastrea pseudo-mas</i>	Fertilised ...	72	144	Farmer and Digby, 1907
<i>L.p.</i> var. <i>polydactyla</i> , Wills ...	Apogamous and aposporous	64—66	132	Farmer and Digby, 1907
<i>L.p.</i> var. <i>polydactyla</i> , Dadds ...	Apogamous ...	90(?)	130(?)	Farmer and Digby, 1907
<i>L.p.</i> var. <i>cristata apospora</i> , Druery	Apogamous and aposporous	60	66(?)	Farmer and Digby, 1907
<i>Marsilia vestita</i> ...	Fertilised ...	16	32	Strasburger, 1907
<i>M. quadrifolia</i> ...	Fertilised ...	16	32	Strasburger, 1907
<i>M. elata</i> ...	Fertilised ...	16	32	Strasburger, 1907
<i>M. hirsuta</i> ...	Fertilised ...	16	32	Strasburger, 1907
<i>M. Drummondii</i> ...	Apogamous ...	32	32	Strasburger, 1907
ANIMALS.				
<i>Ascaris megaloccephala univalens</i>	Sexual ...	1	2	Boveri, 1887
<i>A.m. bivalens</i> ...	Sexual ...	2	4	Boveri, 1887

¹ Twelve "bi-gemini" or partly fused groups of four chromosomes are found. The nuclei and cells of all these tetraploid forms are proportionately larger.

TABLE XIII.—*contd.*

Name.	Reproduction.	Chromosomes.		Author.
		<i>x</i>	<i>2x</i>	
ANIMALS.				
<i>A. lumbricoides</i>				
<i>univalens</i>	Sexual	12	24	Boveri, 1887
<i>A.l. bivalens</i>	Sexual	24	48	Boveri, 1887
<i>Styelopsis</i>	—	—	8 or 4	Julin (361)
<i>Planaria</i>	—	—	6 or 3	Stevens (361)
<i>Helix pomatia</i>	—	—	48 or 24	—
<i>Echinus microtuber-</i>				
<i>culatus</i>	—	9	18	Boveri, 1888
<i>E. microtubercula-</i>				
<i>tus</i>	—	18	36	{ Boveri, 1902 and Stevens, 1902
<i>Asterias vulgaris</i>	—	9(♂)	18	Tennant, 1907
<i>A. Forbesii</i> (?)	—	18	36	Tennant, 1907
<i>Artemia salina</i> , from Cagliari	Sexual	—	42	Artom, 1911
<i>A. salina</i> , from Capodistria	Parthenogenetic	—	84	Artom, 1911
<i>Cyclops strenuus</i>	COPEPODA	11	22	Braun, 1909
<i>C. insignis</i>	"	11	22	Braun, 1909
<i>C. bicuspidatus</i>	"	9	18	{ Braun, 1909 ; Chambers, 1912
<i>C. bicuspidatus</i> var.	"	9	18	Braun, 1909
<i>odessana</i>	"	9	18	Braun, 1909
<i>C. Dybowskii</i>	"	9	18	Braun, 1909
<i>C. fuscus</i>	"	7	14	{ Braun, 1909 ; Chambers, 1912
<i>C. albidus</i>	"	7	14	{ Braun, 1909 ; Chambers, 1912
<i>C. Leuckarti</i>	"	7	14	Braun, 1909
<i>C. serrulatus</i>	"	6 + 2m. ¹	12 + 2m.	Braun, 1909
<i>C. phaleratus</i>	"	6 + 1h. ²	12 + 1h.	Braun, 1909
<i>C. viridis</i>	"	6	12	{ Braun, 1909 ; Chambers, 1912
<i>C. viridis</i> var. <i>par-</i>	"	3	6	Chambers, 1912
<i>cus</i> Herrick				
<i>C. viridis</i> var. <i>ame-</i>	"	5	10	Chambers, 1912
<i>ricanus</i> , Marsh				
<i>C. viridis</i> var. <i>brevi-</i>	"	2	4	Chambers, 1912
<i>spinosus</i>	"	4	8	Chambers, 1912
<i>C. modestus</i>	"	6	12	Braun, 1909
<i>C. diaphanus</i>	"	5 + 1m.	10 + 1m.	Braun, 1909
<i>C. prasinus</i>	"	5 + 1h.	10 + 1h.	Braun, 1909
<i>C. distinctus</i>	"	5	10	Braun, 1909
<i>C. vernalis</i>	"	3	6	Braun, 1909
<i>C. gracilis</i>	"	7	14(♀)	Montgomery, 1901
<i>Harmostes reflexulus</i>	HEMIPTERA	7	14(♀)	Montgomery, 1901
<i>Protenor belfragei</i>	"	7	14(♀)	Montgomery, 1901

¹ m stands for microchromosome = a tiny single or double chromosome.² h stands for heterochromosome = a tetrad-like chromosome smaller than the others.

TABLE XIII.—*contd.*

Name.	Reproduction.	Chromosomes		Author.
		<i>x</i>	<i>2x</i>	
ANIMALS.				
<i>Leptocoris trivittatus</i>	HEMIPTERA ...	7	14(♀)	Wilson, 1909
<i>Chariesterus antennator</i>	„	13	26(♀)	Wilson, 1909
<i>Corynocoris distinctus</i>	„	13	26(♀)	Wilson, 1909
<i>Homo sapiens</i> —				
Negro	—	—	(22(♂) 24(?)(♀)	Guyer, 1910, 1914 Montgomery, 1912
White	—	—	47(♂) 48(♀) 32 33—38 ¹	von Winiwarter, 1912 Farmer, Moore and Walker, 1906 Wieman, 1913

Evidently, in most genera the greater number of species are in the diploid condition, but occasionally, as in *Potentilla*, it would appear either that tetraploidy originated so long ago that several tetraploid species have since been derived from the original mutant, or that the tetraploid condition, being advantageous, had appeared independently and been perpetuated in several stocks. If we assume, as seems probable, that the original *Rosaceæ* possessed 16 chromosomes ($2x$), then in *Potentilla* a majority of the surviving species, so far as our present knowledge extends, are in the tetraploid condition, while in *Alchemilla* this number (32) is the fundamental one in the genus, and the apogamous species, having 64 chromosomes, are octoploid.

Indeed, it appears that species in many cases only become apogamous when they reach the octoploid condition. This would account for the apparent absence of apogamy in *Oenothera gigas*, for the number 28 can only be tetraploid. If the list be examined from this point of view it will be

¹ In cells of embryo.

seen that the apogamous species (with the exception of *Hieracium excellens*, in which the number has apparently been modified by secondary loss of chromosomes, and *Wikstroemia indica*, which is di-triploid) may in many cases be octoploid in comparison with their original ancestors. This applies to the apogamous species of *Alchemilla*, *Antennaria*, *Taraxacum*, *Rosa*, *Nephrodium*, *Athyrium*, *Lastrea*, and perhaps *Marsilia*. On the other hand, as Strasburger has pointed out, apogamy may occur in apparently diploid species, as in *Rumex*, and in *Thismia clandestina*, which appears to contain only six to eight pairs of chromosomes.

Evidently, two phylogenetic doublings of the chromosomes brings about a strong tendency to the omission of chromosome reduction and fertilisation. That apogamy is associated with high chromosome numbers has, of course, long been known, but we may further state that when the octoploid condition is reached the species very frequently becomes apogamous. According to this view, if any species of *Crepis* occurs having 32 chromosomes it should be apogamous. That the rule is not likely to apply strictly, however, is shown by the fact that species of *Rosa* having about 32 chromosomes are apogamous, while species of *Potentilla* having the same number apparently require fertilisation. The same applies to the species of *Viola*.

In this genus the Japanese species have recently been studied by Miyaji (264), who finds the $2x$ numbers to range from 12 to 72. His interesting results show that the chromosomes unite to form close pairs or gemini in diakinesis. In *V. glabella*, which belongs to the sub-genus *Dischidium*, the $2x$ number is 12 and the chromosomes are quite small. The other species examined belong to the sub-genus *Nominium*, in which the chromosome-numbers range from 20 to 72. In *V. phalacrocarpa* the number is 24, while in the closely related and somewhat

stouter *V. japonica* the number is 48—hence tetraploid in comparison with *V. phalacrocarpa*. *V. Patrini*, which has about 72 chromosomes, is again much larger than *V. japonica*. Compared with *V. glabella*, however, *V. japonica* is octoploid ($8x$) and *V. Patrini* dodecaploid ($12x$). The figures of Miyaji show, moreover, that the chromosomes in *V. japonica* are twice as large as in *V. Okuboi* var. *glabra*, while in *V. grypoceras* ($2x = 20$) they are more than twice as large as in *V. japonica*. These are relationships which have not previously been found in any other genus. Notwithstanding these very high numbers, all the species seem to reproduce normally; at least, germinating pollen tubes were found on the stigma. It is to be hoped that the European and American species of *Viola* will be worked out by some one in the same way.

Perhaps the most interesting among the recently discovered cases of tetraploidy is that of *Gyrostachys* (*Spiranthes*) *cernua* (298). *G. gracilis* and *G. cernua* are two common species in Eastern Canada and the United States as far west as Texas. The latter species is distinctly stouter in all its parts, its cells are larger and altogether it seems to form an exact parallel to the case of *Oe. gigas*. It is possible, as Miss Pace suggests, that breeding experiments with *G. gracilis* will show that it even now gives rise to this tetraploid mutant. The fact that both species have the same distribution would perhaps favour this possibility. In any case there seems no reason to doubt that *G. cernua* has originated from *G. gracilis* by mutation at some previous time. Similar relations might be established by experiments with other diploid species having tetraploid relatives.

In the bananas, investigated by Tischler (373), he found that in three different races the $2x$ numbers were respectively 16, 32 and 48, and further that the volumes of their nuclei were exactly in the ratio 1 : 2 : 3. Since the

bananas are sterile, it seems evident that the tetraploid and hexaploid conditions could not have been arrived at through the union of unreduced germ cells, however they may have originated, unless, of course, the changes occurred before they lost their fertility.

In the interesting experiments of the Marchals (258, 259), aposporous diploid gametophytes were produced by wounding the base of the capsule in certain Mosses. It was found that in monœcious species these diploid gametophytes produced sex organs and a tetraploid sporophyte, which produced diploid spores and so fixed the race. In one case, by a repetition of the process the octoploid condition was reached. In this way was "hurried up" a process which in unmolested evolution must usually take a very long time, depending apparently in mosses on chance wounding in the proper manner, and in the higher plants upon causes at present unknown. In one moss, *Phascum cuspidatum*, the diploid gametophyte produced by wounding showed certain mutational changes as well. The new form, although without sex organs, and consequently sterile, reproduced by means of groups of cells resembling propagula.

Another peculiar case of tetraploidy has been observed in the Primulas investigated by Miss Digby (88). The two species *P. floribunda* and *P. verticillata* have each 18 chromosomes ($2x$). *P. floribunda* \times *P. verticillata* gave the hybrid *P. Kewensis* which produced only thrum flowers and was therefore sterile, having also 18 chromosomes. After this plant had been multiplied by cuttings for about five years, a single pin flower appeared on one individual. It was pollinated from a thrum flower and gave rise to a fertile race of *P. Kewensis* having 36 chromosomes. From this a variety, *P. Kewensis farinosa*, having also the tetraploid chromosome number, was afterwards obtained by selection. The reciprocal cross, *P. verticillata* \times *P. floribunda isabellina*, also gave *P.*

Kewensis farinosa having 36 chromosomes. It appears, therefore, that the doubling is not a chance occurrence. Both *P. floribunda* \times *P. verticillata* and its reciprocal have given in some instances matroclinous hybrids and in other crosses *P. Kewensis*. The most probable place of origin of the tetraploid number appears to be in the fertilised egg.

The chromosome numbers in several families, but notably in the Liliaceæ and Amaryllidaceæ among plants (Müller, 1909, 1912) and the Hemiptera among Insects, (Wilson, 1909) are of much interest in any general consideration of the phylogeny of chromosome-numbers, but cannot be taken up here. In the former families the $2x$ numbers run from 10-12 up to 60. In several of the genera there are several pairs of long chromosomes and the remainder are short and rounded, the variations in the different species being undoubtedly caused by transverse segmentation of certain pairs of long chromosomes into several short ones. Among the Hemiptera, where the chromosomes are, as it were, in a state of flux, the number varies in different families from 10 to 38. Several distinct processes appear to have been at work to bring about these changes, and tetraploidy seems to have seldom appeared, although some of the cases may have been obscured subsequently by other types of change.

In the starfishes, Tennant (368) found in a cytological study of the two common American species, *Asterias vulgaris* and *A. Forbesii*, that the sperm of the former species contained nine chromosomes while fertilised eggs of *Asterias* contained in some cases 18 and in others 36 chromosomes. He was inclined to believe that in *A. Forbesii* there were two races, the tetraploid variety being the more common. A form which is perhaps a hybrid between the two species was found to contain 27 chromosomes.

Of great interest are the very recent papers on chromo-

somes in man. From the work of Guyer (167, 168) and of Montgomery (267), it appears that the male negro possesses 22 chromosomes, including 2 accessory or sex chromosomes, from which it may be inferred that the female has, at least in some cases, 24.¹ In the white man, however, von Winiwarter (451) has counted 47 chromosomes in spermatogenesis, including one accessory, and 48 in the oogonial divisions of a woman; while Farmer, Moore and Walker (101) found usually 32 chromosomes in the somatic cells (pathological tissue) presumably of white people, and Wieman (443) counted 33-38 chromosomes in an embryo, the parentage of which is not stated. Though the facts are by no means complete, it would appear that triploid and tetraploid races occur in man. Whether the number in the negro is constantly diploid is not yet certain. Are we to find that the white man originated from a black race as the result of a tetraploid mutation and its consequences? Obviously, these differences in chromosome number might account for the peculiarities of colour inheritance, etc., in white-black crosses, just as the peculiar hereditary behaviour of *Oenothera gigas* is related to its tetraploid condition.

In the genus *Cyclops*, Braun (41) finds that the change in chromosome number has been in the opposite direction, leading to a decrease in number from 22 in *C. strenuus* and *C. insignis* to six in *C. gracilis*. The diminution in number of chromosomes is found also to be correlated with a parallel progressive reduction in the fifth pair of feet and with changes in the receptaculum seminis. The smaller *h* and *m* chromosomes afford strong evidence that the diminution in chromosome number has taken place by the gradual degeneration and disappearance of particular chromosomes—a process similar to that which appears to be taking place with the Y-element of the

¹ Montgomery (267) found that the accessories were irregularly distributed in spermatogenesis.

sex chromosomes in many insects. These changes seem to be very gradual, and thus afford an excellent example of a continuous germinal variation, in contradistinction to a discontinuous germinal change or mutation. Those who are inclined to deny altogether the existence of continuity in germinal variation would do well to focus their attention upon these cases.

That other coincident changes may occur in the nuclei in *Cyclops* has been shown by Chambers (54, 55) in three American varieties of *C. viridis*. This species in Europe has 12 chromosomes, while the three varieties *parvus*, *americanus* and *brevispinosus* have respectively 6, 10 and 4 chromosomes. Those of *brevispinosus* are by far the largest and those of *americanus* the smallest, showing that chromosome fusions and fragmentations have taken place. The size of the organisms seems to be related to the amount of chromatin in their nuclei.

6.—*Analysis of the changes in Oe. gigas*

In 1909, after an extensive series of measurements of cells and nuclei in *Oe. gigas* and *Lamarckiana* (122), it was found that in every tissue examined the dimensions of the cells and nuclei were larger in *gigas*, and in many cases the increase in size was very conspicuous. The comparative measurements and the volumes deduced from them are shown as ratios in Table XIV.

TABLE XIV.

Relative Volume of Cells, *Lamarckiana* : *Gigas*.

Petal epidermis	1 : 1.96
Stigma cells	1 : 3.05
Anther epidermis	1 : 3.837
Inner wall cells of anthers	1 : 3.67
Pollen mother cells during reduction	1 : 1.507
Pollen mother cells in synapsis	1 : 1.506
Nuclei in synapsis	1 : 2.16
Nuclei in synapsis (surface area)	1 : 1.67
Tapetum (multinucleate)	1 : 1.44

It will be seen that the relative volumes of the cells were nearly 4 : 1 in the epidermis of the anther, almost exactly

3 : 1 in the cells of the stigma, 2 : 1 in the epidermis of the petals, and 1.50 : 1 in the pollen mother cells. The nuclei of the pollen mother cells in synapsis were, in accordance with Boveri's law, approximately doubled in volume.

The increase in size of cells was not only far from being equivalent in amount in all the tissues of *gigas*, but, as shown in Table XV, it was, particularly in the epidermal

TABLE XV.

Increase in Dimensions of Cells of *gigas*.

Tissue.	Length increased. per cent.	Width increased. per cent.
Petal epidermis	18.4	39.8
Stigma cells	51.9	32.2
Anther epidermis	72.8	28.4
Inner wall cells of anther	57.7	48.06
Pollen mother cells during reduction	10.9	10.3
Pollen mother cells in synapsis	18.6	10.8

layers, greater in one dimension than in the other. This result is most striking in the anther epidermis, where the increase of the cell in length is 73 per cent. and in width 28 per cent. A much more extensive series of measurements would probably reveal many more interesting relationships of this kind, and aid further in an analysis of the changes which have taken place. It is clear that not only is *gigas* built of larger bricks, but the bricks have altered their shape as well in some instances. In how far the latter change is a result of the former, and in how far the two together account for all the external and physiological changes in *gigas*, remains for further investigation to determine. But it is in any case desirable to press this point of view so far as possible by determining all the changes which may have resulted from an original doubling in the chromosome series.

The relationships of ontogeny are so complex, however, that it is almost impossible to determine which changes are primary and which are merely secondary, *i.e.*, consequent upon the primary change. De Vries believes, and perhaps rightly, that other changes, independent of the chromosome doubling, have occurred simultaneously in this mutation. But thus far nearly all the peculiarities of *gigas* which he has cited as indicating such independent changes have been shown to be reasonably explained as a direct result of the chromosome doubling or the concomitant increase in size of cells and nuclei. The marked changes in the foliage are, however, not so explainable and in this respect the mutation in *gigas* is probably comparable with that induced in the moss *Phascum cuspidatum* (see p. 206) by wounding.

Measurements of *gigas* show that the organs are, in general, stouter in all their parts than in *Lamarckiana*. This has already been referred to elsewhere (p. 118). It extends to the leaves, stems, buds, petals, ovaries, style and stigma, and the seeds. The slower growth and, as a result, the stronger biennial habit of *gigas*, as well as the greater susceptibility of the flowers to frost, may also be expected to result from the increased size of the cells and the increased ratio of volume to surface in the cells. Though the ovaries of *gigas* are proportionally longer and thicker than in *Lamarckiana*, the mature capsules are much shorter, but this is a direct result of the fact that in de Vries's race of *gigas* very few seeds mature, and therefore instead of a new specific character the short fruits are seen to be merely a result of increased sterility, which may be in turn a consequence of the larger and unwieldy cells, or perhaps of incompatible chromosome-combinations resulting from meiosis. In the ovules of the Swedish giant there is little if any more sterility than in *Lamarckiana*, and hence not only the ovaries but also the capsules as well are conspicuously larger than in the latter.

7.—*The Pollen Grains*

Perhaps the most striking change of all in *gigas* is in the pollen grains. While all other species of *Oenothera*, so far as known, have triangular or 3-lobed discoid grains, in the giant races the pollen grains are quadrangular or 4-lobed. This can now be shown to be a direct result of the increase in chromosome number, and not an independent change in any sense. The extra lobe probably represents an adjustment to the increase in the size of the nucleus (which contains 14 chromosomes instead of seven), permitting a proportional increase in the cytoplasm.

TABLE XVI.
Characters of Pollen

Plant.	Total number of grains examined.	% of "good" grains.	"Good" grains.			Remarks.
			% 3-lobed.	% 4-lobed.	% 5 or more lobed.	
<i>Oe. gigas</i> , Palermo ($\frac{2}{1}\frac{2}{2}\frac{7}{7}$)						
(a) No. I. 6 (normal plant)	1050	27.6	6.2	86.6	7.2	
(b) Another normal plant	662	42.6	2.1	90.4	7.5	
(c) No. I. 4 (smaller flowers)	2284	32.6	22.9	74.7	2.3	
<i>Oe. gigas</i> , Sweden ($\frac{2}{1}\frac{2}{2}\frac{3}{3}$)						
(a) No. II. 1	948	36.8	9.5	87.7	2.9	
(b) $\frac{2}{1}\frac{2}{2}$ I. 1 offspring of (a)	188	39.9	1.1	95.2	3.7	
<i>Oe. Lamarckiana</i> (a) ...	910	57.6	100	0	0	
(b) from <i>semilata</i> ($\frac{8}{1}\frac{6}{3}$)	269	48.3	100	0 ¹	0	Two "bad" 4-lobed grains were found. ¹
(c) from <i>lata</i> -like type ($\frac{8}{1}\frac{7}{3}$)	217	24.9	100	0	0	
<i>Lata rubricalyx</i> × <i>rubricalyx</i> ($\frac{4}{1}$). 14-chromosome offspring...	330	78.5	99.6	0.39 ²	0	One "good" and two "bad" 4-lobed grains were observed. ²

TABLE XVI.—*contd.*

Plant.	Total number of grains examined.	% of "good" grains.	"Good" grains.			Remarks.
			% 3-lobed.	% 4-lobed.	% 5 or more lobed.	
<i>lata</i> × <i>lata rubricalyx</i> ($\frac{20}{13}$)	334	76.9	99.6	0.39 ³	0	One "good" and three "bad" 4-lobed grains were observed. ³
(a) No. I. 1 (14 chromosomes) ...	237	59.1	100	0 ⁴	0	One "bad" 4-lobed grain was found. ⁴
(b) No. I. 3 (14 chromosomes) ... <i>rubricalyx</i> × <i>Lamarckiana</i> ($\frac{15}{13}$) ...	469	81.9	98.96	1.04 ⁵	0	Four "good" and one "bad" 4-lobed grain were found. ⁵
<i>lata rubricalyx</i> selfed ($\frac{82}{13}$) (14 chromosomes)	302	67.2	86.2	13.8 ⁶	0	Twenty-eight "good" and ten "bad" 4-lobed grains were found. ⁶
<i>semilata</i> , Sweden ($\frac{84}{13}$) (15 chromosomes)	211	22.8	93.7	6.3 ⁷	0	Three "good" 4-lobed grains. ⁷
Sweden, another culture ($\frac{86}{13}$). No. I. 3 (15 chromosomes) ..	217	23.5	100	0	0	
<i>lata</i> -like, Sweden (15 chromosomes) ($\frac{87}{13}$)	201	24.3	96	4 ⁸	0	Two "good" and five "bad" 4-lobed grains, and one with five lobes. ⁸
<i>rubricalyx</i> × <i>gigas</i> ($\frac{12}{13}$) (21 chromosomes) ...	106	18.9	35	65	0	
<i>gigas</i> × <i>lata rubricalyx</i> ($\frac{30}{13}$) (22 chromosomes)	281	11.4	0 ⁹	87.5	12.5	There were ten triangular grains, all bad. ⁹

In Table XVI are given the results of an examination of the pollen grains in *gigas* races and in various derivatives and hybrids. These examinations, combined with study of meiosis in the pollen mother cells of the same plants, have thrown much light on the subject, and it is now possible to state with some accuracy the relation between the extra lobe and the number of chromosomes contained in the nucleus.

In order to make clear the data in Table XVI, it may be said at once that they appear to show that a pollen grain having seven or eight chromosomes will be triangular, while one having 10 or more chromosomes will have four, or sometimes more lobes. We formerly raised the question whether all 4-lobed grains were diploid and whether it would be possible to determine the frequency of diploid grains by examining the pollen of a given plant. This question is now answered in the negative, although there is nevertheless a definite relation as above stated. Whether 9-chromosome grains will have three or four lobes is uncertain.

That a 4-lobed grain contains more than eight chromosomes, is shown in the first place by the pollen of *semilata*, for although a considerable proportion of the grains in these plants have eight chromosomes, as shown by the fact that their offspring produce about 25 per cent. *semilata* as well as by the meiotic divisions, yet the proportion of 4-lobed grains is almost zero. But while an 8-chromosome pollen grain has three lobes, it appears certain that grains with 10 to 14 chromosomes will possess four or more lobes. The evidence for this is as follows:—

In the cross *gigas* \times *lata rubricalyx*, an individual was produced having 22 chromosomes (see p. 189). Cytological study shows that the heterotypic segregation in this plant is usually $12 + 10$, so that many pollen grains receive these numbers, though owing to the omission of chromosomes from the homotypic mitosis, the number

of chromosomes received by many pollen grains is but nine. Previous examination of the pollen grains showed that there were 265 4-lobed grains (only 28 of them "good") to 10 3-lobed grains (all "bad"). That is, 96.4 per cent of the grains had four or more lobes, while only 3.6 per cent. had three lobes. It seems safe to conclude that pollen grains having at least 10-12 chromosomes will possess four lobes. Again, from Table XVI it will be seen that the plants from *rubricalyx* \times *gigas*, having 21 chromosomes, which produced less than 20 per cent. good pollen, contained amongst this 35 per cent. of 3-lobed grains. In such plants we know that the segregation is usually 10 + 11 and that some chromosomes will also be lost from the nuclei. Hence we may infer that the 65 per cent. of 4-lobed grains possessed probably not fewer than 10 chromosomes. Whether 9-chromosome grains will possess three or four lobes is, as before, uncertain.

We may therefore conclude that while the presence of occasional 4-lobed grains in a diploid plant shows that meiotic irregularities have occurred resulting in the formation of pollen grains with nine or ten or more chromosomes, it is certainly not a proof that the grains are diploid. The irregular 5- and 6-lobed grains occurring, *e.g.*, in the 22-chromosome plant above described, together with many other misshapen and sterile grains, may perhaps contain chromosome combinations which are incompatible with development. This seems the most likely explanation of the fact that only 11 per cent. of the pollen grains in this plant appear viable.

8.—*The Origin of Oe. gigas*

The question whether *gigas* originates through the union of two diploid germ cells, as de Vries believes, or in some other way, has been much debated. We have already concluded that triploidy probably results from the fertilisation of a diploid egg, and since the observation,

by Geerts (158), of a megaspore mother cell in *Oe. Lamarckiana* having 28 chromosomes, it seems probable that from such cells both the triploid and the tetraploid conditions originate. Such a megaspore mother cell might on the one hand complete the reduction processes and so form an embryo sac and an egg which is diploid. The fertilisation of this egg by a haploid male cell would produce a triploid individual. On the other hand, a tetraploid megaspore mother cell might quite conceivably develop aposporously, omitting both the meiotic divisions and fertilisation, and producing directly a tetraploid mutant as the author has suggested (136). Only direct cytological observation can settle this question.

It is, of course, quite possible that similar conditions may occur in the pollen mother cells, but it must at any rate be a much rarer occurrence, for it has hitherto never been observed, although thousands more pollen grains than megaspores have been studied. Very recently, however, in an investigation of the pollen development in the Swedish *gigas*, we have found certain conditions which indicate how diploidy in a pollen grain may originate. A mother cell was found in the stage corresponding to homotypic telophase (see Fig. 73, *f*, p. 188), in which there were three nuclei instead of four. One of these contained about 14 chromosomes, another of the same size was cut but showed 9 chromosomes, all nearly in one plane, while at the opposite side of the cell was a third group much larger containing about 28 chromosomes. If, as appears from the direction of the spindle fibres, and the fact that the chromosomes were all in one plane, such a group forms a single nucleus, then only three pollen grains would be produced from this mother cell, one of them having the unreduced chromosome-number. In the same plant were observed several other mother cells in the homotypic telophase, in which one or more of the nuclei contained approximately 28 bodies. Of course the chromosomes are in ordinary

cases dumb-bell-shaped at this time, and it is possible that the dumb-bells merely break across to form the 28 bodies. But this is not what happens in the other *Oenotheras*, and it is improbable that this is the explanation, because nuclei containing the 28 bodies appear always to be much larger than normal.

The Swedish *gigas* differs from all the other *Oenotheras* we have studied, in that the chromosome-halves during interkinesis and the homotypic prophase, instead of being closely held together by mutual attraction, show a distinct tendency to separate from each other. It may well be that if these bodies during interkinesis become quite independent of each other, the nucleus will fail to divide and a pollen grain will thus be formed having 28 chromosomes. This matter is being more fully investigated. It certainly increases the probability that diploid grains may occur in *Lamarckiana*. It should also be pointed out that in the Swedish giant, as in *gigas* itself, an irregular heterotypic distribution of chromosomes sometimes occurs (Fig. 73, e), giving 15 + 13.

In this connection it may be pointed out that Geoffrey Smith (343) has found that in hybrid pigeons in which synapsis fails to take place in spermatogenesis, the homotypic mitosis was almost wholly suppressed, thus giving rise to giant spermatozoa. Similarly, Hartman (173) has recently discovered in the grasshoppers that secondary spermatogonia are sometimes found having about 46 instead of 23 chromosomes.

9.—A 27-Chromosome Mutant

In Table XVI is listed a plant (No. I. 4) in the offspring of *gigas* from Palermo, grown in 1912, which first attracted our attention (146) by the smaller size of its leaves and flowers, although they otherwise agreed closely with their *gigas* parent. The petals were not greatly longer than in *Lamarckiana*, though broader (45 × 60 mm.). Examina-

tion of the pollen (see Table XVI) showed about 23 per cent. of triangular grains, while normal *gigas* contains only 2 per cent. to 6 per cent. of such grains. The cytological material was only sufficient to show that many small extra nuclei are formed in the pollen mother cells, and that frequent irregularities occur. A considerable number of chromosome counts in the somatic tissues of the flowers showed the presence of 27 chromosomes and no more (Fig. 73, *g*). In 13 clear cases in somatic prophase and metaphases the number of chromosomes was 27, and in one case clearly 26. Of course, the matter is a difficult one to prove, and scores of metaphase groups were discarded as insufficiently clear for demonstration. It should be mentioned that the conclusion that there were 27 chromosomes and not 28, was reached independently on two occasions separated by an interval of more than a year, during which time we had forgotten the previous determination and had not looked up the records. Hence we feel quite certain that the result is correct. Fig. 73, *g* shows one of these metaphase groups. The odd chromosome accounts for the large number of irregularities in meiosis. This leads to many chromosomes being left in the cytoplasm, and hence probably to the formation of a considerable number of triangular grains.

As regards the origin of this plant, it evidently came from the union of germ cells having respectively 13 and 14 chromosomes, through an irregular distribution of one chromosome such as has been observed in *gigas* several times. If the relation between this plant and normal *gigas* were a purely quantitative one, depending on the lack of 1 chromosome in 28 from the nuclei, then the plant might be supposed to be only $\frac{1}{28}$ smaller than *gigas* in its various organs. The decrease in size is, however, much greater, and in the size of several parts the plant is intermediate between *gigas* and *Lamarckiana*. This seems to show that other changes

accompanied the loss of a chromosome. But if the chromosomes are unlike, this conclusion does not necessarily follow.

The narrow-leaved plant (Fig. 53, p. 129) in the offspring of de Vries's *gigas* was quite sterile though its anthers contained both triangular and quadrangular grains. Its reduction divisions have not been studied, but the chromosome number is 27 or 28. We have as yet been unable, from the few mitoses available in the tapetum, to determine between these two numbers. It is therefore impossible at present to determine the significance of this narrow-leaved form. If it has only 27 chromosomes, then there are different types of 27-chromosome mutants, just as there are of 15-chromosome mutants. If it has 28, then the sterility and aberrant character of this, as well as several other forms which appear in the offspring of *gigas*, may result from the occurrence in meiosis of new combinations of the double chromosome series.

It will, we think, be evident that although the cytological work is arduous it is fundamental to any understanding of the nature of the mutations in *Oenothera*. Without this cytological knowledge we should still be drifting about in hypothetical speculation on many points which are now reasonably clear. On the other hand, like all scientific advances, the cytological results probably raise as many questions as they answer. These questions concern particularly the ever-present and almost insoluble problem of the relation between the chromosomes and the cytoplasm, and the way in which their interaction works out in the development of what we are accustomed to call external characters. Even the small steps taken in this direction are, however, not without their value, and in particular the effect of the presence (if one may use the phrase) of the extra chromosome in plants furnishes interesting comparisons with the accessory and supernumerary chromosomes in animals.

CHAPTER VII

HYBRIDISATION

THE hybridisation experiments with *Oenothera* have been prodigious, and in the space at our disposal we will endeavour merely to summarise the results so as to show the various types of hereditary behaviour which occur. The extensive and complicated experiments of de Vries have recently been recorded in a book (*Gruppenweise Artbildung*) to which the reader should refer. Many of my results have confirmed those of de Vries, and in the present account my own experiments will be chiefly chosen for illustration, in addition to those of de Vries.

The dogma of the Mendelian school, that all characters segregate in inheritance and are unmodified by crossing, has been so persistently adhered to by some writers that it is necessary to emphasise the fact that other equally well-defined types of hereditary behaviour exist. Notwithstanding the great value and importance of these numerous cases of Mendelian inheritance, especially conspicuous in the colours of the petals of flowers and the coats of mammals, of which so much has been made in recent years, it is a profound error to suppose that all inheritance can be explained in terms of the simple conception of the segregation of unmodified "factors." These conceptions, while of great service in many cases of analysis, have introduced a rigidity into all the thinking on the subject which ill corresponds with the facts observed in

many hybrid organisms. Instead of the familiar, and we believe correct, conception of plasticity and variability of protoplasm and of organisms, we are presented with conceptions of rigidity and unmodifiability which differ but little if at all from those of inorganic matter. But it seems clear that the plasticity and adaptability of organisms is one of their main properties which has made evolution possible. On the other hand, the "tenacity" of heredity in perpetuating even small differences for long periods is essential if evolution is to have any cumulative effect.

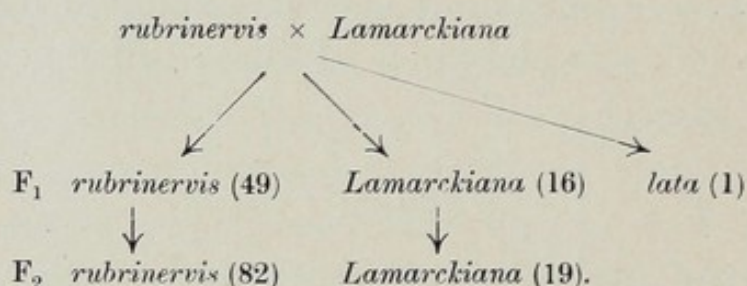
In *Oenothera* the types of hereditary behaviour may be divided into four main classes: (1) mutation crosses, (2) Mendelian splitting, (3) blending and modification of characters, and (4) twin hybrids. In a given cross, more than one type of behaviour may be exhibited by different characters. The explanation of these differences will be considered later.

1.—*Mutation Crosses*

The fundamental difference that exists between mutation crosses and Mendelian hybrids has not been realised, and indeed many workers appear to be unaware of the existence of the former type of behaviour, so effectually has it been buried beneath the accumulation of Mendelian cases in which the F_1 is uniform and splitting occurs in the F_2 and later generations of hybrids. De Vries showed, many years ago, that when *Oe. Lamarckiana* is crossed with certain of its mutants, e.g., *rubrinervis*, *lata*, and *nanella*, splitting occurs in the F_1 . Both parent types appear, and both breed true in subsequent generations. Thus in 1907 he obtained from *Lamarckiana* \times *nanella* in four crosses a total F_1 of 771 plants, which included *Lamarckiana* and in addition 17 per cent. to 34 per cent. *nanella*. The reciprocal cross gave similar results, and *nanella* \times *brevistylis* and *nanella* \times *laevifolia* also produced both

parent types in F_1 . In the same way, *Lamarckiana* \times *rubrinervis* and its reciprocal both gave *Lamarckiana* and *rubrinervis* in F_1 . The total number of F_1 offspring in the first case was 6,430, of which 59 per cent. were *rubrinervis*;¹ and in the reciprocal (*rubrinervis* \times *Lamarckiana*), in a total F_1 of 3,639 there were 50 per cent. *rubrinervis*.¹

We have obtained the same results. Thus in 1906 the cross *rubrinervis* \times *Lamarckiana* was made twice, producing in the first case an F_1 of 38 plants, of which 32 were *rubrinervis*, five *Lamarckiana*, and one undetermined. In the second case the F_1 contained 66 plants, of which 49 were *rubrinervis*, 16 *Lamarckiana*, and one *lata*. One of these *rubrinervis* selfed gave 82 offspring, all *rubrinervis*, and one of the *Lamarckiana* similarly gave an F_2 of 19 *Lamarckiana*. This is shown in the accompanying diagram:—



In Table XVII (page 223) are several similar results, though the numbers are small.

In Mendelian hybrids, when there is splitting in the F_1 it may be at once assumed that one or both parents are heterozygous. But that this is not the explanation in mutation crosses is shown by the fact that, after the F_1 splitting, *both* the types of offspring breed true in F_2 and later generations. From this fact it is reasonable to conclude that when the original cross was made, some individuals were determined in the fertilised egg, through the ascendancy of *Lamarckiana*, to become *Lamarckiana* plants; others were at the same time determined as

¹ De Vries has since (425) recognised that the *rubrinervis*-like plants in this F_1 differ from the *rubrinervis* mutant chiefly in being less brittle, and he has called them *subrobusta*.

rubrinervis. Both came from the union of a *Lamarckiana* with a *rubrinervis* germ cell, but in each case the effect of one germ cell was completely obliterated through the ascendancy of the other. This view is confirmed by the fact that both of the F_1 types show in their offspring no trace of the presence of the other parent. Instead of a heterozygous condition, in which the characters of one parent are more or less completely concealed by those of the other, the fertilisation reaction is such that the effect of one parent or the other is completely obliterated. The *Lamarckiana* and *rubrinervis* conditions are so sharply

TABLE XVII
Mutation Crosses

Date.	Cross.	No. of off-spring.	Types of offspring.
1909	<i>Lamarckiana</i> \times <i>rubrinervis</i> , F_1 .	68	<i>Lamarckiana</i> 22 + <i>rubrin.</i> 45 + 1 mutant.
1910	<i>Lamk.</i> \times <i>rubricalyx</i> , F_1 ...	11	<i>Lamk.</i> 2 + <i>rubrin.</i> & <i>rubricalyx</i> 8 + 1 mutant.
1910	<i>rubricalyx</i> \times <i>Lamk.</i> F_1 ...	4	<i>Lamk.</i> 1 + <i>rubricalyx</i> 3.
1907	<i>rubrinervis</i> \times <i>nanella</i> , F_1 ...	42	<i>Lamk.</i> 20 + <i>rubrin.</i> 20 + <i>lata</i> 1.
1907	<i>rubrinervis</i> \times <i>nanella</i> , F_1 ...	3	<i>Lamk.</i> 1 + <i>rubrinervis</i> 2.
1910	<i>rubrinervis</i> \times <i>nanella</i> , F_1 ...	79	<i>Lamk.</i> 25 (?) + <i>rubrin.</i> 52 (?) + 2 aberrant.
1910	<i>rubricalyx</i> \times <i>nanella</i> , F_1 ...	42	<i>Lamk.</i> 7 + <i>rubricalyx</i> 35.
1907	<i>lata</i> \times <i>rubrinervis</i> , F_1 ...	4	<i>Lamk.</i> 3 + <i>lata</i> 1. The <i>Lamk.</i> remained true in F_2 and F_3 .

alternative that when one is developed the other cannot even be present in a latent or recessive condition. This is obviously a very different thing from Mendelian dominance, for instead of both characters being represented in the sporophyte and afterwards segregating in the germ cells, the essential reaction which obliterates one or the other takes place in fertilisation.

The same explanation must apply *pari passu* to *Lamarckiana* \times *nanella*, for in this cross the F_1 again contains both *Lamarckiana* and *nanella*, and both types afterwards breed true. At first, such behaviour appears unlikely or even

incredible, but we may perhaps get a picture of what happens by considering *lata* \times *Lamarckiana*. Here again the split is in the F_1 , and in this case we can see that it must be so because of the presence and behaviour of the extra chromosome (see p. 179). The F_2 of this cross, however, differs from the previous crosses in that the mutant itself gives both *lata* and *Lamarckiana* offspring.

De Vries (425, p. 281 ff.) has formulated his ingenious hypothesis of pangens in three conditions to account for just such cases as these. While the explanation is a formal one, the manner in which he has applied it in detail to a vast body of breeding experiments concerning both the origin of the mutants and their subsequent hereditary behaviour is quite remarkable. In brief, a pangen may be in one of three conditions, (a) active, (b) inactive, and (c) labile. A mutation occurs when a pangen passes from one condition to the other, and new pangens may also be added.

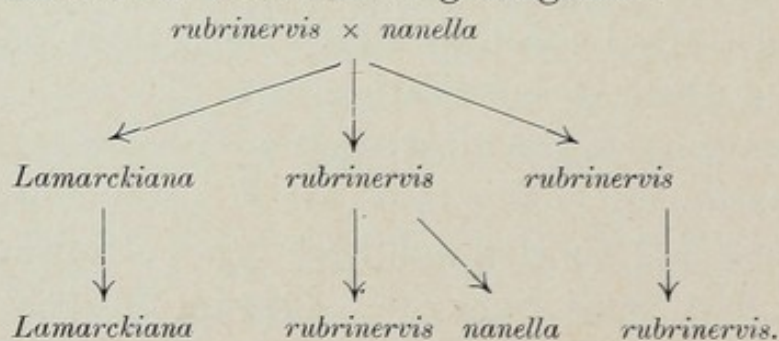
It is further assumed that—

inactive pangen \times labile pangen = split in F_1 ,

inactive pangen \times active pangen = split in F_2 .

In the origin of *nanella* as a mutation, the *alta*-pangen for height has passed into an inactive condition, from the labile condition which it occupies in *Lamarckiana*. Hence *Lamarckiana* \times *nanella* or the reciprocal will split in the F_1 . On the other hand, *rubrinervis* \times *nanella*, as is well known, produces an F_1 composed of *Lamarckiana* and *rubrinervis*. The former breeds true in F_2 , while the latter splits into *rubrinervis* and *nanella* (see also p. 227).

This is shown in the following diagram :—



This cross is in itself another proof that the mutants are not due merely to the loss of different "factors" from *Lamarckiana*; for if that were the case the above cross should give *Lamarckiana* only (just as two white races of sweet pea produced the Sicilian sweet pea again), but *rubrinervis* always appears as well in the F_1 . It is also known that *rubrinervis* never produces *nanella* as a mutant. These two independent facts, (1) that *rubrinervis* is apparently incapable of producing dwarfs, (2) that *rubrinervis* \times *nanella* only splits off dwarfs in F_2 and not in F_1 ; are both explained by the single assumption that in *rubrinervis* the *alta*-pangen is changed from the labile to the active condition. This being the case, it (1) does not, like *Lamarckiana*, give rise to dwarf mutants, and (2) active \times inactive in *rubrinervis* \times *nanella* (corresponding to presence \times absence in the Mendelian terminology) shows dominance and F_2 splitting. In *Oe. muricata* \times *nanella* the behaviour is similar, dwarfs only appearing in the F_2 .

Whatever else may be said of this hypothesis, it has the distinct merit of bringing under one point of view several classes of otherwise unrelated facts, which fully justifies its formulation; and it must be remembered that this explanation applies not only to crosses with the mutants of *Oe. Lamarckiana*, but also to a number of wild species. Whether the germinal representatives of the various character-differences be called pangens or factors is immaterial, but the pangen theory explains two distinct classes of facts where the Mendelian presence-absence hypothesis breaks down. That these crosses do not conform to the Mendelian scheme is shown by the fact that, e.g., *Lamarckiana* \times *nanella* gives dwarfs in F_1 , while *rubrinervis* \times *nanella* first produces dwarfs in F_2 .

2.—Mendelian Characters

We have already seen that some crosses between mutants, such as *rubrinervis* \times *nanella*, give essentially, although

not wholly, Mendelian results. Two of the mutants, unlike the others, behave in Mendelian fashion when crossed with the form from which they were derived. Thus in *Lamarckiana* \times *brevistylis* the peculiarities of *brevistylis* behave as a Mendelian recessive, reappearing in the F_2 , but the ratios often depart widely from Mendelian expectation (see p. 93). Again, *rubricalyx* appeared as a new Mendelian dominant character from *rubrinervis*. The original mutant was heterozygous and its offspring produced 25 per cent. *rubrinervis* (p. 104). In Table XVIII are presented the results of several crosses with *rubricalyx*, which show that its behaviour is the same as that of *rubrinervis*. The query is as to whether some of the offspring (rosettes) were *rubrinervis*, since the *rubricalyx* parent was probably heterozygous. Very likely pure *rubricalyx* \times *rubrinervis* would give F_1 all *rubricalyx* and F_2 3 : 1, though this point has not yet been finally determined.

TABLE XVIII.

Oe. mut. rubricalyx crosses.

Date.	Cross.	No. of off-spring.	Result.
1910	<i>rubricalyx</i> \times <i>Lamk...</i>	81	F_1 . <i>rubricalyx</i> 54(?) + <i>Lamk.</i> 26 + 1 mutant.
1910	<i>Lamk.</i> \times <i>rubricalyx...</i>	45	F_1 . <i>rubricalyx</i> 32(?) + <i>Lamk.</i> 9 + 4 aberrant.
1910	<i>rubricalyx</i> \times <i>nanella</i>	42	F_1 . <i>rubricalyx</i> 35(?) + <i>Lamk.</i> 7
1910	<i>rubricalyx</i> \times <i>rubrinervis.</i>	47	F_1 . (?)
1910	<i>biennis</i> \times <i>rubricalyx</i>	34	F_1 . <i>velutina</i> + <i>laeta</i> (twins)

In crosses with other species, e.g., *Oe. grandiflora* and *Oe. biennis*, the *rubricalyx* pigmentation is dominant, although there is a decrease in the amount of pigment-

¹ These plants remained rosettes and it was uncertain whether they were all *rubricalyx* or whether some *rubrinervis* appeared in the F_1 .

development. In F_2 there is sharp splitting, though in different ratios. For a summary of the results, see *grandiflora* \times *rubricalyx*, p. 255.

Oe. brevistylis and *rubricalyx* are the only mutants which show simple Mendelian behaviour when crossed with their parent, one of them being recessive, the other dominant, though the evidence in the case of *brevistylis* is not conclusive.

3.—Dwarf Crosses

The unexpected appearance of large numbers of dwarfs in interspecific crosses has been a feature of our F_2 hybrids of *grandiflora* \times *rubricalyx* (154) and its reciprocal; and Davis (80) has obtained similar results in *grandiflora* \times *biennis*. While their appearance in the cultures was a surprise, it was found on looking up the records that they might have been expected to appear. In 1909 the cross *rubricalyx* \times *nanella* was made, the mother plant being heterozygous for red. The F_1 offspring consisted of *Lamarckiana*, *rubrinervis*, and *rubricalyx*, and one of the latter was used to make the cross *grandiflora* \times *rubricalyx*. The *grandiflora* parent was shown to give uniform offspring when selfed. The above cross yielded 147 plants, which were uniform except with regard to the heterozygous *rubricalyx* character. Approximately half the plants possessed and half lacked this character. Five F_2 families were raised, and two of these contained dwarfs. This pedigree is shown in Table XIX. The numbers were 60 tall : 22 dwarf, and 23 tall : 50 dwarf. That is, a ratio of practically three tall to one dwarf in one family, and one



FIG. 78—Dwarf rosette from *Oe. grandiflora* \times *Oe. rubricalyx*.

tall to two dwarfs in another. A young rosette of one of these dwarfs is seen in Fig. 78, and a full-grown plant in Fig. 79. Fig. 80 shows one of these dwarfs in bloom. It is very much larger than *nanella*, and yet it has short internodes, characteristic branching, and very brittle leaves and stems.

Dwarfs of the same type appeared in the reciprocal



FIG. 79.—Dwarf type in F_2 of *Oe. grandiflora* \times *Oe. rubricalyx* and reciprocal.

cross, but in this case they were inherited from the *grandiflora* parent. The pedigree is shown in Table XX. It will be seen that the *grandiflora* parent was capable of producing dwarfs which bred true, in the proportion of about one dwarf to 7.6 tall. The F_1 contained only tall, but two of the nine F_2 families contained dwarfs. The latter appeared in the ratio 1 : 6.4, showing that the tendency

to produce dwarfs in the ratio of about one dwarf to seven tall was inherited from the *grandiflora* grandparent.

TABLE XIX.

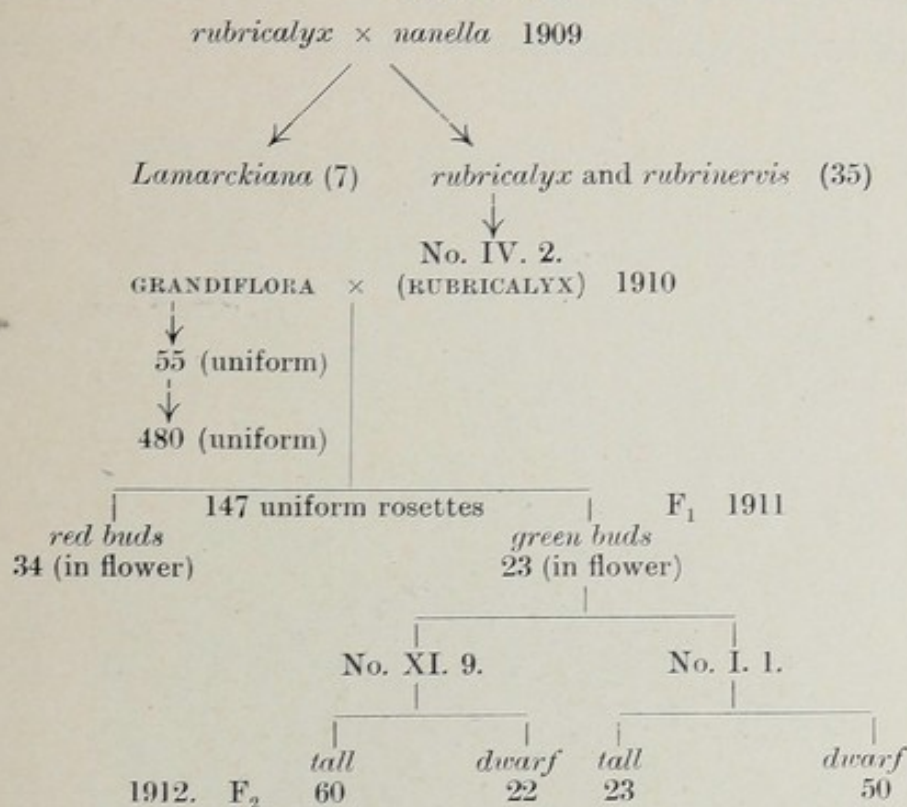
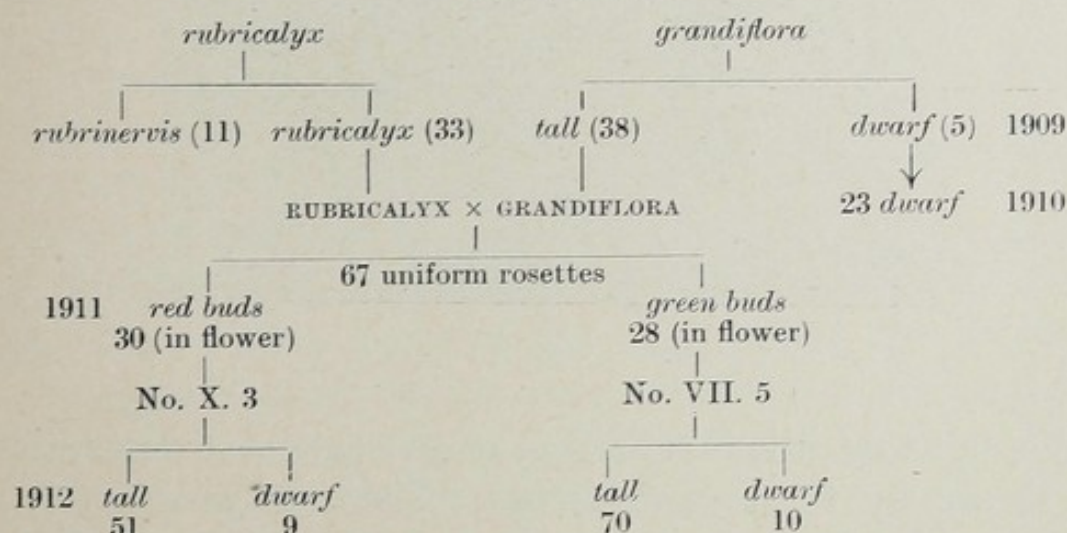


TABLE XX.



These facts propound a nice question as to how this race of *grandiflora* acquired the power of producing more than 11 per cent. of dwarf offspring. It appears that about 22 per cent. of the pollen or egg-cells or both must

be carrying the capacity for producing dwarfs, and that these dwarfs must be regarded as mutants, although their frequency is much higher than has been previously recorded. How this high capacity has been produced is a question which cannot be answered at the present



FIG. 80.—Dwarf type of Fig. 79 in bloom.

time, but that it is inherited from generation to generation is shown by these experiments. That the problem is a different one from that in the reciprocal cross (Table XIX) where nanism was introduced by crossing with a dwarf, is shown by the very much larger and entirely different ratios (3 : 1 and 1 : 2) produced in the latter case, although the type of dwarf was the same.

The F_3 cultures from *grandiflora* \times *rubricalyx* and its reciprocal are in general agreement with these results except that the fluctuations in percentages are wider. Thus in 1913, we grew 14 F_3 families (2,263 plants) from *grandiflora* \times *rubricalyx*. Three families contained fewer than 20 plants each so they are not considered, but four of the remaining 11 families contained dwarfs as in Table XXI.

TABLE XXI.

Dwarfs in F_3 families of *grandiflora* \times *rubricalyx* and reciprocal.

F ₃ Culture.	Offspring.		Ratio.	Parent F ₂ Culture.		Parent F ₂ plant.
	Tall.	Dwarf		Tall : Dwarf.		
$\frac{103}{13}$	107	2	53.5 : 1	$\frac{53}{13}$	60 : 22	$\frac{53}{13}$ No. II.3, tall
$\frac{104}{13}$	222	48	4.6 : 1	$\frac{53}{13}$	60 : 22	$\frac{53}{13}$ No. II.11, tall
$\frac{105}{13}$	34	249	1 : 7.3	$\frac{54}{12}$	23 : 50	$\frac{54}{12}$ No. I.13, dwarf
$\frac{106}{13}$	18	2	9 : 1	—	23 : 50	$\frac{54}{12}$ No. II.19, tall
$\frac{120}{13}$	275	3	91.7 : 1	$\frac{56}{12}$	115 : 0	$\frac{56}{12}$ III. 5, tall
$\frac{125}{13}$	220	12	18.3 : 1	$\frac{58}{12}$	119 : 0	$\frac{58}{12}$ II. 4, tall
$\frac{133}{13}$	56	1	56 : 1	$\frac{60}{12}$	51 : 9	$\frac{60}{12}$ III. 1, tall
$\frac{134}{13}$	38	1	38 : 1	$\frac{60}{12}$	51 : 9	$\frac{60}{12}$ III. 2, tall

Hence we see that in the F_2 family which contained 3 tall : 1 dwarf, two of the tall plants self-pollinated produced dwarfs, one in a greatly diminished and the other in a slightly diminished proportion. Again, in the F_2 family ($\frac{54}{12}$) which contained 1 tall to 2 dwarfs, one of the dwarfs when selfed produced 1 tall to 7.3 dwarfs—a great increase in dwarfs,—while one of the tall plants produced 9 tall to 1 dwarf, a correspondingly large decrease. These facts furnish the best evidence that the proportion of tall and dwarf depends in some way upon a varying ascendancy or prepotency among the germ cells as regards this character. The fact that dwarfs give rise to some tall puts out of court the Mendelian conception of dominance in this case, as well as the conception of multiple factors,

unless, forsooth, it be assumed that a sufficient number of "factors" for dwarfing will overcome a single factor for tall stem. But what advantage has such a view over one of varying prepotency? The wide fluctuations in the percentage of types in many *Oenothera* crosses must be explained in a similar manner.

Of the reciprocal cross, *rubricalyx* \times *grandiflora*, we grew, in 1913, 34 F_3 families (2,738 plants.) Eleven of these, which contained fewer than 20 plants each, will not be considered, but four of the remaining 23 families contained dwarfs. It will be remembered that the *grandiflora* in this cross was producing 1 dwarf to 7.6 tall, while two of the F_2 families produced dwarfs in the ratio of about 1 : 6.4. In the F_3 , just as the dwarf-containing families were much less frequent than in the reciprocal cross (four in 23 instead of four in 11), so the percentage of dwarfs was also much less in these families. In these respects the F_3 furnishes a confirmation of the F_2 results. Further, the frequency of dwarf-producing F_3 families, four in 23 or about one in six, is in general agreement with the frequency—1 in 7.4—of dwarfs in the dwarf-producing families. The facts are given in the latter half of Table XXI. But the dwarfs are much rarer in F_3 than in F_2 . In one case their frequency is down to about 1 per cent., and the highest frequency is only 5.5 per cent. In 1910, we made the double reciprocal cross (*grandiflora* \times *rubricalyx*) \times (*rubricalyx* \times *grandiflora*), which yielded 45 tall : 8 dwarfs (5.6 : 1). One of the tall offspring was selfed and produced 141 tall : 11 dwarfs (12.8 : 1) in 1913, showing again a falling off in the frequency of dwarfs.

Turning now to the results of Davis, he obtained in *Oe. grandiflora* \times *Oe. biennis* 141 dwarfs in an F_2 of 1,451 offspring from one individual (see Table XXII). This is 1 : 9.3 or a frequency of 9.7 per cent. A sister plant of the F_1 (10.30 Lb) produced 992 offspring, of which 147 or 1 : 5.7 (14.8 per cent.) were dwarfs. But curiously enough, the

dwarfs in the two cases were unlike. In the former case they were etiolated, narrow-leaved rosettes which gradually outgrew their etiolation and produced dwarfs having variable foliage and irregular branching.

TABLE XXII.

		<i>grandiflora</i> × <i>biennis</i>			
1910.		10.30 La.		10.30 Lb. F ₁	
1911.		tall 1310	dwarf 141	11.42 f.	tall 845
1912.		tall 241	dwarf 18	48 dwarfs.	dwarf 147
				tall 54	dwarf 8
				tall 357	dwarf 20
					65 dwarfs. F ₃

The size of flower also varied greatly. This type bred true in F₃, and one of the tall F₂ plants produced the same type of dwarf in F₃ to the number of 18 in 259 (= 1 : 13.4 or 7 per cent.). Thus the frequency of dwarfs in the F₃ (7 per cent.) was not a wide departure from that (9.7 per cent.) of the F₂.

The other type of dwarfs, which also bred true, appeared in F₂ with a frequency of 1 : 5.7 or 14.8 per cent., but in F₃ with a frequency of only 1 : 17.9 or 5.3 per cent. Thus there is a tendency, although less marked than in our cultures, for the dwarfs to be less numerous in F₃ than in F₂. These dwarfs differed markedly from those described in the previous paragraph. There was no etiolation, but the rosettes were very small, the stems unbranched and the leaves narrow.

It is a matter of much interest that in these independent experiments by Davis and the author such concordant results should have been reached. Davis did not discover the source of his dwarfs, but probably one or the other parent of his cross (perhaps *grandiflora*) was throwing dwarfs.

It is to be hoped that this point may be determined by further breeding experiments.

The experiments of de Vries with *nanella* (425) have been much too extensive even to summarise here. But a single result may be mentioned. *Oe. mut. nanella* \times *Oe. biennis* produces in F_1 two types of dwarfs, one much larger than the other, with, in some cases, a small percentage of tall plants. The dwarfs are called *debilis* and *semi-alta*, and both breed true. We have made this cross several times, using an American race of *biennis*, and obtained usually an F_1 composed of tall plants, the same as *Lamarckiana* \times *biennis*. Only occasionally, in larger cultures, did dwarfs appear in F_1 . Thus in de Vries's crosses the F_1 offspring were mostly dwarfs, while in our crosses using other races they were mostly tall. From the fact that tall and dwarfs both appear in the F_1 of this cross, de Vries concludes, as previously explained (p. 224), that in the pollen of *biennis*, the *alta*-pangen is in the labile condition.

4.—Gigas Crosses

It is interesting to compare the inheritance of nanism with that of giantism. The differences are striking. In the first place, the giant crosses are more difficult to make, and the hybrids show much greater sterility. This is undoubtedly a result of the unbalanced chromosome numbers and the meiotic irregularities to which they lead, as described in Chapter VI. In this respect *gigas* behaves in the traditional way for a distinct species, and shows that a condition of sterility in crosses may arise suddenly and is therefore not necessarily a mark of gradual divergence between two species. The important fact is proven in the case of *lata* and *brevistylis*, that a sterile form may arise suddenly by one step from a fertile one, and this moreover not as the result of a cross but after a germinal change. The existence of *gigas* in the same way shows

that a new form may arise suddenly the hybrids of which with related species are often almost completely sterile. Similarly, Osawa (289) has suggested with considerable probability that *Daphne odora*, which has 28 chromosomes and is sterile, has originated through a mutation (or is perhaps the survivor of a series of mutations) from one of the related species, all of which have 18 chromosomes.

De Vries has made a large number of crosses between *gigas* and several wild species. These include reciprocal crosses with *Hookeri*, *Cockerelli*, *biennis*, *muricata*, *biennis* Chicago, and *cruciata*, and also *gigas* \times *Millersi*. In all these cases the reciprocal crosses gave similar results, with sometimes slight differences. The hybrids were in general intermediate between the parents in all cases, and all the F_1 hybrids were completely sterile. In all the families a varying number of individuals with small or linear leaves appeared, as they do in cultures of *gigas*. The total number of plants from these crosses was 1,273. In *cruciata* \times *gigas* the flowers of the F_1 though intermediate in size were all cruciate; *gigas* \times *cruciata* produced 105 plants, of which 14 flowered, 13 of them having cruciate and one broad-linear petals.

It is noteworthy that *biennis* \times *gigas* and *gigas* \times *biennis* both give a single type which is intermediate between the parents, for this contrasts with *biennis* \times *Lamarckiana* in which the twin types (*laeta* and *velutina*) appear (see p. 245). From the fact that *gigas* produces only one F_1 type in all these crosses, de Vries concludes that in it the *laeta*-pangen has changed from the labile to the "associated" condition. Whatever the meaning of it, we have here a striking change in hereditary behaviour. And since this change from producing two types of pollen grain (*laeta*- and *velutina*-producing) to one, can scarcely be supposed to result from the mere doubling in the number of chromosomes, de Vries believes it necessary to consider this an independent change.

Gigas \times *Lamarckiana* gave in one case a fertile hybrid which continued relatively constant for five generations. The same type, intermediate between the parents, is produced by *Lamarckiana* \times *gigas*, as well as by *gigas* \times *brevistylis*, *gigas* \times *rubrinervis* (17 plants) and *rubrinervis* \times *gigas* (236 plants). All these hybrids have 21 chromosomes, except perhaps the narrow-leaved plants which appear occasionally in all the crosses. Geerts claims that he obtained F_2 plants of *gigas* \times *Lamarckiana* which were identical with the F_1 plants and yet contained only 14 chromosomes. Of course it is quite possible that, owing to meiotic irregularities, some of the F_2 offspring may have only 14 chromosomes. Indeed, this is to be anticipated if the pollinations are made late in the season. But it is highly improbable that such plants have the same external features as plants with 21 chromosomes.

The cross *lata* \times *gigas* is perhaps of greatest interest. De Vries (414) grew from this cross, in 1907, 133 plants, 68 of which were intermediate between *lata* and *gigas*, and 65 intermediate between *Lamarckiana* and *gigas*. We now know from the work of Miss Lutz that the former possessed 22 chromosomes and the latter 21. In 1909 Miss Lutz (239) obtained 40 offspring from *lata* \times *gigas*. They belonged to three types: (1) *lata* (two plants, each having 15 chromosomes); (2) *gigas* (6 plants, with about 30 chromosomes each); (3) an intermediate and somewhat variable lot of 32 plants having 21, 22, or 23 chromosomes (see Table XII, last lines, p. 180). It is to be supposed that the *lata* plants came from the apogamous development of diploid *lata* eggs, the intermediates respectively from 7 + 14, 8 + 14 or 7 + 15, and 8 + 15 chromosomes. The *gigas* plants are less certainly accounted for, but they probably originated from the fertilisation of a diploid *lata* egg by a *gigas* male cell, hence 15 + 14 (= 29) or 15 + 15 (= 30) chromosomes. This affords indirect evidence that diploid eggs occur in *lata* and that they

can be fertilised, but the matter awaits direct observation.

Nanella \times *gigas* is a still more difficult cross to make, and we have not yet succeeded in getting seeds which would germinate. From four crosses de Vries (425) obtained 75 seedlings, of which four were dwarfs, *i.e.*, miniature *gigas*. The tall plants had the appearance of *Lamarckiana* \times *gigas*, as did also the F_1 of *rubrinervis* \times *gigas* (236 plants). The F_2 of the latter cross contained 16 plants, of which 10 were *rubrinervis*, the remainder like the F_1 . These reversions to *rubrinervis* are no doubt a result of the omission of chromosomes from the pollen nuclei.

Miss Lutz (241) states that the triploid (*semigigas*) mutants are different from the corresponding hybrids, having 21 chromosomes, but the differences appear to be of a very minor character.

Oe. gigas thus behaves as all true species were formerly supposed to do, in giving intermediate and more or less uniform and constant hybrids which are for the most part sterile. This is in strong contrast to some of the other mutants.

Very few secondary crosses with *gigas* have yet been made, and they are very difficult on account of the high degree of sterility. But (*gigas* \times *Lamarckiana*) \times *gigas* and its reciprocal have yielded de Vries (425) a hybrid race (120 plants) which is again intermediate between *gigas* \times *Lamarckiana* and *gigas*. The plants had larger flowers than the hybrid parent, stouter buds, shorter and broader leaves which were more closely arranged on the stem. The chromosomes of these hybrids are being studied by Miss Lutz. Since *gigas* \times *Lamarckiana*, when the meiotic processes are regularly carried through, produces germ cells having 10 and 11 chromosomes, and since the germ cells of *gigas* contain 14 chromosomes, these secondary hybrids should have for the most part $10 + 14 = 24$ and $11 + 14 = 25$ chromosomes. When loss of chromosomes

from the germ cells leads to a diminution in these numbers, then individuals should appear which more closely resemble *gigas* \times *Lamarckiana*.

Oe. (gigas \times *Lamarckiana)* \times *Lamarckiana* and its reciprocal also produced 120 plants of which 30 bloomed. They were somewhat earlier and taller than the hybrids described in the last paragraph, with long inflorescences and buds somewhat thicker than in *Lamarckiana*. They appeared like tall and stately *Lamarckianas* and were thus again intermediate between their parents. Hence in these crosses it is clear that instead of sharp alternation there is blending and fractionation of characters in these hybrids. Their chromosome numbers should be (a) 10 or 11 + (b) 7, hence $10 + 7 = 17$, or $11 + 7 = 18$. It is probable that closer observation will show differences to exist between these two types.

It is to such series of secondary crosses as these that we may look for an ultimate solution of the question as to the precise relation between chromosome-number and the external features in *Oenothera*.

For *gigas* hybrids see also p. 189 ff., and Figs. 74 to 77.

5.—*Lata* and *semilata* Crosses

Unlike *gigas*, the *lata-semilata* series of forms gives hybrids which split in F_1 . This is obviously concerned with the behaviour of the extra chromosome. De Vries considers that, since *lata* splits in this way in crosses with the other mutants and *Lamarckiana*, its *lata*-pangen is in the labile condition. This may be expressed in terms of the chromosome facts by saying that an unbalanced (labile) condition with production of two kinds of germ cells is bound to result from the presence of the extra chromosome and the fact that the chromosomes usually behave as whole individuals.

The following crosses with *lata* are taken from de Vries

(425, p. 244 ff.). The cross *lata* \times *Lamarckiana* has been made many times, yielding a total of 3,180 plants. About 20 of these are *lata*, and the remainder *Lamarckiana*, except occasional mutants. We have obtained a similar result with small numbers, one F_1 family consisting of five *lata* and eight *Lamarckiana*. Again, *lata* \times *rubrinervis* produced 534 plants, of which 13 per cent. were *lata*.

Nanella, on the other hand, produces three types in F_1 , *lata*, *Lamarckiana*, and *nanella*, about a third of each. That is, *lata* \times *nanella* splits in F_1 both as regards the *lata* characters and height, from which it is concluded that the *alta-pangen* in *lata* is in the same (labile) condition as in *Lamarckiana*. There should be also in this cross some *lata nanella* having 15 chromosomes.

The crosses with other species are of even greater interest. Thus *Lamarckiana* \times *biennis* gives a single intermediate type, but *lata* \times *biennis* produces two types in F_1 , one having certain *lata* and certain *biennis* features, the other intermediate between *Lamarckiana* and *biennis*. These, no doubt, have respectively 15 and 14 chromosomes. *Lata* \times *biennis* gave, in an F_1 of 258 plants, 53 per cent. having *lata* characters.

Lamarckiana \times *Hookeri* gives the twin types *laeta* and *velutina* in F_1 (see p. 242); and as might now be expected, *lata* \times *Hookeri* produces four types, *Lamarckiana-laeta*, *Lamarckiana-velutina*, *lata-laeta* and *lata-velutina*. Although they have not been examined, there can be no doubt since the author's work with Miss N. Thomas on the chromosomes of *lata rubricalyx* and *lata biennis*, that *lata-laeta* and *lata-velutina* also have 15 chromosomes. These two forms will both doubtless split in their offspring into the ordinary and the *lata*-like form. The *lata-laeta* plants were, however, sterile in their pollen, but the *lata-velutina* continued to split as above stated.

A pollen-producing race of *lata*, which seems to be the same as my *semilata*, produced in the F_4 two dwarf mutants,

one of which resembled *Lamarckiana* and the other *lata* in foliage (425). The former bred true while the latter (*lata nanella*, doubtless, having 15 chromosomes) produced 27 dwarfs, 18 of which had the ordinary characters and nine those of *lata*. This shows again that wherever the extra chromosome is present splitting will occur in the offspring, no matter with what other features the *lata* characters may be associated.

The hereditary behaviour of *lata* is thus perfectly clear and consistent throughout. It is in no sense Mendelian, but is concerned with the presence and distribution of the extra chromosome. The resulting odd number of chromosomes brings about what de Vries calls the labile condition of the *lata*-pangen.

The hereditary behaviour of *semilata* is essentially the same as that of *lata*, except that in its offspring are included some *lata* as well as *semilata*. The nature and cause of the difference between *lata* and *semilata*, which is only one of degree, is not at present clear.

In summarising the various behaviours of the mutants on crossing, we may say that several distinctive types of hereditary behaviour are exhibited. (1) *Oe. rubrinervis* and *nanella* (as well as *scintillans*, *oblonga*, and *laevifolia*), when crossed with *Lamarckiana*, split in F_1 and afterwards breed true; (2) *lata* and *semilata* under the same conditions split in F_1 and continue to do so in later generations; (3) *rubricalyx* and *brevistylis* behave in some crosses though not in all,¹ respectively as dominant and recessive Mendelian characters; (4) *gigas* and *semigigas* give intermediate blends which usually breed true although very largely sterile.

It is evident that the type of hereditary behaviour of a mutant is a criterion indicating to some extent the nature of the change which has taken place in its origin, and it

¹ *Rubricalyx* \times *brevistylis* gave a hybrid which was intermediate in nearly all its features (see p. 94, footnote).

is of much theoretical interest that from this point of view the mutants can be classified into several distinct categories.

6.—*Heterogamous and Isogamous Species*

In this section we wish to consider the hereditary behaviour of the wild species of *Oenothera*. They have been classed by de Vries on the basis of his extensive crossing experiments, as isogamous and heterogamous. The former are those species the reciprocal crosses of which give the same result, and hence the pollen and egg cells of which are carrying the same potentialities. To this series belong *Oe. Hookeri*, *Oe. Cockerelli*, *Oe. strigosa*, and *Oe. Lamarckiana*. Thus *Hookeri* \times *Cockerelli* and its reciprocal both produced intermediate hybrids, which were closely similar except that the former had rather broader, less pubescent leaves. Otherwise they agreed, both having leaves shorter than in *Hookeri* and with points bent aside less than in *Cockerelli*, less red than in *Hookeri*, less bluish than in *Cockerelli*; flowers of intermediate size, self-pollinating.

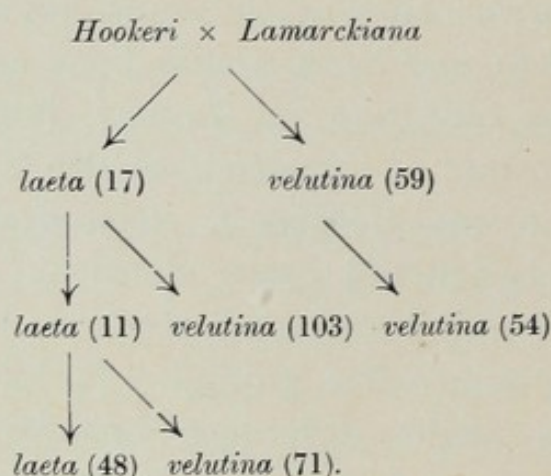
In the same way *Hookeri* \times *strigosa* and its reciprocal were nearly though not quite identical. Thus the latter was more red and had looser rosettes, which were more closely appressed to the ground. Perhaps we may conceive of this slight difference between the reciprocal crosses in isogamous species as brought about in the following way. If x and y represent respectively the germ cells of *Hookeri* and *strigosa* which unite to form the cross, then, remembering that the male cell consists only of a nucleus while the egg contains cytoplasm as well, the reciprocal crosses would be as follows:—

$$\begin{aligned} \textit{Hookeri} \times \textit{strigosa} &= (x \text{ nucleus} + x \text{ cytoplasm}) + y \text{ nucleus} \\ \textit{Strigosa} \times \textit{Hookeri} &= (y \text{ nucleus} + y \text{ cytoplasm}) + x \text{ nucleus} \end{aligned}$$

These slight divergences between the reciprocal crosses may then result from the initial difference in the cytoplasm of the two species. Such an explanation cannot, however, apply to the numerous patroclinous hybrids in *Oenothera*.

Another important point regarding these species-hybrids is that, in addition to constituting a single uniform intermediate type, they breed true, and thus fulfil all the conditions which were formerly supposed to hold universally for species-hybrids.

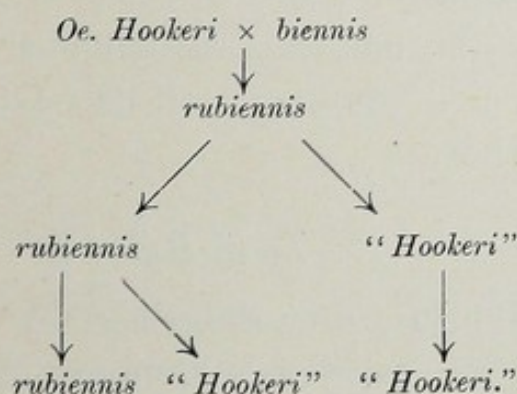
An important difference between *Lamarckiana* and the other isogamous species is that, although its reciprocal crosses with wild isogamous species are the same, yet both produce instead of a single hybrid type the twins *laeta* and *velutina* (see p. 244). This is true of *Hookeri* \times *Lamarckiana*, *Cockerelli* \times *Lamarckiana*, *strigosa* \times *Lamarckiana*, and their reciprocals. The same result is obtained when *Lamarckiana* is replaced by *nanella*, *brevistylis*, and other derivatives. Thus *Hookeri* \times *Lamarckiana* gave de Vries the following result :—



If now we examine the heterogamous species we find that their reciprocal crosses are quite unlike, showing clearly that their pollen grains and egg cells are carrying different qualities. The species shown to be in this condition are *Oe. biennis*, *Oe. muricata*, *Oe. cruciata*, *Oe. Millersi*, and *Oe. biennis* Chicago. This remarkable condition has also been found by Miss Saunders (328) in her experiments with Stocks. Perhaps, however, it is not so remarkable as it first appears. For in all hermaphrodite plants and animals there is a regular segregation of the sexes at some point in the ontogeny, and in higher plants of course this

must occur independently in the development of every flower, at the time the primordia of the anthers and ovaries become separated. From this point of view we really have in heterogamous plants a case of sex-limited inheritance, one character being carried only by the male element and the other only by the female. In many of these cases, however, the pollen may be carrying only one character while the eggs carry both, or *vice versa*. Hence such characters are not strictly sex-limited, and it has been considered probable that in these cases half the pollen, namely, that which carries the missing character, aborts. This may be the significance attaching to the frequent occurrence of 50 per cent. of sterile pollen grains in *Oenothera* species, although it has never been shown that the aborting grains are two from each tetrad of spores. A more probable explanation, depending on the failure of certain classes of hybrid embryos to develop, will be considered in the next section.

In *Hookeri* \times *biennis*, however, it is found that in the F_1 hybrids (*rubiennis*) the egg cells bear only the *Hookeri* characters while the pollen bears the (segregated) characters of both parents. Thus, unlike the other hybrids in the series, *Hookeri* \times *biennis* splits in F_2 , splitting off a form resembling *Hookeri*. The following diagram shows what happens:—



An understanding of the constitution of heterogamous species is obtained by crossing them reciprocally with

species which have been shown to be isogamous. These reciprocal crosses are of course unlike. In this way it was found by de Vries (425) that in most heterogamous species the characters carried by the pollen nearly represented the external features of the species, while those borne by the egg cells were quite different. In other words, in heterogamous species the functional male and female germ cells are unlike in their latent capacities.¹ Thus, to take an instance, *Cockerelli* \times *biennis* gave an F_1 type which was uniform except that some of the plants were yellowish and weak. This hybrid bred true in subsequent generations, and it nearly resembled the pollen-parent, *biennis*. The reciprocal, *biennis* \times *Cockerelli*, gave a uniform green and constant type called *conica*, which resembled most strongly the pollen parent. Similarly, *biennis* \times *biennis* Chicago and *biennis* \times *Hookeri* produce a *conica* type. On the other hand, *biennis* \times *cruciata*, *biennis* \times *muricata*, and *Lamarckiana* \times *cruciata* produce a type called *gracilis*.

In all these cases there is nothing resembling the Mendelian recombination of many independent characters, but the various hybrid types remain for the most part constant and uniform in later generations, except in an occasional character such as flower-size. They thus follow in a general way the traditional rules for species-crosses. A striking feature of these crosses is that single characters do not behave independently but the hybrid organism acts as a whole and all its parts are more or less modified together.

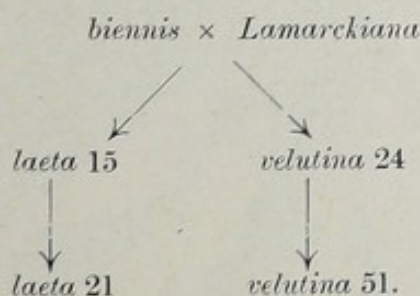
7.—*Twin Hybrids*

The twin hybrids, first described by de Vries in 1907, introduce another type of behaviour. Like the mutation

¹ It may be that the heterogamous condition is, in some cases, the result of a heterozygous condition and the selective elimination, not of germ cells, but of embryos after fertilisation.

crosses, there is F_1 splitting into two types, but instead of these types being the same as the parents they are widely unlike either parent and in some features they cannot be said to be intermediate. Thus *Lamarckiana* and several of its derivatives produce the twin types *laeta* and *velutina* in F_1 when crossed either way with the isogamous species *Cockerelli*, *Hookeri*, and *strigosa*. They also produce the same twin types when crossed as pollen parent with *biennis*, *muricata*, and *Millersi*, and when used as seed-parent in crossing with *biennis* Chicago. These twin types both breed true in later generations, except when *nanella* is the pollen parent. Then the *laeta* remains constant, while *velutina* splits off dwarfs in the second and later generations. In some cases, however, dwarfs appear in F_1 . Thus in *biennis* \times *nanella*, we obtained in 1910 an F_1 of 43 plants, of which 28 were *velutina*, seven *laeta*, six dwarfs and two aberrant.

The rosettes of *laeta* and *velutina* from *biennis* \times *Lamarckiana* are shown in Figs. 81–82, and the flowering shoots in Figs. 83 and 84. The rosette leaves in *laeta* are broader, more crinkled, and darker green than in *velutina*. The stem-leaves in the latter are also narrower, furrow-shaped, and gray-green in colour. The results obtained from this cross were as follows:—



Similar results were derived from *biennis* \times *laevifolia*, *biennis* \times *rubricalyx* and *biennis* \times *nanella*. There is therefore no doubt that this is a characteristic type of behaviour.

Although both twin types breed true, their male and



FIG. 81.—Rosette of *laeta* type in F_1 of *Oe. biennis* \times *Lamarckiana* (cf. Fig. 82).



FIG. 82.—Rosette of *velutina* type from *Oe. biennis* \times *Lamarckiana*.

female germ cells are unlike, as is shown by crossing them reciprocally. *Laeta* \times *velutina* then gives both parent types, while *velutina* \times *laeta* gives 100 per cent. *laeta*. Also *biennis* \times *laeta* produces only *laeta* and *biennis* \times *velutina* only *velutina*. By ingenious reasoning from these and other results, de Vries concludes that in *laeta* the



FIG. 83.—*Laeta* twin type from
Oe. biennis \times *Lamarckiana*
(cf. Fig. 84).



FIG. 84.—*Velutina* twin type from
Oe. biennis \times *Lamarckiana*.

laeta-pangens of the pollen are in the active and the egg cells in the labile condition, while in *velutina* they are in the inactive condition in both eggs and pollen.

When *biennis* Chicago and *cruciata* are pollinated by *Lamarckiana* or its derivatives, another pair of twin types, *densa* and *laxa*, are produced, and *densa* remains constant while *laxa* splits off a third type called *atra*.

Fresh light has recently been thrown on the twin hybrids and certain other hereditary peculiarities of the *Oenotheras* in an important paper by Renner (316A). By an examination of the seeds and embryos of several species and hybrids he has shown that certain types of character-combinations regularly fail to produce viable embryos. Thus, using a peculiar race of *Oe. muricata* from Venedig, he found that *muricata* \times *biennis* produced only small seeds which contained no embryos. When examined microscopically it was observed that the young embryos were very irregular in shape and soon ceased to develop altogether. In *muricata* \times *Lamarckiana* the embryos degenerated still earlier.

On the contrary, in *biennis* \times *Lamarckiana* (obtained from de Vries), which produces the twin types, there were no degenerating embryos, and the seeds when examined were all found to be good. The reciprocal cross, *Lamarckiana* \times *biennis*, produces a single hybrid type and Renner found that half its seeds were smaller and contained undeveloped embryos. The numbers of seeds ran very close to equality (173 good : 169 bad). Evidently, then, one of the twin types, corresponding to *laeta*, is unable to develop owing to some constitutional incompatibility, though both are formed as in the reciprocal cross. It is probable that selective elimination of embryos will thus occur in many cases where the pollen and egg cells are carrying different qualities, as is the case in *biennis*.

In the same way it was found that *biennis* \times *muricata* and *muricata* \times *biennis* when self-pollinated give 50 per cent. of bad seeds. They are thus constantly heterozygous, the two homozygous types failing to develop in each generation of embryos. It appears, however, that pure *biennis* and *muricata* produce only good seeds, so that the heterogamous condition of these species cannot be explained in this way.

Renner applies the same reasoning to *Lamarckiana*, in

which de Vries found that only one-third of the seeds germinate. He discovers that half the bad seeds contain very small embryos while the other half are without embryos. The mutants *nanella* and *rubrinervis* also produce 50 per cent. of bad seeds, from which it is concluded that they as well as *Lamarckiana* are always heterozygous for the *laeta-velutina* factor, the two types of homozygous embryos degenerating. Selective elimination of embryos thus furnishes an additional means of explaining the hereditary peculiarities of the *Oenotheras*, and it will no doubt apply to other plants. In animals, the fact that, *e.g.*, homozygous yellow mice never appear is already well known. The causes of such marked differential viability are at present obscure.

8.—*Double Reciprocal Crosses*

Another interesting type of behaviour which has been investigated in *Oenothera* is with regard to the results of double reciprocal crosses. Thus *muricata* \times *biennis* in many crosses gave always a uniform F_1 (130 plants) which was strongly patroclinous and continued to breed true in the second, third, and fourth generations, in all features except size of flower. Similarly, the reciprocal, *biennis* \times *muricata* produced a uniform F_1 which remained constant in four generations of breeding. The latter hybrid was also patroclinous, resembling *muricata* more closely than *biennis* and hence unlike the reciprocal. *Biennis* and *muricata* are both heterogamous species, carrying different potentialities in their eggs and pollen grains, whence arises this result.

By crossing these constant hybrids with each other, de Vries (421) obtained double reciprocal hybrids. Thus, using B and M to stand for the species, two double reciprocal hybrids are possible, $(B \times M) \times (M \times B)$ and $(M \times B) \times (B \times M)$. The former was found to produce a hybrid almost identical with *biennis*, and the

latter with *muricata*; that is, there is in both cases reversion to the "outside" grandparents. Certain features, such as size of petals, are exceptions to this rule. The characters of the grandfather are not transmitted through the mother, and those of the grandmother are not transmitted through the father. Goldschmidt (162) suggested an explanation of this through merogony, the male nucleus being supposed to develop in the egg cytoplasm while the egg nucleus degenerated. Later study by Renner (316) has not borne out this explanation, but instead normal fertilisation was found to take place. It seems probable that this behaviour results from the elimination of certain types of embryos as in the twin hybrids.

Several other double reciprocal crosses—with *biennis* and *biennis* Chicago, *biennis* and *cruciata*, *biennis* and *strigosa*, *biennis* and *Hookeri*, and *biennis* and *Lamarckiana*—gave similar results. It was also found that in the *biennis-muricata* series (*muricata* \times *biennis*) \times *muricata* [= (M)B \times M] gave *muricata*, and (*biennis* \times *muricata*) \times *biennis* [= (B)M \times B] gave *biennis*. In the same way (M)B \times B produced (M)B and B \times (B)M = (B)M. These are known as sesquireciprocal hybrids.

In the next section it will be shown that *grandiflora* does not follow this interesting type of behaviour, at least in crosses with some species. In such cases, probably all the hybrid embryos develop.

9.—Grandiflora Crosses ¹

We have made extensive series of crosses between *grandiflora* and *Lamarckiana*, and between *grandiflora* and *rubricalyx*, and Davis (77, 79, 80) has studied *grandiflora* \times *biennis*. First let us consider *grandiflora* \times *rubricalyx* and its reciprocal. The results can only be briefly summarised. The parents are compared in Table XXIII.

¹ The full results of these crosses in F₁ and F₂ are given in my paper (154), to which reference should be made.

TABLE XXIII.

Comparison of the Main Characters of the Parents.

<i>Oe. grandiflora</i> , Solander.	<i>Oe. mut. rubricalyx</i> , Gates.
1. Leaves of rosettes thin, nearly or quite smooth, with <i>pale red blotches</i> on the surface; petioles and midribs always wholly <i>green</i> on ventral surface and usually also on <i>dorsal</i> surface.	1. Leaves of rosettes thicker, more pubescent, considerably <i>crinkled</i> , without red blotches on the blade; petioles and midribs more or less bright red on the <i>ventral</i> surface, and to a lesser extent on the dorsal surface. (The ventral red is nearly always well developed at one stage of the rosette, but if that stage is missed the plant becomes indistinguishable from <i>rubrinervis</i> until the buds appear.)
2. Rosette stage more or less <i>evanescent</i> and often entirely omitted, the plants being physiologically " <i>early</i> " in their development.	2. <i>Rosette stage well developed</i> , the plants being physiologically <i>later</i> in their development.
3. Later rosette leaves characteristic in shape, long and rather broad-pointed, with long, irregularly margined petiole. ¹ (See Figs. 85, 86, and 1, p. 13).	3. Leaves of mature rosette rather narrow-pointed.
4. Stem leaves thin, <i>smooth</i> , <i>pointed at both ends</i> ; petioles green. (See Fig. 89, p. 261)	4. Stem leaves thicker, <i>crinkled</i> , <i>broad and sessile or aurate at base</i> , except the lower ones; petioles red ventrally and sometimes less so on the dorsal surface.
5. Buds <i>green</i> throughout or with a small amount of red on the sepals (see Fig. 87).	5. Hypanthium and sepals, especially their median ridges, <i>deep red</i> (see Fig. 36, p. 105).
6. Buds <i>slender</i> and <i>rounded</i> , sepals <i>thin</i> , sepal tips long and setaceous (Fig. 87).	6. Buds <i>stouter</i> , <i>quadrangular</i> , sepals <i>thick</i> , sepal tips shorter and stouter (Fig. 36).
7. Buds wholly <i>glabrous</i> , or covered only with a soft, inconspicuous pubescence of <i>short hairs</i> .	7. Buds covered with soft pubescence, and in addition a conspicuous <i>long, pointed type of hair</i> arising from <i>red papillae</i> .
8. Flowers usually somewhat smaller than in <i>rubricalyx</i> and others of the <i>Lamarckiana</i> series (petals 30-40 mm. in length).	8. Petals about 40 mm. in length.

¹ The most characteristic type of leaf, with prominent basal lobes, is always omitted under the usual conditions of culture, so it need not be considered here.

THE PARENT TYPES

The two types differ from each other in every feature throughout all stages of their development.

The F_1 and F_2 results have already been published, but

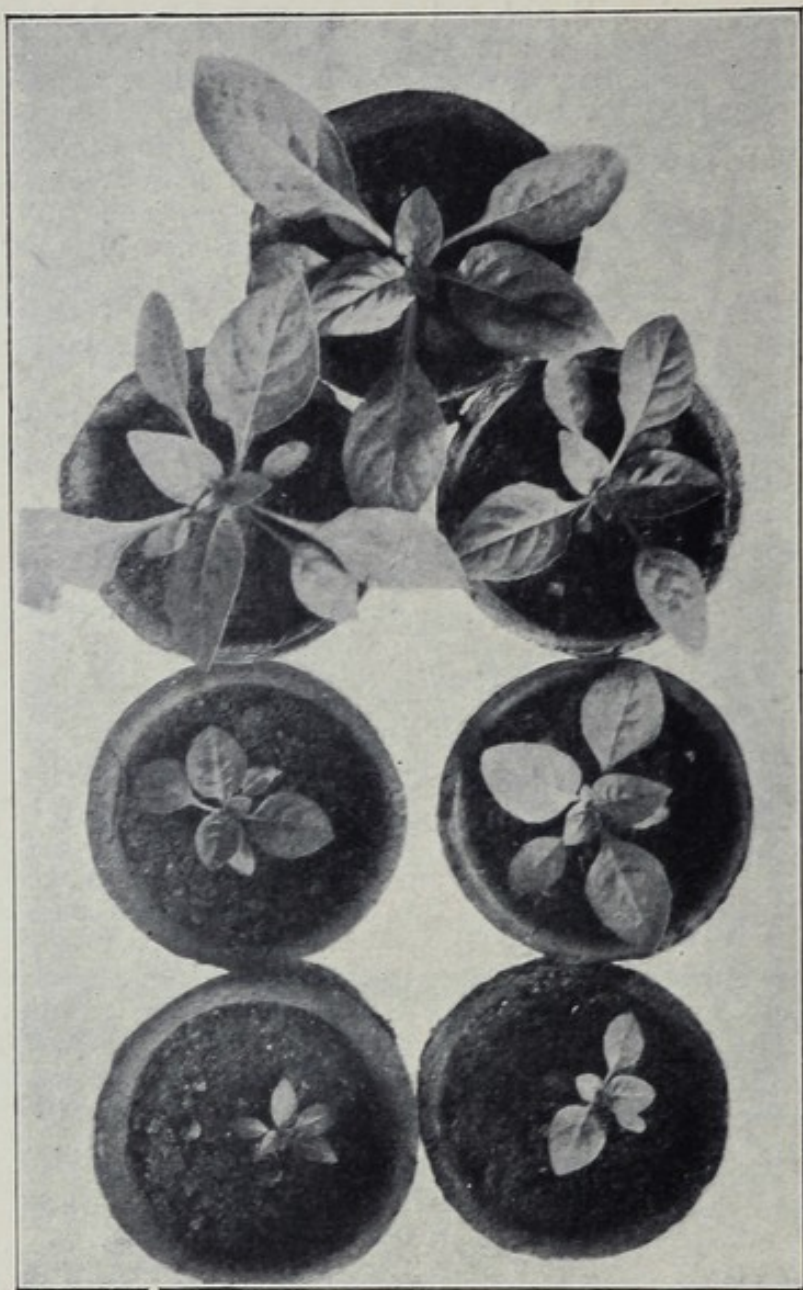


FIG 85.—Seedlings of *Oe. grandiflora*.

the F_3 , grown in 1913, will be included here as well. We have already described the inheritance of dwarfism in these crosses (see p. 227). We may consider next the inheritance of the red pigmentation (R) which distinguishes *rubricalyx* from *rubrinervis* and all the other forms.

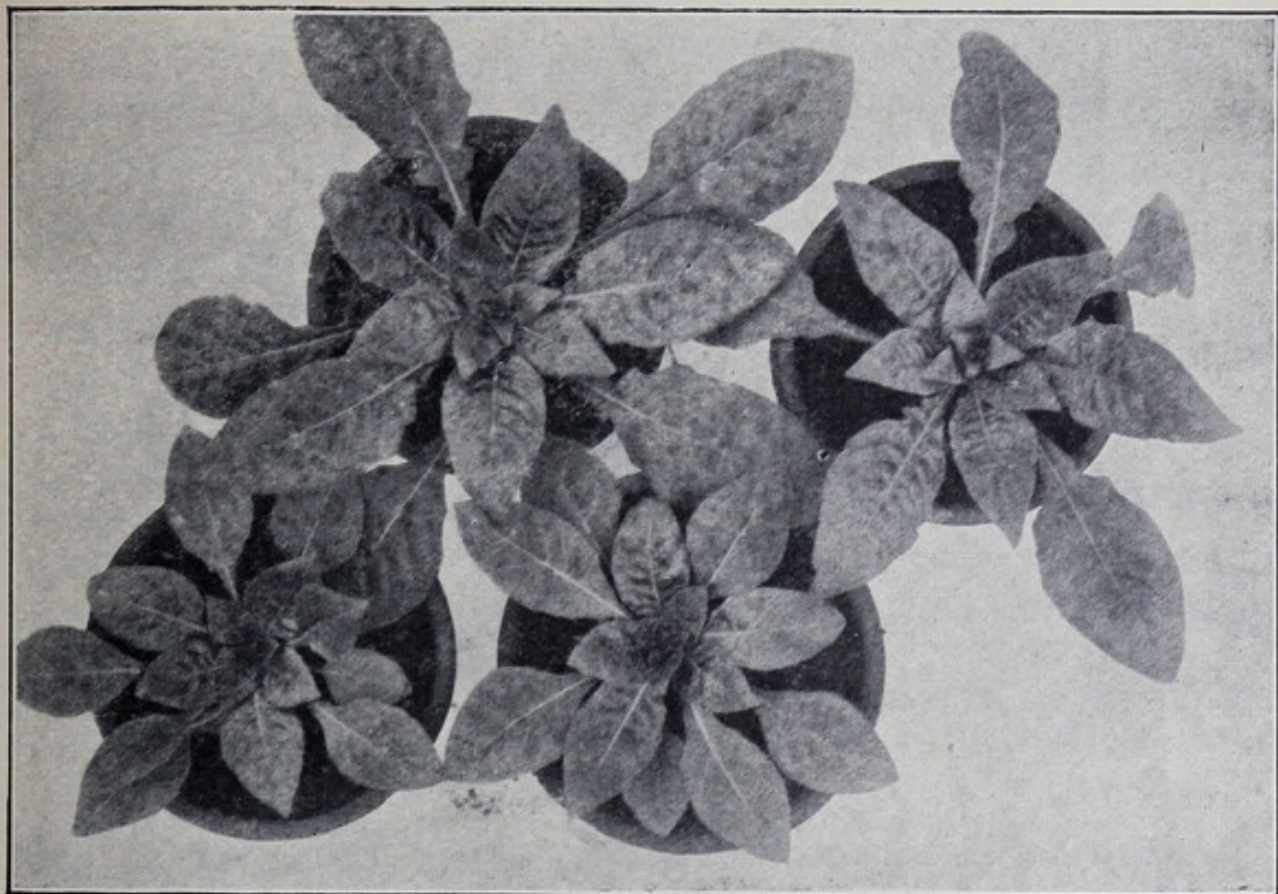


FIG. 86. —Young rosettes of *Oe. grandiflora* from Alabama.

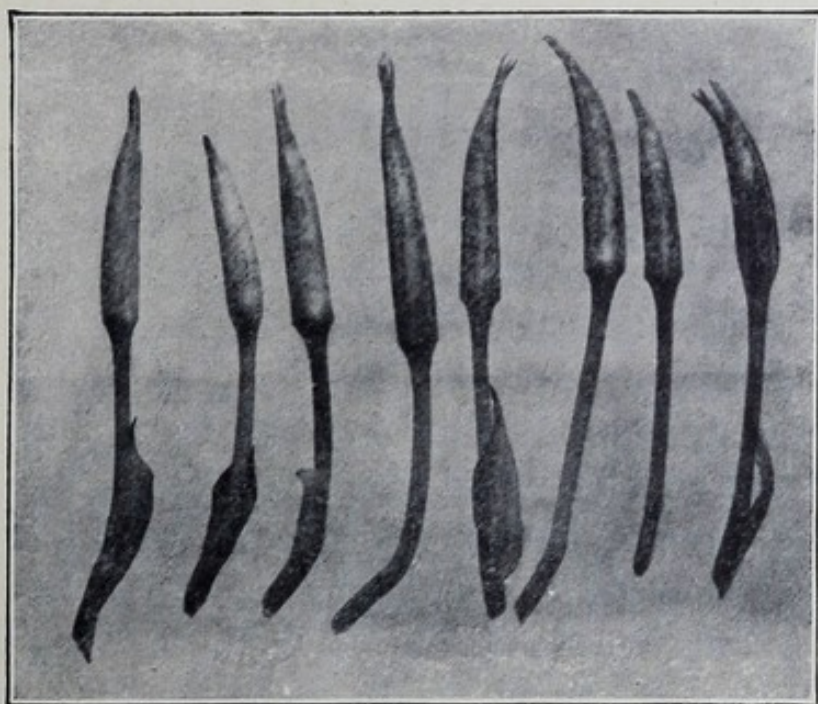


FIG. 87. —Buds of *Oe. grandiflora* (cf. Fig. 36, p. 105).

9A.—*Inheritance of R*

The origin of R through a mutation is explained elsewhere (see p. 102). In the first cross with *grandiflora* it behaves as a sharp dominant Mendelian unit. In both *grandiflora* \times *rubricalyx* and its reciprocal the *rubricalyx* parent was heterozygous for R and so gave about 50 per cent. offspring with red buds and 50 per cent. with green (see p. 106). The number of plants in the F_2 and the various back-crosses and double reciprocal crosses, which were grown in 1912, is shown in Table XXIV.

TABLE XXIV.

Summary of *grandiflora-rubricalyx* hybrids.

Cross.	No. of families.	No. of plants.
<i>grandiflora</i> \times <i>rubricalyx</i> , F_2	5	504
<i>rubricalyx</i> \times <i>grandiflora</i> , F_2	12	1039
(<i>grandiflora</i> \times <i>rubricalyx</i>) \times <i>grandiflora</i> ..	3	373
(<i>rubricalyx</i> \times <i>grandiflora</i>) \times <i>grandiflora</i> ..	4	579
(<i>rubricalyx</i> \times <i>grandiflora</i>) \times <i>rubricalyx</i> ..	1	44
(<i>rubricalyx</i> \times <i>grandiflora</i>) \times (<i>grandiflora</i> \times <i>rubricalyx</i>)	1	62
(<i>grandiflora</i> \times <i>rubricalyx</i>) \times (<i>rubricalyx</i> \times <i>grandiflora</i>)	3	193
	29	2794

The proportions of red-budded and green-budded plants in the various F_2 families are given in Table XXV. A 3 : 1 ratio might have been anticipated but it will be seen that the ratio R : r varies from 3 : 1 to 4 : 1, 5 : 1, 6 : 1, 10 : 1 and even 33 : 1. Again, it will be seen that in Table XXV, the ratios fall into three main groups. Cults. 55, 63, and 64 are all derived from one F_1 plant (No. VII. 2), and all show approximately the same 5 : 1 ratio. Hence it must be concluded that different F_1 plants, though externally alike, have the capacity of producing the dominant and recessive characters in different proportions.

TABLE XXV.

Distribution of the Dominant Character, R, in F_2 .

No. of 1912 culture.	No. of F ₁ parent plant.	Character of buds in parent F ₁ plant.	Offspring.		Ratio.
			R.	r.	
I. <i>grandiflora</i> × <i>rubricalyx</i> , F ₂					
Cult. 48 (a)	IX. 4	red buds	68	16	4.25 : 1
Cult. 49 (b)	VI. 6	red buds	142	15	9.5 : 1
Cult. 50 (c)	III. 2	red buds	133	4	33.25 : 1
			343	35	9.8 : 1
II. <i>A. rubricalyx</i> × <i>grandiflora</i> . F ₂					
Cult. 55 (a)	VII. 2	red buds	66	13	5.0 : 1
Cult. 59 (b)	IV. 4	red buds	45	14	3.2 : 1
Cult. 60 (c)	X. 3	red buds	47	3 ¹	15.7 : 1
Cult. 61 (b)	VIII. 1	red buds	134	44	3.04 : 1
Cult. 62 (a)	VI. 1	red buds	67	13	5.15 : 1
Cult. 63 (a)	VII. 2	red buds	82	13	6.30 : 1
Cult. 64 (a)	VII. 2	red buds	77	15	5.13 : 1
			518	115	4.50 : 1

If ratios of 3 : 1 and 15 : 1 only were obtained, then the Mendelian hypothesis of multiple factors might apply, but the frequency of the 5 : 1 ratio shows that it does not, and some other explanation must be sought. Before suggesting that explanation we may examine the F_3 ratios, obtained in 1913. These are given in Table XXVI.

TABLE XXVI.

Distribution of R in F_3 families.

No. of 1913 culture.	No. of F ₂ parent plant.	Character of buds in F ₂ parent plant.	Offspring.		Ratio.
			R.	r.	
I. <i>grandiflora</i> × <i>rubricalyx</i> , F ₃ .					
93	42. II. 18	red buds (R)	280	0	4.125 : 1 4.23 : 1
95	49. I. 2	red buds (Rd)	312	0	
96	49. IV. 2	red buds ..	6	0	
97	49. VI. 2	red buds ..	231	56	
98	50. III. 2	red buds ..	237	56	
99	50. IV. 8	red buds ..	4	0	

¹ Also one plant exactly intermediate between R and r, and 9 dwarfs whose buds, through an oversight, were not recorded.

TABLE XXVI.—*contd.*

No. of 1913 culture.	No. of F ₂ parent plant.	Character of buds in F ₂ parent plant.	Offspring.		Ratio.
			R.	r.	
I. <i>grandiflora</i> × <i>rubricalyx</i> , F ₃ .					
100	50. V. 2	red buds ..	275	0	
101	50. VI. 5	red buds ..	97	0	
102	53. — 15	<i>rubrinervis</i> (ru)	0	5	
103	53. II. 3	green buds (r)	0	109	
104	53. II. 11	green buds (r)	0	270	
105	54. I. 13	intermediate in pigmentation.	283		
106	54. II. 19	intermediate in pigmentation.	20		
II. <i>rubricalyx</i> × <i>grandiflora</i> , F ₃ .					
108	55. I. 3	red buds (R)	57	31	1.84 : 1
109	55. I. 4	red buds (R)	155	0	
110	55. I. 5	red buds (R)	6	0	
111	55. I. 6	red buds (R)	22	6	3.7 : 1
112	55. II. 1	red buds (R)	2	3	
113	55. II. 4	green buds (r)	0	181	
114	55. III. 1	red buds (R)	112	69	1.6 : 1
115	55. IV. 1	red buds (R)	13	0	
117	56. II. 1	red buds (R)	12	2	
118	56. II. 7	green buds (r)	0	53	
120	56. III. 5	red buds (R)	278 ru.		
121	56. IV. 1	green buds (r)	0	22 gr.	
123	58. I. 2	<i>rubrinervis</i> buds ru.	21 ru.	17 gr.	
124	58. II. 2	green buds (r)	0	5 gr.	
125	58. II. 4	green × red buds (R).	182	29	6.3 : 1
126	58. IV. 1	green × red buds R.	4	2	
127	58. IV. 2	green × red buds gr.	0	18 gr.	
133	60. III. 1	red buds (R)	55	2	27.5 : 1
134	60. III. 2	red buds (R)	37	2	18.5 : 1
138	62. I. 2	red buds (R)	14	0	
141	62. II. 4	red buds (R)	166	0	
142	62. IV. 1	red buds (R)	72	6	
143	63. II. 12	green buds (gr)	0	63 gr.	
144	63. III. 1	red buds (R)	59	1	59 : 1
145	63. IV. 1	red buds (R)	79	37	2.1 : 1
146	63. V. 2	red buds (R)	5	3	
147	64. II. 1	green buds (r)	0	185	
148	64. IV. 1	red buds (R)	80	34	2.4 : 1
149	65. III. 12	intermediate buds.	186		
150	65. III. 5	green buds (gr)	0	88 gr.	
156	66. IV. 1	green buds (ru)	28 ru.		
157	66. IV. 9	green buds (ru)	165 ru.		

From this table several interesting facts appear. Among the 13 F_3 families from *grandiflora* \times *rubricalyx*, in six the dominant character R bred true, in three the recessive character r came true, in two families an intermediate condition of pigmentation came true without any indication of segregation, and in two families there was sharp splitting in a ratio approximately 4 : 1. Of course, the numbers in families 96 and 99 are so small that splitting might have occurred in them. But without considering these, there remain four large dominant families which failed to split, while only two families segregated. The segregation in these families was, however, sharp and clear. Moreover, of the families which failed to segregate, some had constantly more anthocyanin than others. Thus the buds in family 95 were constantly darker red (Rd) than in number 93, showing that they were producing more anthocyanin. Comparison of Tables XXV and XXVI shows that the F_3 family No. 98, which split in the ratio 4 : 1, was derived from F_2 family No. 50, which contained only four r to 133 R.

In the F_3 families Nos. 105 and 106 a new condition of stability is reached as regards pigmentation, both in the tall and dwarf plants (see Table XXVI, p. 256). The buds in all these individuals were intermediate, the sepals, including usually the median ridge, being pale red, with very pale red on the hypanthium. This condition was uniform in both cultures, with very little tendency to vary and no suggestion whatever of segregation. The pigment was very weakly distributed over the whole bud. Indeed the quantity was probably no greater than in *rubrinervis*, though its distribution was more nearly that of *rubricalyx*.

These various facts taken together clearly exclude the possibility of applying any multiple factor hypothesis.

If now we examine the 32 F_3 families from the reciprocal, *rubricalyx* \times *grandiflora*, we find that five of them bred

true to R (although only two of these families are large enough to show that they are certainly homozygous); eight produced only r, lacking the red hypanthium; three families (Nos. 120, 156, and 157) bred true to the *rubrinervis* pigmentation of the buds (ru); one (No. 123) did not properly split as indicated in the table, but showed a range of conditions in the buds, from *rubrinervis* to *grandiflora*; one family (No. 149) was derived from an F_2 plant the bud-pigmentation of which was intermediate. The bud cone was weak red (colour pattern 7) with streaks of pale red on the hypanthium. This intermediate condition was inherited in the 186 offspring. Their buds varied somewhat. All had the colour pattern 5 on their sepals. In some the hypanthium appeared green to the naked eye, and from this condition a complete series was found from the merest traces of red on the hypanthium to weak red throughout. This race therefore fluctuated about a new centre of variability.

In the 14 remaining families splitting took place, the ratio R : r varying enormously (see Table XXVI), from 1.6 : 1 to 6.3 : 1 and even 59 : 1. In four of the larger cultures it was near 2 : 1, and in one of them about 6 : 1. There is again not the slightest evidence in favour of the operation of two independent "factors" for red. Indeed, when we consider the fact that intermediate conditions can be formed and when so formed apparently breed true (or rather, vary about their new centre of stability), the suggestion becomes absurd. It should be pointed out that splitting is the rule, and a blended condition arises less frequently, but apparently whenever it occurs it breeds true. Among 2,794 plants in the F_2 families, 20 such intermediates were observed.

The F_3 families thus strengthen the interpretation of the F_2 , and the only hypothesis we have been able to formulate which meets all the facts regarding the inheritance of pigmentation in the buds is one of varying prepotency in

different individuals. In any case, an hypothesis of rigid duplicate "factors" is excluded.

It is, we think, not difficult to understand why instead of a 3 : 1, widely varying ratios are obtained in F_2 and F_3 . The 3 : 1 ratio may be usefully regarded as the result of a condition of *balance*. When two organisms agree in all characters but a single one, as in *rubricalyx* \times *rubrinervis* and many Mendelian crosses, sharp alternation results, with development or non-development of the dominant character. But if, as in *rubricalyx* \times *grandiflora* and its reciprocal, the cross be made with a different species the metabolism and physiological development of which are diverse, then the condition of balance is lost; with the result that the unit-character, even though it originated suddenly by a mutation, is modified in its development and may with further crossing be fractionated until it is unrecognisable or lost altogether.

As will be seen from Table XXIII (p. 251), *grandiflora* and *rubricalyx* differ from each other in every feature, and especially in their physiology and rate of development. It is not therefore surprising that, as these experiments have shown, *grandiflora* has an inhibiting effect in not only reducing the percentage of R's in the offspring when used in secondary crosses, as (*rubricalyx* \times *grandiflora*) \times *grandiflora*, but also in reducing the quantity of anthocyanin produced in the R individuals.¹ For the experiments on which this is based see (154).

When, therefore, individuals are crossed which are in agreement except for one or a few unit-character differences, their germ cells fit into each other like lock and key; but in crosses between distinct species which differ from each other in their physiological metabolism there is no such fit. The hybrids which develop as the result

¹ That this inhibiting effect is not due merely to the action of an "inhibiting factor," is shown by the fact that in F_2 families the proportion of R individuals is often much greater than 3 : 1.

of the interaction of two more or less conflicting metabolisms, differ from either parent in nearly all their features. They give blends, and when crossed back with one of the parents these blends may be blended again.

9B.—*Inheritance of Foliage-characters*

Blended conditions in these hybrids are shown as regards the pubescence, shape of buds, rate of development,



FIG. 88.—*Oe. grandiflora* grown at St. Louis, Mo.

time of flowering, and foliage. In all these cases, there is intermediacy in the F_1 , with a variable condition running



FIG. 89.—*Oe. grandiflora* as grown in England.

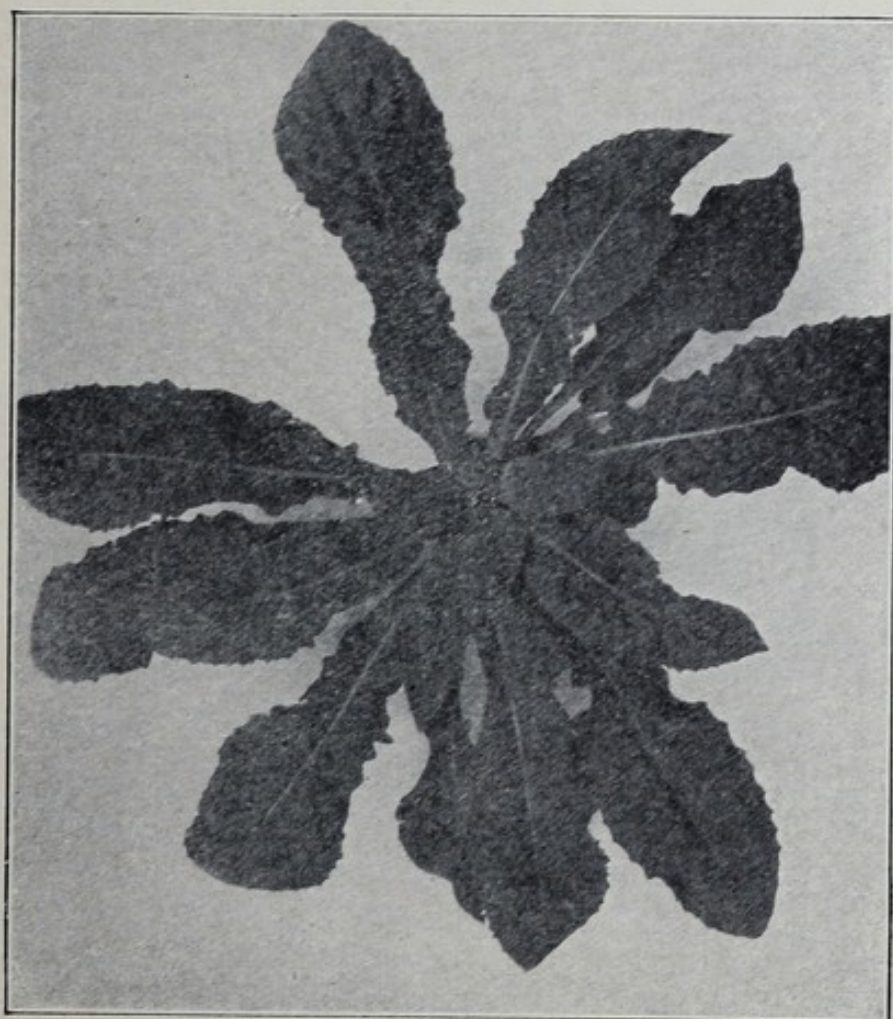


FIG. 90.—*Oe. grandiflora* × *rubricalyx*, F_1 rosette.

towards both parents in F_2 . East, in particular, has endeavoured very persuasively to show investigators that there is some advantage in supposing such a condition to arise through the chance distribution of numbers of rigid multiple "factors" for each character. But it is clearly impossible to apply this conception with any

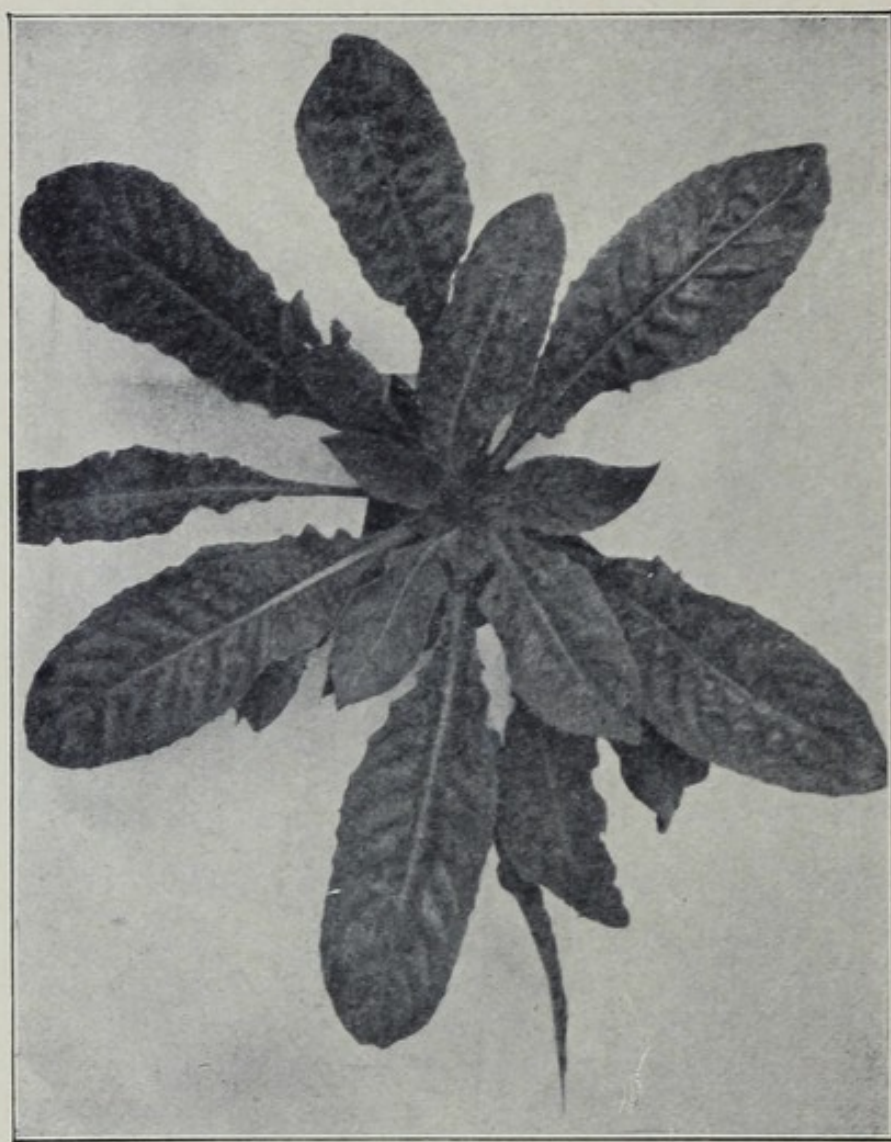


FIG. 91.—*Oe. mut. rubricalyx* \times *grandiflora*, F_1 rosette.

advantage to the foliage characters in these *Oenothera* crosses.

Among blending characters, on which we have made a large amount of detailed observation, we can consider here only the main facts regarding the foliage in crosses between *grandiflora* and *rubricalyx*. Figs. 1 (p. 13)

and 34 (p. 103) show rosettes of the parent species, and Figs. 88, 89 and 35 (p. 104) the full-grown plants. The F_1 rosettes of the reciprocal crosses are uniform, intermediate between the parents, and somewhat unlike each other (see Figs. 90 and 91). The same is true of the fully developed F_1 plants (*cf.* Fig. 92 with Figs. 89 and 35).



FIG. 92.—*Oe. rubricalyx* \times *grandiflora*, F_1 .

In the F_2 , of which we grew five families from *grandiflora* \times *rubricalyx* and 12 families from *rubricalyx* \times *grandiflora*, numbering in all 1,543 plants, a complete series of intermediate forms is found, and these are, in general, the same for both reciprocal crosses. A few of them are illustrated in Figs. 93 to 97. Each family, for



FIG. 93.—*Oe. grandiflora* × *rubricalyx*, F₂. Foliage $\frac{b}{2}$ – b. $\frac{c}{4}$.



FIG. 94.—*Oe. grandiflora* × *rubricalyx*, F₂. Foliage p – b. s.

the most part, gave the whole series of F_2 forms, though there were certain differences between families. There were, however, apparently no complete reversions to the foliage of either parent.

The 45 F_3 families, which were derived from different



FIG. 95.—*Oe. grandiflora* \times *rubricalyx*,
 F_2 . Foliage p.s.

F_2 individuals, were in many cases very uniform, fluctuating around the condition of the F_2 parent. In some families this fluctuation was extremely narrow, and a number of such uniform and characteristic races were produced. Other families were more variable in certain features, and a few showed a considerable range of variation.

The great bulk of the plants came nearest either parent, but a number of new blended races also occurred. These are real blends, and not merely combinations of factors, for they breed true and the foliage, buds, and pigmentation all show *modifications* of the original characters. The



FIG. 96.—*Oe. rubricalyx* × *grandiflora*, F_2 .
Foliage p.s.

conception of “purity of the gametes” does not apply here; there is blending instead.

As a means of classifying roughly the main foliage-characters we have used the following symbols: *p* = leaf pointed at base, *b* = broad at base; *c* = crinkled, *s* = smooth or free from crinkling. Intermediate conditions were represented by fractions. A large number

of the F_2 plants were carefully classified so far as this system would permit, but it must be understood that the variation is really continuous and cannot be represented accurately by any classification. In this system *p.s.*, for example, indicates a plant having leaves nearly



FIG. 97. — *Oe. rubricalyx* \times *grandiflora*, F_2
Foliage *p.s.*

smooth and pointed at base, hence resembling *grandiflora*, and $\frac{b}{2} \cdot \frac{c}{4}$ means having leaves averaging about half as broad at base as *rubricalyx*, with a quarter the amount of crinkling. Similarly n = the amount of long hairs on the buds of *rubricalyx*, and fractions of this the number present in the hybrids.

With these symbols, Fig. 98 represents one of the plants (No. $\frac{9.5}{1.3}$ I. 1) in an F_3 family numbering 312 individuals, whose foliage is indicated by the formula $\frac{b}{2} \cdot s$. This family was derived from an F_2 plant ($\frac{4.9}{1.2}$ I. 2, see Table XXVI), having the same foliage-formula. The whole culture fluctuated about this mean. The buds also varied somewhat in pubescence, having $\frac{a}{4}$ to 0 long hairs, and the sepals were all very uniformly dark red



FIG. 98.—*Oe. grandiflora* \times *rubricalyx*, F_3 .

(Rd) in colour. Fig. 99 shows another F_3 plant (No. $\frac{9.8}{1.3}$ XII.4), derived from an F_2 plant (No. $\frac{5.9}{1.2}$ III. 2) having the formula $b \cdot \frac{s}{2}$, i.e., whose leaves were as broad at base as in *rubricalyx* but only half as much crinkled. This F_3 culture contained 293 plants, and exhibited the whole range of variation between the two original parents. The individual in Fig. 99 stood rather close to *rubricalyx*.

Fig. 100 represents one plant (No. $\frac{1.0.3}{1.3}$ V. 1) in a remarkably uniform F_3 family of 109 individuals derived from



FIG. 99.—*Oe. grandiflora* × *rubricalyx*, F_3 ,
buds red, stout.



FIG. 100.—*Oe. grandiflora* × *rubricalyx*,
 F_3 family.

No. $\frac{53}{12}$. II. 3. This race stood much nearer *grandiflora* than *rubricalyx*, but had peculiarly narrow, closely repand-denticulate foliage. The buds resembled those of *grandiflora*, being slender but somewhat smaller. They were slightly squarish, covered with fine pubescence, with only rare long hairs, the sepals yellowish-green. In another F_3 family (No. 105) derived from a dwarf (No. $\frac{54}{12}$



FIG. 101.—*Oe. grandiflora* \times *rubricalyx*, F_3 , in offspring of dwarf F_2 type. Cf. Figs. 78 to 80 (p. 227 ff.).

I. 13) the 34 tall offspring were all of one type, as shown in Fig. 101. The leaves were $\frac{b}{2} \cdot \frac{c}{4}$ drooping, the branches spreading; the buds glabrous, slender to stouter and squarish, and the pigmentation of the buds was clearly intermediate and nearly uniform, being pale red on the sepals and very pale on the hypanthium. Such a race shows peculiarities in every feature, and if found wild

might well be described by "splitters" as a species. Many other equally distinct F_3 races were obtained.

These are only a few samples from the F_3 races which were derived from *grandiflora* \times *rubricalyx*. We have obtained numbers of equally unexpected races from seeds of the intercrossing *Oenotheras* at Birkenhead.



FIG. 102.—*Oe. rubricalyx* \times *grandiflora*, F_3 , buds green, slender. From same F_3 family as Fig. 103.

Among F_3 families from *rubricalyx* \times *grandiflora*, Figs. 102 and 103 are from culture No. 113, showing the range of variation in this relatively uniform *grandiflora* race. The buds varied from rounded, slender, greenish and smooth as in *grandiflora* (Fig. 87) to stouter, squarish, and with $\frac{n}{4}$ long hairs (Fig. 36). These plants also differed



FIG. 103.—*Oe. rubricalyx* × *grandiflora*, F₃,
buds green, rather stout (cf. Fig. 102).



FIG. 104.—*Oe. rubricalyx* × *grandiflora*, F₃,
buds red.

considerably in foliage, though they all had smooth leaves resembling *grandiflora*. The stems, and the midribs of the leaves were red. Another F_3 family (No. 115)—a very handsome type—is represented by Fig. 104. The buds were light red, somewhat squarish, soft-pubescent



FIG. 105.—*Oe. rubricalyx* \times *grandiflora*, F_3 .

without long hairs; the leaves $\frac{p}{2}$. s, nearly smooth, midribs white. Finally, Fig. 105 shows a plant from another F_3 culture (No. 149 . VIII. 20). This family numbered 186 plants. It was derived from an F_2 plant (65. III. 12) whose foliage was b. $\frac{3c}{4}$. and the pigmentation of the buds intermediate between *rubricalyx* and *rubrinervis*. The offspring came true, not only to the intermediate

pigmentation but in foliage as well, the leaves being recorded as $b. \frac{c}{2}$. with white midribs and little variation.

The cross (*rubricalyx* \times *grandiflora*) \times *rubricalyx* yielded an offspring of 44 plants which were again on the average intermediate between their parents in foliage,



FIG. 106.—(*Oe. rubricalyx* \times *grandiflora*)
 \times *rubricalyx*. Foliage $b. \frac{c}{2}$.

although they showed considerable variation. One of them is illustrated in Fig. 106. The buds in all were dark red. Figs. 107, 108 and 109 are taken from the offspring of three different individuals in the above cross. The cultures were grown in 1913 and numbered respectively 157, 17, and 98 plants. The buds were dark red in all. In

the first culture the foliage varied from smooth to considerably crinkled. The second culture, which was derived from a plant (No. $\frac{79}{2}$ II. 2) which was almost identical with *rubricalyx*, consisted of 17 individuals, 15 of which were indistinguishable from *rubricalyx* (cf. Figs. 108 and 35), one was *lata* and one probably *oblonga*. Hence in this



FIG. 107.—(*Oe. rubricalyx* × *grandiflora*)
× *rubricalyx*, F_2 (cf. Fig. 106).

family, there was complete segregation to one parent. The third culture came from a plant whose foliage-formula was recorded as $\frac{b}{2} \cdot \frac{c}{4}$. The same type of leaf is found in the offspring, as shown by Fig. 109.

If now we examine the results of (*rubricalyx* × *grandiflora*) × *grandiflora*—a cross which was made four times with a total of 300 plants—we again obtain hybrids



FIG. 108.—(*Oe. rubricalyx* × *grandiflora*) × *rubricalyx*, F_2 (cf. Fig. 35, p. 104).



FIG. 109.—(*Oe. rubricalyx* × *grandiflora*) × *rubricalyx*, F_2 (cf. Figs. 107, 108).

intermediate between the parents, although with some variation. One of these (from Cult. No. $\frac{67}{12}$) is shown in Fig. 110. Figs. 111 and 112 are different offspring of the same cross (Cult. No. $\frac{71}{12}$), the latter having narrow foliage. They are all obviously nearer *grandiflora* than *rubricalyx*. They constitute a new blended though variable type



FIG. 110.—(*Oe. rubricalyx* \times *grandiflora*) \times *grandiflora*.
Foliage p.s. (cf. Fig. 89, p. 261).

which is about $\frac{3}{4}$ *grandiflora* and $\frac{1}{4}$ *rubricalyx*. From two plants of the latter cross (Cult. No. $\frac{71}{12}$), families were grown in 1913. They contained respectively 15 and 10 plants. One of the latter is shown in Fig. 113. The buds are *spotted* with red, the colour pattern being broken up, as not infrequently happens in this back-cross with *grandiflora*. The foliage is also characteristic, resembling that of *grandiflora* but with some crinkling.

These few selected cases will be sufficient to show the endless variety of forms occurring in these crosses, and the hopeless impossibility of trying to apply to them a conception of fixed segregating units. This is all the more



FIG. 111.—(*Oe. rubricalyx* × *grandiflora*)
× *grandiflora*. Foliage p.s.

impossible because frequently there is a considerable range of variation in the foliage of a single individual.

On the other hand, there is a distinct tendency for characters to vary independently. In some F_3 families certain bud characters are variable while the foliage is relatively uniform, and in other families the reverse may be the case. Again, there appears to be a tendency for

the population to return towards the original parent types, though this is very difficult to estimate when such a host of character-differences is concerned. The objection to the application of the conception of Mendelian units to these characters is therefore that, although they vary



FIG. 112.—(*Oe. rubricalyx* \times *grandiflora*) \times *grandiflora*. Foliage p.s. narrow.

more or less independently, they do not come out "pure," but modified and blended. The idea that the characters of organisms are mutually independent of each other has therefore been over-emphasised, for they are really dependent upon each other in various ways for the manner and degree of their expression in the organism and inheritance in later generations.

We have already pointed out that in various double-reciprocal hybrids of *Oenothera* there is segregation in such a way that one or other of the grandparental types reappear. This is not true, however, of the double reciprocal crosses between *grandiflora* and *rubricalyx*. Thus (*rubricalyx* \times *grandiflora*) \times (*grandiflora* \times *rubricalyx*) ought in this



FIG. 113.—(*Oe. rubricalyx* \times *grandiflora*) \times *grandiflora*, F_2 . Buds red-spotted.

way to produce pure *rubricalyx*. But it gives instead series of forms like the other *grandiflora* hybrids. One of the plants from this cross in F_2 is shown in Fig. 114. It clearly resembles *grandiflora* rather more than *rubricalyx*. A number of other second generation families from these double-reciprocal crosses gave similar results.

In closing this account of crosses between *rubricalyx*

and *grandiflora*, we may conclude that although the character R, which originates through a mutation, is dominant in its morphological aspect, *i.e.*, as regards the extent and distribution of the pigmentation, yet the amount of pigment produced or the capacity of the cells for antho-



FIG. 114.—(*Oe. rubricalyx* × *grandiflora*) ×
(*grandiflora* × *rubricalyx*), F₂.

cyanin-production is quantitatively inherited. Usually there is a sharp distinction between presence and absence of this character,¹ but in occasional cases intermediate conditions in distribution as well as quantity of pigment occur, and breed true. The wide variations in the ratio

¹ This is believed to be due to the fact that the character-difference, R, resides in one chromosome. See Chapter IX.

R : r in different F_2 families is also incompatible with the shuffling of fixed Mendelian units. All that can be said is that *grandiflora* exerts an inhibiting effect on anthocyanin-production (though the percentage of R plants in F_2 is increased), and that different hybrid plants vary in their prepotency as regards the proportion of R plants they can produce. The same is true of the inheritance of dwarfs, except that dwarfness is a recessive character in which, however, some dwarfs can give a certain percentage of tall offspring.

As regards the foliage it need only be added that not only intermediacy and blending occur, with modifications of many characters, but a certain amount of segregation (for the most part impure) gives rise to a large number of new F_3 races, which breed perfectly true in some cases and exhibit a varying degree of variability in others.

In contrast with these results we have made an equally extensive series of crosses between *Lamarckiana* and *grandiflora*, carrying the hybrids to the F_3 generation. These crosses give a strikingly different kind of behaviour, which is more in harmony with the results obtained by de Vries in crosses between *Lamarckiana* and other species. Thus the F_1 contained two sharp and distinct types unlike either parent, and these afterwards bred true except for splitting into two types in some cases. Why these hybrids should be so different from those with *rubricalyx* does not appear, but the fact remains that they were. Perhaps one may describe the difference by the statement that in some crosses the tendency to segregate into well-defined types is clear, while in other crosses this tendency is more or less obliterated by the tendency to form blends.

10.—*Summary*

In *Oenothera*, several types of hereditary behaviour have been demonstrated. These types of behaviour seem to depend in part, in the case of mutation-crosses and

Mendelian characters, on the condition in which the character is present in the organism. Mere presence or absence of a "factor" is insufficient to explain the behaviour in mutation-crosses. Other types of behaviour apparently depend upon the nature of the character concerned. Thus we have blending in the *gigas* crosses, in which the hereditary phenomena are obviously limited by the chromosome behaviour, and we have F_1 splitting in *lata* hybrids for the same reason. Again, the chemical nature of the pigmentation-character R is probably connected with its sharply alternative inheritance in contrast to the usually blended condition of the foliage, although even here we have seen that R also blends in certain respects and in some cases.

The Mendelian 3 : 1 ratio apparently depends upon a condition of balance in the organism. If that balance is disturbed by crossing with a species having a different metabolism, then the expression and inheritance of the characters are both modified. This shows that even although characters may be inherited more or less independently of each other, they are never really independent of the particular organisms in which they find expression.

CHAPTER VIII

THE RELATION BETWEEN HYBRIDISATION AND MUTATION

THE consideration of the phenomena of hybridisation in Chapter VII, and of mutation in previous chapters, shows that these two classes of phenomena are distinct. Cytological studies in particular have served to controvert the Mendelian conception that mutation is only Mendelism in another guise. The study of the chromosomes in *Oenothera*, by showing what changes have actually occurred in the origin of several of the mutants, has been a most valuable instrument of analysis, and has proven further that the processes of change are themselves diverse as regards different mutations. While thus affording a remarkable insight into the nature of these germinal changes, it has checked those speculations which attempted to explain all the phenomena in terms of one idea. Combined with breeding experiments, the cytological work has been the most successful means of elucidating many phenomena which must of necessity have remained obscure if only the external characters of the plants were investigated.

But notwithstanding the fact that mutations and hybridisation are distinct processes, yet they are intimately related and sometimes difficult to disentangle, and the former is perhaps in some cases occasioned, or rather accentuated, by the latter. The exact nature of this causal nexus between hybridisation and mutation is an interesting

one to trace. It should perhaps be pointed out here that, although in *Oenothera* such a relation appears to exist, in other organisms the cause of mutations may be of an entirely different nature, and even in *Oenothera* numerous mutations are now known without previous crossing. The recent discovery (426) that *Oe. Lamarckiana* identical with the present cultures was originally an endemic species in North America, goes far to discount crossing even as an indirect cause of mutations in this species. The only feature which all mutations have in common is that they result from germinal disturbance in the organism, and it is obvious that such disturbances may be brought about by a variety of agencies.

One peculiarity which mutants not infrequently share with hybrids is sterility. A condition of partial or complete sterility is, therefore, not in itself a proof of hybridisation, for sterility may arise suddenly in connection with the origin of a mutation, as in the pollen of *Oe. lata* and the ovules of *Oe. brevistylis*. The presence of bad pollen grains is therefore not necessarily an indication of crossing. Geerts (158) has shown that partial sterility of the pollen is of widespread occurrence in the Onagraceæ, a large number of the species having about 50 per cent. of bad grains. But there are relatively few plants in which crossing is more unlikely to take place than in *Oe. biennis*, for the flowers are close-pollinated and in the great majority of cases might as well be cleistogamous. It is, therefore, very unsafe to conclude that crossing has taken place in all these cases.

We are inclined rather to regard the high frequency of bad pollen grains as a result of the peculiar cytological condition of *Oenothera*, in which the chromosomes in meiosis are very loosely paired and hence form irregular combinations (we are not referring now to changes in number) which may be incompatible with development. The weak attraction between homologous chromosomes, which results

in this loose pairing, may be merely an indication of some fundamental peculiarity in the condition of the germ plasm. In any case, the degeneration of a portion of the germ cells in an organism cannot be looked upon as in itself a proof of previous crossing. For example, this degeneration regularly occurs, as shown by Morgan, in half the sperms (namely, those lacking the *x*-chromosome) of certain Phylloxerans. There is at present, however, no evidence to show that in *Oenothera* the approximation to 50 per cent. of bad pollen grains is due to the regular degeneration of half the members of each pollen tetrad. It may ultimately be found that sterility of a portion of the germ cells is as likely to be an indication of mutation as of crossing. From this point of view, the suggestion of Osawa that *Daphne odora* has acquired its sterility through having originated by a mutation is at least as plausible as the belief that the sterility is a result of cultivation. In this case, the possibility of crossing as a cause of the sterility seems to be eliminated through the absence of relatives with which to cross.

The proof that hybridisation and mutation are separate processes, and that true germinal changes and the hybrid recombination of characters may both occur in the same germ cell, has been furnished by correlated cytological and experimental study. In Chapter VII were described the results of series of crosses between *grandiflora* and *rubricalyx*. Here we wish to point out the occurrence of certain mutants in the F_2 of these crosses. There were ten such individuals, as listed in Table XXVII (page 287).

Certain of these mutations were teratological or somewhat pathological. Similar aberrant forms have been obtained in other cases, and they serve to show that there is no sharp line between ordinary mutations and teratological malformations. The first plant in the list was chiefly peculiar in having an abortive bud in the angle between each flower and its bract, the petiole of

the latter being continued as a ridge down the stem. The anthers were also nearly empty of pollen, and the capsules long and slender. The last plant in the list (see Fig. 61, p. 160) was strikingly aberrant, having very narrow, linear leaves which were somewhat fleshy, speckled with yellow, and not quite healthy in appearance. An exactly parallel mutant has been obtained by de Vries (425, Fig. 109, p. 303) in *Oe. muricata* \times (*biennis* \times *muricata*) which gives a race of pure *muricata*.

TABLE XXVII.

Mutants in F_2 hybrids of *grandiflora* and *rubricalyx*.

Cult.	No. of plant.	Mutation.
49	VIII. 10	Mutant (?) teratological.
50	I. 8	Same as last, but small and poorly developed.
50	II. 3	<i>Lata</i> -like, leaves crinkled, many somewhat sickle-shaped; plant small.
50	III. 13	Leaves sickle-shaped; pathological?
50	VI. 6	Plant small, with very narrow, imperfectly developed leaves.
53	II. 7	Near <i>semilata grandiflora</i> (see Fig. 41, p. 114).
60	I. 20	<i>Lata rubricalyx</i> .
60	I. 13	Same as last; died in July.
62	I. 7	<i>Semilata grandiflora</i> .
67	II. 6	Leaves very narrow and linear. Pathological? (See Fig. 61, p. 160).

Two other plants which were called *semilata grandiflora* (see Fig. 41) combined certain peculiarities of the *semilata* foliage with those of *grandiflora*. They no doubt possessed 15 chromosomes. Perhaps most interesting were two plants called *lata rubricalyx*, which occurred in the F_2 of *rubricalyx* \times *grandiflora*. One of them died but the other reached maturity. In foliage, habit, and buds it closely resembled *lata*, while the anthers produced plenty of pollen and every part was suffused with anthocyanin. *Lata* usually produces no red pigment at all, but these plants possessed all the pigmentation features of *rubricalyx*. The capsules were also, unlike *lata*, very large and filled with seeds.

This plant, *lata rubricalyx*, possessed 15 chromosomes (see p. 183). It is therefore obvious that this mutant originated through an irregular meiotic distribution of the chromosomes, a process superimposed upon the regular processes of hybridisation. This is further shown by its offspring, of which we grew 44 in 1913. They were nearly uniform, all having the red pigmentation of *rubricalyx*, but were intermediate between *rubricalyx* and *grandiflora* in foliage and buds. The leaves were nearly all free from crinkling. The plants which were examined had 14 chromosomes, as was doubtless the case with all of them. Hence in the absence of the extra chromosome the ordinary hybrid characters reappeared as in other F_2 families from this cross. Curiously enough, although this *lata rubricalyx* mutant was crossed both ways with several other forms the offspring (few in number) which developed proved to be all of 14-chromosome types. Since there was an abundance of pollen, it would appear probable that many of the grains must have received the extra chromosome and that the latter was frequently lost during the divisions in the pollen tube.

These facts then flatly contradict the Mendelian hypothesis of mutations, and show that the origin of a true mutation must be regarded as a process entirely distinct from its subsequent inheritance. The nature of these germinal changes will be further considered in the next chapter. The fact that mutations and hybrid segregation may bear a superficial resemblance to each other has led several writers to the false conclusion that any mutations which occur in a hybrid race are necessarily a result of the previous cross. Thus Davis (82) has used this argument in connection with the occurrence of mutants in *Oe. biennis* \times *Oe. biennis cruciata* as described by Stomps (351). But the latter has since shown the falsity of the argument by observing similar mutations in a pure race of *Oe. biennis* (354). Now that mutations are known to occur

in pure species, it can never again be assumed that because mutations appear there has been previous crossing.

In the account of his crosses between *Oe. grandiflora* and *Oe. biennis*, Davis (85) describes several forms which are obviously mutants. The dwarfs, which occurred in large numbers (see p. 232), were probably inherited from an earlier mutation or capacity for mutation in one of the parents. In addition, there appeared one *semigigas* form having at least 21 chromosomes; and the F_2 generation contained a plant (II 42 l) which, judging from the figure, resembled *semilata* and probably possessed 15 chromosomes. The 117 offspring of this plant were variable but contained some individuals like the parent plant. Another F_2 mutant in these crosses (II. 42 j) resembled *elliptica*, having very narrow leaves and sterile anthers. This plant was pollinated from one of the *grandiflora*-like F_2 hybrids, and its offspring included 5 like *elliptica* and 41 large-leaved and variable.

These forms obviously must be considered as mutations. Whether they would have appeared with equal frequency in either of the two parent races without crossing, could only be determined by cultivating the original races in sufficient numbers.

We may compare with this behaviour the results of the studies of Bengt Lidforss (230) on the genus *Rubus*. He believed that the mutations which he found to occur were the result of earlier crossing. In *R. polyanthemus* 1 per cent. to 15 per cent. of aberrant individuals were obtained from pure seed. These included (1) a giant form; (2) a dwarf type; (3) a form with much anthocyanin, resembling *R. affinis*, Wh. and N.; (4) a type having leaves white tomentose beneath, like some F_1 hybrids of *R. tomentosa* \times *R. polyanthemus*, and (5) a wholly distinct form with deep green foliage, pyramidal leafy inflorescence and deep red flowers. Giants also occurred in the offspring of *R. insularis*, *R. radula*, and *R. tiliaceus*.

The appearance of mutant-like forms in the offspring of hybrid beetles of the genus *Leptinotarsa* has also been described by Tower (377). He placed colonies of three species, *L. decemlineata*, *L. oblongata*, and *L. multitaeniata*, together in natural conditions and observed the successive changes in later generations of the hybrid population. Such colonies were started in the Balsas Valley and on Mount Orizaba in Mexico, and at Tucson, Arizona. In all cases the three species interbred freely and the hybrid races were found to be most successful. But the hybrid race which ultimately survived was found to be different in all three cases, these differences being ascribed to the environment. The surviving hybrid races were found, at least in one case, to be a sort of compound blend having certain features of resemblance to all three original species. They were found, moreover, to give rise to occasional sporadic mutants, though the characters of the latter are not described. These divergent individuals when inbred were found to be stable and hence they appear to have been due to germinal changes.

When we compare the aberrant forms appearing in various genera such as *Rubus* and *Oenothera*, we are struck with the frequent parallelisms between them. Dwarfs and giants in particular seem to be of usual occurrence, and of course in many cultivated species the changes are rung on the same series of colour varieties. De Vries, in his *Mutationstheorie*, pointed out the significance of this fact for an understanding of variability. He directed attention to the frequent occurrence of such variations as laciniation of petals or leaves and loss of pubescence, as recorded in the varietal names *laciniata*, *glabra*, etc. The widespread occurrence of such cases makes it evident that it is easier for protoplasm to vary in certain directions than in others, at least when the variation is by definite discontinuous steps. It appears that there is a limited number of definite paths which discontinuous variations are likely to

take. Whether the more infrequent mutations are of such nature that they complete the circle of possible directions of variation, or whether these too are confined to certain definite paths so that there is not only discontinuity between parent and offspring but discontinuity between adjacently placed mutations, is not at present clear. It may be that protoplasm can produce marked variations in every conceivable direction, but looking at variability as a whole, it is certain that mutations occur in some directions much more frequently than in others, and this might perhaps be expected from what we know of the constitution of protoplasm as a mixture of complex colloidal stereoisomeric substances.

We are still, however, far from being able to conjecture why certain paths of variation are easier than others, although we may look forward to the time when the essential chemical or physical nature of the change in the cell producing each type of mutation will be understood. The pangen theory of de Vries affords at present a convenient notation in dealing with these questions, but the details of the picture as regards the changes in chemical or morphological structure of the cell are sure to be filled in with later knowledge.

In conclusion, we may again point out that although crossing may in some cases increase the frequency of mutations or even initiate a condition of germinal instability, yet there is no necessary relation between crossing and mutations. For the latter may occur in the absence of crossing, which shows not only that mutation is an independent process but that it is in many cases, although probably not in all, due to other causes than hybridisation. It would appear that for recurring mutations two things are necessary, (1) a condition of delicate balance or easily disturbed stability on the part of the germ plasm, and (2) an environmental influence which disturbs or makes more insecure that condition of balance.

CHAPTER IX

A GENERAL THEORY OF MUTATIONS

1.—*Definition of Terms*

THE purpose of the present chapter is not so much to furnish a complete theory of mutations as to indicate certain lines along which it seems desirable that such a theory should develop. This is all the more necessary because the neo-Mendelian philosophy of evolution, founding everything upon the presence-absence hypothesis, has led to conceptions which sometimes border upon the grotesque. Some of these ideas will be referred to later, but before proceeding to a discussion of the nature of mutations it will be well to define our terms, because the words designating these and related processes have been used, by various writers, in many senses. As our knowledge of the processes involved increases, the connotation of such terms as variation, mutation, and fluctuation of necessity also undergoes modification.

Biologists are, we believe, generally agreed that the term variation should be used in a general or generic sense to include all types of change or difference, and that is the sense in which the term is used in this book. The various biological schools of the present day are, to a large extent, defined by the categories into which they divide variations, and the relative importance attached by them to these different categories. Experimental biologists appear to be agreed that variations should be

divided for the most part into two categories. The two experimental schools differ, however, as to the manner in which these two main categories are to be delimited. The Mendelians consider that the distinction between these two classes, which we may call mutations and fluctuations,¹ is that the former are inherited while the latter are not. Others, including some at least of the mutationists, hold that mutations and fluctuations are both inherited but not in the same way.

Our own view, recently expressed (153), is that mutations are *completely* inherited, either in a portion or in all their offspring, while some fluctuations are *partially* inherited and so give a progeny exhibiting a continuous series of degrees in the development of any fluctuating character. As de Vries has shown, questions of environment, nutrition, and the "inheritance of acquired characters" come in to an extraordinary extent in the consideration of the inheritance of fluctuations, partly because in these cases the data cannot well be treated individually, but must be considered *en masse*, but chiefly because of the difficulty in disentangling these various factors in their effects on the ontogeny of the organism.

As an outgrowth of these points of view, we have defined fluctuations, by contrast with mutations, as "continuous changes arising from the effects of environment or nutrition, which are only partly inherited and hence show Galtonian regression, the whole population forming a continuous series in regard to a fluctuating character."

On the other hand, we have defined a mutation as "a discontinuous germinal change arising from a physical or chemical alteration in the structure of the organism (in micro-organisms) or of one or both of the germ-cells (in higher organisms) which produce a new individual, or from such a change arising in certain cells elsewhere

¹ Bateson's classification of variations into meristic and substantive is made from another point of view.

in the life-cycle of the organism, this change being capable of complete inheritance, at least in some of the offspring, although reversion may occur in the others."

Briefly stated, a mutation is a germinal change which is completely inherited in a varying percentage of the progeny while the others may revert.

Mutations and fluctuations are thus contrasted with each other both from the point of view of variation and from that of inheritance. For (1) fluctuations are continuous while mutations are discontinuous, and (2) mutations are completely inherited, with or without reversions, while many fluctuations are partially inherited in varying degrees in the offspring, and thus form a continuous graded series ranged on one or both sides of the parental condition according to the place occupied by the parent organism in the original series.

In addition to these partially inherited fluctuations, Johanssen's experiments show that there are also non-inherited or somatic variations. Some of the latter are wide or discontinuous, though they are usually narrow or continuous. These would both belong to Weismann's category of somatogenic variations. Professor Poulton (312) has suggested that mutations (for which he prefers Galton's term *transilients*) should be classed as *magnigrade* or *parvigrade* according to whether the change is large or small—a jump or a step. Somatogenic variations or somatogens (to use Poulton's term) might of course be similarly divided, but the classification would in this case have less utility, for the existence and size of small somatogenic variations (or *parvigrade* somatogens) is so intimately concerned with the incidence of environmental effects. Besides, over-classification defeats its own ends, for it must be remembered that the lines between these various categories are by no means hard and fast. There is always a transition zone somewhere, the boundaries of which are faint and indistinct.

It is an interesting and probably a significant fact that while in recent years discontinuity has been receiving more attention in biology, it has also been creeping more and more into the fundamental conceptions of physics. Witness, for example, the quantum theory of radiation, a view which would scarcely have been conceivable twenty years ago, still less, seriously advocated. Yet this view, although so recent, appears to be gaining adherents. Physical even more than biological conceptions show how narrow and tenuous the line between continuity and discontinuity may become, but in biology at any rate there is little doubt that discontinuity will play an important if not a predominant part in the progress of the next half century. The great danger probably lies in the over-emphasis of discontinuity at the expense of continuity.

2.—*The Explanation of Mutations*

Before the cytological work with *Oenothera* was begun, we already knew from the researches of de Vries the peculiar variability of *gigas* and the peculiar hereditary behaviour of *lata*. But it remained for the study of the germ cells to show why *lata* must be inherited in a peculiar way, and why *gigas* might exhibit an extreme and characteristic form of variability in its offspring.

We may go further, and say that not only has the study of the nuclei in *Oenothera* solved some of these problems up to a certain point, but it has made possible a general hypothesis of mutations which is in accord with all the facts of variation, heredity and structure. Our knowledge of the chromosome history in *Oenothera* is still, however, far from complete, and it may be anticipated that further important discoveries will yet be made by more prolonged investigation of these processes. Particularly is this true of the megaspore and embryo sac

and embryo development which, on account of technical difficulties, have as yet only been imperfectly studied.

Since the first paper on the cytology of the mutating *Oenotheras* (116) was published by the writer in February, 1907, a number of investigators have contributed to this rapidly growing subject. Although certain points in that early paper were afterwards found to be inaccurate, yet the situation disclosed showed at once that an important basis for the interpretation of mutation would be furnished by cytological study. The plants investigated were believed to be *lata* \times *Lamarckiana*, but it was afterwards found that they were, unfortunately, not from guarded seeds, so that the male parent remained uncertain. However, one plant was discovered to have about 14 chromosomes, and another about 20 chromosomes as sporophyte number.

It may be of interest to note some of the views which were expressed in this, the first paper on the subject, and it will be seen that they included several of the essential conclusions which have since been drawn from later investigations. On p. 106 is the statement, "It seems highly probable that mutations in *Oenothera* will be found to originate during the reduction mitoses, and perhaps from irregularities in the distribution of chromosomes." This has since been abundantly verified in certain instances. Finally we find, "The inference seems justifiable that the mutations of *Oe. Lamarckiana* arise during the reduction divisions and that pollen grains which will give rise to mutants differ in their potentialities and probably also in chromatin morphology from the ordinary pollen grains of the plant." This statement still requires no modification, except the limitation of its application to exclude mutations which originate elsewhere in the life-cycle.

As soon as we consider the individual mutations of *Oenothera* we find that, cytologically considered, they differ among themselves in their manner of origin. They

are in no sense steps in a series, but each has originated through its own peculiar type of change. This we believe to be one of the most important facts demonstrated by the cytological work. It confirms and gives a basis of fact for the view of de Vries that the mutants are in many directions. If these facts had been understood by Heribert-Nilsson (184) he would not have tried to formulate his theory that the mutants are merely plus and minus expressions of the various characters of *Oe. Lamarckiana*. The knowledge of the cell structure also, in our opinion, explains another peculiarity of the mutants which was emphasised by de Vries, namely, that in nearly all, if not all, the mutations the whole plant has been altered in every part.

These many correlated changes, as in *lata*, result from a change in the nucleus of every cell, the new condition being determined in fertilisation and merely handed down from cell to cell by mitosis. Even in the case of *rubricalyx*, where the pigmentation alone is changed, the pigment-producing capacity of cells in all parts of the plant has been greatly increased, showing that a change has taken place in the original mutated cell, which has been transmitted to all the others through mitosis.

The various correlated changes exhibited by the mutations are, therefore, merely external expressions of an alteration in cellular structure of the fertilised egg, which was propagated by mitosis to all the cells of the organism. The difference between *lata* and *Lamarckiana*, for example, appears to result from the duplication of one chromosome, or in other words, from an original nuclear complex of 15 instead of 14 chromosomes. The fact that parallel effects are produced when the extra chromosome occurs in *Lamarckiana*, *biennis*, or in *grandiflora* hybrids, seems to justify this point of view.

It is probable that all the cell changes involving mutations really occur in the nucleus. Otherwise they could

not be handed on so accurately to all parts of the organism, and still less could they be transmitted to subsequent generations. In *lata*, *semilata*, and *incurvata* we have a vivid picture of a nuclear change from 14 to 15 chromosomes being passed on in this way, the extra chromosome having originated as such through finding its way into the wrong cell. To us, the cytological condition of *Oenothera* is a sufficient explanation of these chance occurrences, a very slight environmental influence being adequate to produce the irregularity.

It should be stated here also, as the author pointed out in 1908 (119, p. 28), that if the chromosomes are unlike in their potentialities then their loose pairing during meiosis should lead not only to both members of one pair of chromosomes (*A*) passing to one end of the spindle (and hence into the same germ cell), as in the origin of *Oe. mut. lata*, but more rarely to cases in which at the same time both members of a second pair of chromosomes (*B*) pass to the opposite pole of the spindle. In such cases the chromosome numbers and the chromosomes themselves would remain unchanged, yet two mutated germ cells would have arisen simultaneously, one of which possessed two *A* chromosomes and no *B* chromosomes, while the other possessed two *B* chromosomes and no *A* chromosomes. It is specifically to be observed that a mutation here depends upon the *A* and *B* chromosomes being unlike,¹

¹ Shull (340) has recently suggested that "duplicate determiners" for Mendelian characters may in some cases arise through exchange of mates on the part of the members of two pairs of chromosomes, a process which of course leads to the result mentioned above. In this way he explains with much plausibility the simultaneous origin of the recessive mutant *Bursa Heegeri* and the duplicate condition of determiners for capsule-form in *B. bursa-pastoris*. For if, in a meiotic division, the pair of chromosomes containing the determiner for capsule-form should be mismated and both pass into the same germ cell, that germ cell would possess two determiners for capsule character, as is found to be the case in *B. bursa-pastoris*, while the other germ cell would lack both these determiners and hence produce the recessive mutant *B. Heegeri*.

Shull points out that the same result could be attained by a deter-

while in *Oe. mut. lata*, according to present knowledge this is not *necessarily* the case.

In the case of *gigas* and *semigigas*, the exact place in the life-cycle where the doubling of one or both chromosome series takes place, to give 21 or 28 chromosomes, is still unsettled. But triploid mutants probably originate, at least in the great majority of cases, through the union of a diploid egg with a haploid male cell. And the tetraploid giants probably arise from a suspended mitosis either before megaspore formation or after normal fertilisation, or possibly from the union of two diploid gametes. In any case it seems desirable again to call upon the environment to furnish a *raison d'être* for the rare occurrence of this change in a particular cell. Again, the amount of environmental influence required is but slight.

If now we consider *rubricalyx*, in which the chromosome-number is unchanged, the alteration in the character of the cells is obviously of quite a different kind. It is chemical, rather than physical or morphological as in the cases above, and we believe it may be reasonably "explained" in the following manner. Since the original mutant was heterozygous, the essential change occurred in one germ cell only and has since been propagated through division of that cell or its nucleus.

In recent years, numbers of mutations in bacteria have been described, particularly those in which the bacterial cell suddenly alters certain of its physiological properties. Thus Massini, in 1907 (see Dobell, 90), cultivated a strain called *Bacillus coli mutabile*, and found that it was giving rise to colonies which could ferment lactose. This power was suddenly acquired by certain individuals while the others remained unchanged. Further cultures showed that the non-lactose-fermenting individuals continued to

minor located in the end of one chromosome becoming attached to the adjacent end of another chromosome when the spireme segments in mitosis.

split off individuals which gave rise to constant lactose-fermenting colonies. R. Müller (278) showed similarly that *Bacillus typhosus* behaved in the same way towards rhamnose. Colonies grown on a medium containing this sugar give rise to certain individuals which have permanently acquired the power of splitting rhamnose. Again, F. Wolf (454), in 1909, by growing *Bacillus prodigiosus* on culture media containing very small amounts of potassium bichromate and other salts, was able to induce permanent changes in colour. And Madame Victor Henri (179) has recently produced marked mutations in *Bacillus anthracis* by subjecting them to ultra-violet rays.

These and other experiments show clearly that hereditary changes arise spontaneously or may be induced in Bacteria. These mutations consist frequently in change of function, such as the sudden acquiring of the ability to split certain sugars. We believe this may throw an important light on the nature of certain mutations in higher organisms, for if a bacterium can undergo a sudden constant change of function, the same may reasonably be expected to happen to a chromosome. The change is no more, and no less, incomprehensible or unlikely in one case than in the other. Thus we may think of the *rubricalyx* mutation as having occurred through a sudden change in activity or function on the part of a chromosome (one member of a pair) either at or after separation from its mate in the reduction division, or at least during some period of meiosis.¹ The other functions of this chromosome may have remained unmodified, just as in the Bacteria. Its change

¹ Of course, both homologous chromosomes forming a pair might have undergone the change simultaneously before their separation, in which case two mutated germ cells would be produced, and if both functioned (as might be the case with pollen grains but not with megaspores) then two mutated individuals should result. Occasionally, *lata* and *semilata* mutants appear in pairs in a family, and it is probable that in such cases the meiotic change took place in one pollen mother cell rather than independently in two megaspore mother cells.

in function was such as to lead to a greatly increased capacity for anthocyanin-production in the cell as a whole. The change may even be considered to be quantitative in nature, since the parent *rubrinervis* also produces red pigment but in much smaller quantity.

Although we have spoken of the change as one in the activity of a chromosome, it is probable that in ultimate nature it is an alteration in the chemical constitution of the chromosome or a portion of it. This may be thought of as a stereochemic re-arrangement in the complex molecule of the nucleic acid or as some other type of chemical change involving the formation of slightly modified protein substances.¹

A view closely similar to this, but without the analogy of bacterial mutations, was suggested by Spillman (349) in his teleone hypothesis. It seems not unlikely that many mutations occur in this way, through the sudden loss of a function or change of a function owing to a chemical change on the part of a chromosome. The criticism may of course be made, that this merely transfers the process into a chromosome without further analysing it, to which it may be rejoined that such a change is at any rate analogous to what is actually known to occur in Bacteria, and in the latter case the change has not been analysed either.

If we consider other mutations, such as *brevistylis*, *nanella*, *albida*, or *elliptica* from *Oe. Lamarckiana*, or *sulphurea* and *cruciata* from *Oe. biennis*, it is evident that the cellular changes involved must be equally diverse, though they have not yet been analysed by cytological study. The most obvious classification of all these changes is into those which are fundamentally or chiefly physical or morphological, and those which are chemical or physio-

¹ Some writers appear to think that by calling the new character-determiner a "gene" they have silenced all inquiry concerning the nature of the change.

logical in nature. Whether such a change as the chromosome-doubling in *gigas* is accompanied by independent rather than consequent physiological changes, is uncertain, but at any rate this should not be assumed unless such an assumption is necessary to account for all the new phenomena.

From the point of view of Bateson's classification of variations into meristic and substantive, *gigas* might perhaps be regarded as an example of the former and *rubricalyx* of the latter, but a classification into mutations which are fundamentally morphological or chemical in nature seems more appropriate in the present instance.

With regard to the origin of recessive mutants which Bateson (18) believes are easily accounted for by "some slip in the accurate working of the mechanical process of division" by which "a factor gets left out" (p. 91), it seems more probable that the change occurs by the loss or alteration of an activity on the part of a chromosome or other cell constituent. This being the case, the character or activity may not always be lost irrevocably, but may occasionally reappear, causing a "reversion." Bateson's conception of a positive or negative mutation as resulting from a "pathological accident" in cell division is, therefore, we think, not applicable to a case like that of *rubricalyx*, though it applies admirably to the origin of *lata*.

Finally, having regard to the various directions which the derivatives from a mutating species may take, it seems useful to consider such mutations as a result or an expression of a condition of germinal instability in the species. This conception we have found very useful, although it may appear rather vague, and consequently unsatisfactory, to some. Analysis of the various germinal changes is the only way in which it can be made more definite, and this is steadily going on. The hypothesis that each change is connected with the alteration of a particular pangen,

gives the process a "local habitation and a name" but does not add to our knowledge of it. But if we assume that the change is concerned with a particular chromosome or portions of one, we make the matter still more concrete, and the hypothesis can, at least in some cases, be verified by observation and experiment. In this way the chromosome hypothesis (which is already proven in certain cases) should, we think, be used as supplementary, and not contradictory, to the pangen hypothesis of de Vries.

In the mutations of the pumice-fly, *Drosophila*, although some characters are sex-linked and others not, Morgan (273, etc.) has found that the eye-colour varieties all come in one series, and they are all considered to be negative in character. The same appears to be true of the numerous wing mutations, though the published data are perhaps not sufficiently complete to enable one to judge on this point. But the general result appears to be that, although the mutations are much more numerous than in *Oenothera*, yet they are in fewer directions and do not affect so markedly the whole organism, as is the case in *Oenothera*, but chiefly single organs. Is it too speculative to suggest that in *Oenothera*, changes in the distribution or functions of whole chromosomes are usually concerned; while in *Drosophila*, where the changes are more numerous but in fewer directions and affecting in each case mainly single organs, the mutations result from changes in single particles or portions of a chromosome? Morgan's view of the processes of mutation and inheritance in *Drosophila*, based on Janssen's chiasma type of chromosome behaviour in maturation, is in harmony with this conception.

As regards the ultimate nature of mutations, we are therefore inclined to look upon them as the result of various types of change in the nucleus: (1) morphological changes (*a*) in number, (*b*) in shape and size of the chromosomes, or in the arrangement of their substance; (2) chemical or functional changes in (*a*) whole chromosomes or (*b*)

portions of particular chromosomes, by which a function may be modified or lost; (3) two simultaneous mutations may occur through mismating of the chromosomes in two pairs so that each germ cell receives both members of one pair; (4) changes may perhaps occur in the mysterious karyolymph or gel which forms the groundwork of the nucleus. Such changes may be thought of as alterations in chemical structure or even in polarity, and may also be supposed to extend to the ground-substance of the whole cell. But the real nature of all such changes as those last mentioned is at present highly speculative.

It seems that an understanding of mutations can be advanced more securely by an analysis (through cytology and breeding) of the many individual cases now known, than by an attempt to group all instances under some generalised theory. For the present, the more speculative part of the subject appears to be sufficiently served by the pangen theory of de Vries. Its obvious advantages, and indeed necessity, in obtaining a co-ordinated view of all the breeding experiments in *Oenothera* have already been pointed out (see p. 224). At the same time there are evident difficulties in applying it in detail to the chromosome changes in *lata* and *gigas*, and we are inclined as far as possible to base views upon the visible cytological facts, as affording the best means of further insight into the ultimate nature of these processes. The cytological facts, while not in conflict with the pangen theory, afford, we think, the most promising basis for future hypotheses.

We should also point out here that negative mutations, or in Mendelian terms loss of unit factors, can quite well be explained as the result of the loss of a special activity by a particular chromosome. If, in one germ cell such a loss takes place while in the others no change occurs, and such a cell is fertilised by a normal germ cell, then

the resulting individual is heterozygous in that the members of one pair of homologous chromosomes differ in possessing or lacking this activity or property. When these chromosomes separate in meiosis in the next generation, half the germ cells of both sexes will contain one of them and half the other. The result will be that the character, whether dominant or recessive, will be inherited in Mendelian fashion in case the gametes come out "pure" and unmodified as they frequently appear to do. The loss of unit factors, on which Mendelians lay so much stress, is therefore probably a loss from particular chromosomes, and the simple Mendelian 3 : 1 or 1 : 2 : 1 ratio in inheritance is exactly as though this were the case.

3.—*Relation of the Chromosomes to External Characters*

In the development of any theory of variation or heredity, definite views are necessary both as to the respective rôles of nucleus and cytoplasm in the cell, and concerning the relation of nuclear structure to external characters. We wish to point out first that we know very little regarding the nature of chromosomes, whether they are composed of enzymes—a plausible suggestion—or of other substances. The fact that a variety of types of nuclear division occur in Protozoa can scarcely be without significance. Dobell (91) has recently shown that while the nucleus of *Amoeba lacertae* can scarcely be said to divide mitotically, in two other species, *A. glebae* and *A. fluvialis*, definite and apparently constant numbers of chromosomes (16 and 12 respectively) appear in mitosis. This seems to show that even when a single cell is the whole organism there is advantage or necessity in the equitable distribution of this limited number of bodies to the daughter cells, and the number of these bodies is much the same as in the nuclei of higher organisms. It appears reasonable to conclude, at any rate, that the

whole process of mitotic division was evolved before organisms advanced from the unicellular to the cell-colony or multicellular condition, although the process has been perfected in detail since.

This furnishes a further reason for the conclusion that the chromosome-number is a fundamental property of the cell and not merely of the species. Loose statements regarding variation are frequently made, implying that variations in chromosome number are no more significant than fluctuation in any external feature, such as the number of petals in a flower. But we believe it is important to emphasise the fact that the chromosomes come in a unique category. They are almost the only primary morphological features transmitted as such directly from the previous generation. The constitution of the nuclei in any organism is determined at the time of fertilisation, while in higher organisms all other features of the adult (the so-called external characters) are secondary in origin, developing as the result of interaction between nucleus and cytoplasm in the cell. Moreover, regeneration of the cytoplasm can and does take place, but no such thing as regeneration of a chromosome is known, and experimental cytology makes it highly improbable that such a process ever occurs.

There is another point which we wish to emphasise in this connection, namely that the nucleus of the cell is probably the conservative part of the germ plasm, remaining unmodified by conditions which alter the activities of the cytoplasm, and hence modify such products as the cell walls and various other features of the tissues, which result from the interaction of nucleus and cytoplasm. MacCallum (242) and others have shown that the nuclear membrane plays an important rôle in preventing the entrance into the nucleus of many substances which are commonly found in the cytoplasm. The fact that the nucleus is thus hedged round except when the chromosomes

are in the compact condition of mitosis, can scarcely be without significance, and has received insufficient attention in general views on the material basis of heredity and the nature of the difference between germinal changes and non-inherited or partially inherited modifications. Just as we know that various germinal changes are occasioned by or at least accompanied by alterations in nuclear structure, so it appears equally probable that fluctuations result from cytoplasmic alterations which are insufficient to disturb the equilibrium of the nucleus.

4.—*Mutations in Other Organisms*

In concluding this chapter it seems desirable to attempt to give some idea of the range and variety of mutations in other organisms than *Oenothera*. An adequate treatment of this subject would require a volume, since such cases have been accumulating with great rapidity in recent years. We shall only produce here, however, in slightly modified form, a classification of mutations which was published in a recent paper (153). The classification is of course incomplete, but it serves to indicate the great variety of types of mutational change now known to occur. From the great number of instances available in the literature a few have been selected. They include both plants and animals, and the name of the organism is followed in each case by the name of the discoverer or investigator of the mutation. We think the futility of attempting to describe all these mutants in terms of one idea—the Mendelian presence-absence hypothesis—will be apparent to anyone examining this table.

As already mentioned, there exists a borderland of transition between mutations and fluctuations, partaking somewhat of the nature of both. Here we are inclined to place such variations as striped flowers, which, according to de Vilmorin, originate through partial reversion from

TABLE XXVIII.

Mutations.

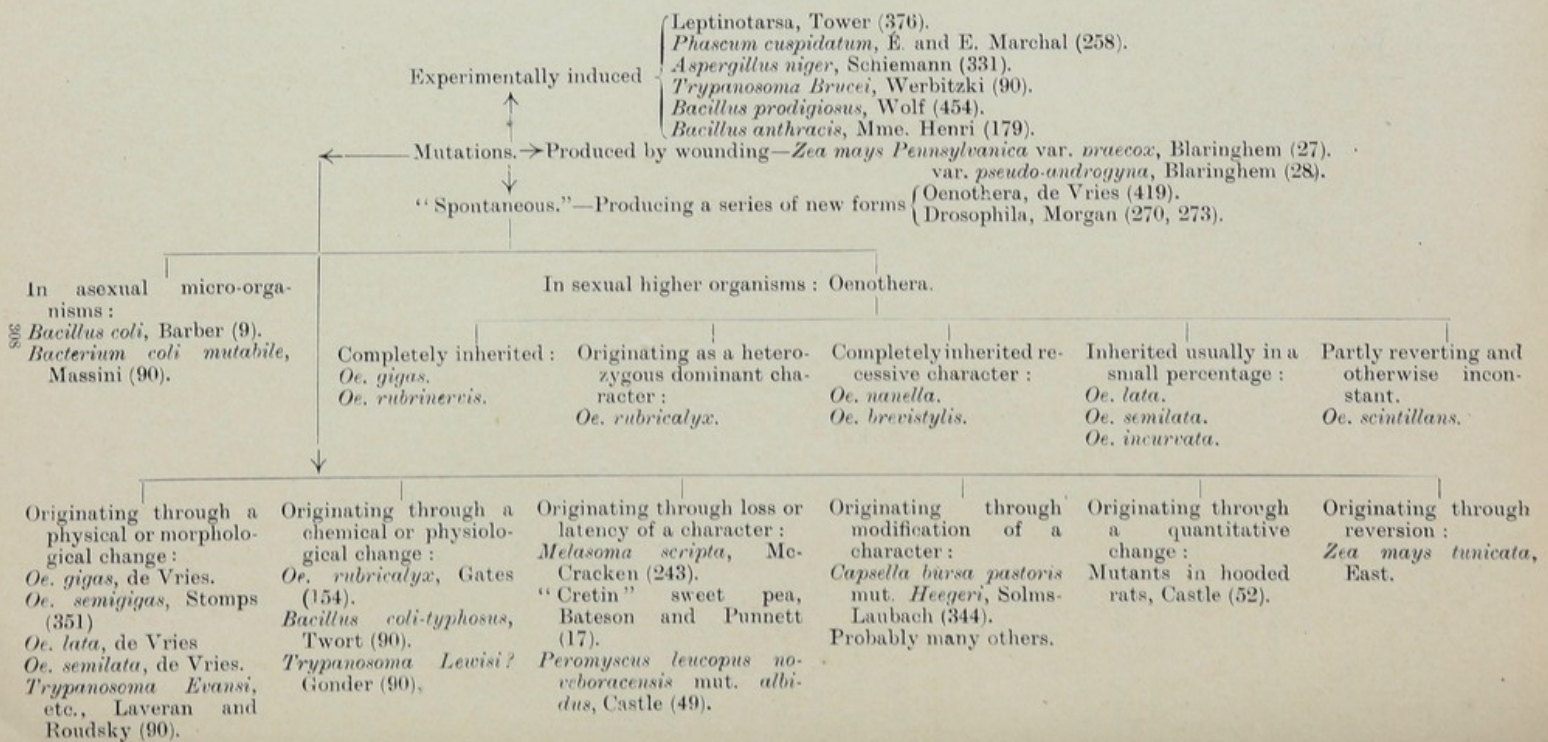


TABLE XXVIII (continued).

Originating.

In the wild.

Peromyscus leucopus noveboracensis mut. *albidus*, Castle (49).
Potentilla verna mut. *monophylla*, Domin (92).
Helianthus lenticularis mut. *coronatus*, Cockerell (57).
Amphidasys betularia var. *doubledayaria*, Bateson (18).
Cereba (*Certhiola*) *saccharina* var. *atrata*, Bateson (18).

In cultivation.

Primula officinalis mut. *horticola*,
 Domin (92).
Melandrium album with small leaves, Baur (21).

Originating.

In meiosis:

Oe. lata.
Oe. rubricalyx.
Oe. biennis semigigas.
H. lenticularis mut.
coronatus, Cockerell.

In fertilisation or subsequently:

Oe. gigas?
 Periclinal and sectorial
 chimeras? Baur (19).

As vegetative mutation.

In pure races:

Phaseolus vulgaris,
 Johannsen (200).

Through segregation in
 somatic cells of hetero-
 zygous races:

Solanum tuberosum, East
 (96).
Veronica longifolia × *V. l.*
alba, de Vries (398).

Through change in somatic cells from
 homozygous to heterozygous condition.
Mirabilis Jalapa variegata, Correns (67).

Originating.

In pure races:

Hordeum distichum, Kiessling (212).

In crosses:

Many probable cases.
Bombyx mori, Toyama (378).
Antirrhinum majus, Baur (20).

New dominant characters:

Oenothera rubricalyx (137).
Zea mays, albinistic ear, Collins (61).
Helianthus lenticularis coronatus, Cockerell (57).
Primula sinensis, giant, Keeble (210).

New recessive characters:

Many dwarf varieties.
 Many white varieties of flowers, and albino animals.

Historical mutations.

1. *Chelidonium majus laciniatum*, 1590. Sprenger.
2. *Mercurialis annua laciniata*, 1719. Marchant.

3. *Fragaria vesca monophylla* (Fries. Lapland.
1761. Versailles.
4. Copper beech, 17th century.

Originating in prehistoric time: *Gyrostachys cernua* and many other tetraploid species (see p. 197).

white varieties which have been crossed ; also some types of variegation in foliage. The latter is a very common variation, and the changes involved are probably of various kinds, but we should include here such cases as *Acer striatum variegatum*, Godron, described by de Vries (419). The "ever-sporting varieties" of de Vries should also perhaps be relegated to this transition zone.

In the next chapter, certain further comparisons of mutation with other processes will be made.

CHAPTER X

THE EVOLUTIONARY SIGNIFICANCE OF MUTATIONS

1.—*The Mutation Concept as Related to Heredity and Ontogeny*

FROM the few mutations of which a classification was attempted in the previous chapter, it will be obvious that the changes we now call mutations are of many and diverse kinds. The nature of each one can only be fully understood by making a cytological, anatomical and breeding analysis of it. Such analyses show that although the essential change usually occurs during meiosis, yet not infrequently it may take place in some other part of the life cycle. They show, moreover, the composite nature of the mutation process as a whole, since a variety of types of germinal change occur.

In the present chapter we wish particularly to consider the evolutionary bearings of this diversity, for if germinal changes are of many kinds this is a very important fact for evolutionary theory. We believe that the significance of this fact, which emerges from recent genetic experiments, has been generally overlooked. The most recent consideration of mutation is that of Bateson, in his *Problems of Genetics*, and his conclusions invite comment and criticism, since he has not taken account of these points of view. Having classified all character-changes into dominants and recessives, he apparently considers this distinction so fundamental that no other class or

classification is conceivable. He himself says (p. 93) that the distinction between dominant and recessive characters has become to most geneticists a "permanent and continual obsession."

Bateson finds it easy to understand the appearance of a recessive character through the loss of a "factor" (we have given our view of the origin of recessives in the last chapter), but with regard to the origin of "dominant factors" he says (p. 94): "Whether we look to the outer world or to some re-arrangement within the organism itself, the prospect of finding a source of such new elements is equally hopeless." If the presence-absence hypothesis leads thus to a *cul de sac*, is it not possible that the point of view needs to be modified?

To quote again from the same work, after finding an understanding of the causes of meristic variations impossible, we read (p. 86): "Of the way in which variations in the substantive composition of organisms are caused we have almost as little real evidence, but we are beginning to know in what such variations must consist. These changes must occur either by the addition or loss of factors." It appears to the writer that it is from this somewhat dogmatic assertion, and the points of view growing out of it, that many difficulties which might otherwise be obviated arise. We feel that the possibilities of germinal change are unnecessarily restricted by confining them to Mendelian dominants and recessives resulting from the addition or loss of "unit factors."

Again, on page 90 we read: "Somehow or other, therefore, we must recognise that dominant factors do arise. Whether they are created by internal change, or whether, as seems to me not wholly beyond possibility, they obtain entrance from without, there is no evidence to show. If they were proved to enter from without, like pathogenic organisms, we should have to account for the extraordinary fact that they are distributed with fair constancy to half

the gametes of the heterozygote." To those who believe in the segregation of character-determiners in meiosis, as the chromosomes segregate, the above view appears to mystify unnecessarily the facts regarding the origin of heterozygous mutants—facts which, as explained in the previous chapter, offer no serious difficulties on the chromosome hypothesis. The cytological facts are, moreover, in harmony with the facts of Mendelian behaviour.

The difficulty of the view here discussed evidently arises from the failure to consider germinal changes as consisting in anything else than the loss or addition of "unit-factors." May we not say that the root of the trouble lies with the presence-absence hypothesis and its supposed universality? This hypothesis has proved its usefulness in dealing with Mendelian inheritance. But, as we have already seen, the phenomena of mutation, by which new forms originate, lie outside this category, mutation being one type of variation.

Surely we may agree that the thing which is called a "factor" is only a *difference* in the structure of the cell or some part of the cell, and it may apparently be of any kind whatever. That difference has been produced by a change, and the change constitutes what we call a mutation. In certain cases the germinal change is such that the new character is a dominant, in other cases it is a recessive, in still more numerous instances it is neither, but intermediate in crosses. It is now fairly clear that whether the new or modified character behaves in one or another of these ways depends, at least to some extent, upon its chemical or morphological nature. The application of chemical and physical conceptions to cell changes suggests that the usual classification of all new characters into dominants due to "addition of a factor" and recessives due to "loss of a factor," is not the most illuminating method of dealing with the changes involved.

Instead of looking for "dominant factors" to enter

the germ plasm, like pathogenic organisms, from without, surely the reasonable explanation to adopt is that of an "internal change" or a modification in the structure of the cell or some part of it. This is the view which we tried to develop in Chapter IX, the change being considered to affect (1) the functions or chemical composition of a chromosome, or, (2) a portion of a chromosome, (3) the number of chromosomes, or (4) perhaps in some cases the groundwork of the whole nucleus or cell. In any case the change must come from a modification in the cell or some element in it, and can scarcely be supposed to arise through a representative particle of any kind being injected into it from without. It is probable that whenever the new character is inherited in Mendelian fashion the change has been in the functioning of one chromosome or a portion of one.

Professor Bateson adds a note to his argument (p. 94), in which he advocates the possibility at least that all germinal changes are merely due to the "loss of factors." This obviates the difficulties he finds in conceiving how "dominant factors" may arise. Each now makes its appearance through the loss of an inhibitor for that factor. The difficulties with this view become apparent when it is pushed to its logical consequences. We must then suppose that the primordial form or forms contained "inhibitors" for every character which has since appeared, and that evolution has consisted in the loss of these inhibitors *seriatim*.

This is the outlook to which, so far as we can judge, the Mendelian philosophy leads. It is difficult to see wherein this conception of the loss of inhibiting factors in evolution differs in general outlook from the *emboîtement* theory of embryology developed by Bonnet in the eighteenth century. That theory was the extreme expression of the "evolution" view as contrasted with the epigenetic view of embryological development. According to it, the egg

of the chick contained another egg ready to unfold in its turn, that contained another, and so on *ad infinitum*. But epigenesis soon triumphed in embryology when it was found by observation that the egg did actually develop from an undifferentiated to a complex condition; and the emboîtement theory of Bonnet has long been of interest only as an historical curiosity. It is scarcely thinkable that biologists to-day could be induced to return to a conception of evolution as crude and elementary in its way as was this eighteenth century theory of Bonnet in embryology.

The truth is that Mendelism is a theory of inheritance, and as such is not adapted to deal with the question of origins at all. It is false logic to assume that the inheritance of a character *necessarily* throws any light at all upon its origin. Characters of a race which have been acquired gradually may be suddenly lost or altered and thus give a Mendelian pair; or characters which have suddenly appeared may be gradually modified, by crossing with different species or by other means. It is curious how many have been misled by the logical fallacy above mentioned, and assume that if they can prove that the *inheritance* of a new type is Mendelian, they have at the same time shown its *origin* to be a Mendelian phenomenon. Nothing could be further from the truth, and it should be kept clearly in mind that the mode of origin of any character is one thing and the subsequent inheritance of that character is a very different thing.

If the doctrine of the fixity and universality of unit-characters should find general acceptance (which is not likely to be the case) it might retard the progress of biology as seriously as did the dogma of species-fixity. It would seem that the failure of modern Mendelians to recognise the limitations of Mendelism, both as a method and as a doctrine, is the chief source of weakness in Mendelism at the present time. Mutation deals with

origins in so far as they can be considered discontinuous ; Mendelism, on the other hand, concerns itself with discontinuity in inheritance. Galton, though using other terms, recognised the importance of such a distinction as this, in his *Natural Inheritance*.

In considering this phase of the subject, it is remarkable how closely interwoven and interdependent our conceptions of heredity, ontogeny, and evolution have become. As one part of the problem of the origin of species we have to consider the origin of Mendelian characters. The writer's conception is that every such character, whether dominant or recessive, arises through an alteration in a chromosome, or a change which affects, and thus becomes incorporated in, a chromosome. If, in the course of time, a number of such changes take place in the different chromosomes of two races which have become isolated, we may in this way obtain two distinct species which Mendelise in a number of characters when crossed, as Baur (20) has shown with species of *Antirrhinum*. Baur's (21) view of the nature of Mendelian character-differences agrees essentially with that here expressed. When such characters do not Mendelise they may have originated in some other way, either through a different kind of mutation or perhaps by a more continuous change.

In this connection we should like to direct attention to the clearness and simplicity, as well as the complete adequacy, of the chromosome explanation of the phenomena formerly known as "coupling of characters" and "spurious allelomorphism" or "repulsion." If two organisms differ in two characters A and B, the manner of inheritance of these characters depends in some cases upon whether the characters are both derived from the same parent or separately from the two parents. Thus, if A and B represent the changed characters and *a* and *b* the absence of these changes, in amended terms of the presence-absence hypothesis, then in the cross

$A B \times a b$ all the gametes may be either $A B$ or $a b$, while if the parents are $A b \times a B$ the gametes may be wholly $A b$ or $a B$. In the former case there would be complete coupling of A and B ; in the latter, complete repulsion or spurious allelomorphism.

Emerson (97A) was, we believe, the first to point out that if A and B enter from the same parent and are represented in the same chromosome, then they would show complete coupling, with a 3 : 1 ratio $A B : a b$ in F_2 , because this chromosome separates from its mate in reduction. Further, in $A b \times a B$, if the changes leading to the production of A and B have taken place respectively in homologous chromosomes of a pair, then half the gametes will contain A and half B , and there will be complete repulsion or spurious allelomorphism. Again, if A and B are "contained in" *separate* chromosomes of the x series, they will Mendelise independently whether they enter from the same parent or from different parents, giving the F_2 ratio 9 : 3 : 3 : 1 if there is dominance.

In the authenticated cases of the existence of two or three independent "factors" for the same character, as in Nilsson-Ehle's factors for red in wheat, where the ratios 3 : 1, 15 : 1, and 63 : 1 are all obtained, it is reasonable to suppose that the condition has arisen through the same germinal change having occurred independently in two or three different chromosomes of the x series.

The cytological evidence is thus completely in accord with the theoretical requirements and the experimental facts. There is a further phenomenon which was formerly called "partial coupling," but has since been rather cryptically referred to by Bateson and Punnett (17) as "reduplication." In this case the character-differences A and B when they enter from the same parent are usually, but not invariably, found together in the F_2 offspring. Such a condition was first studied by Bateson and Punnett (16A) in a cross between two varieties of the Sweet

Pea, Emily Henderson. It was found that the purple colour of the corolla was associated with long pollen grains, and red corolla with round pollen grains in such a way that F_2 individuals having purple corolla and long pollen occurred about 14 times as frequently as those having purple corolla and round pollen. Purple corolla was thus partially, although not completely, coupled or linked with long pollen grains. Similar phenomena have since been observed in various other cases, and, in *Drosophila*, Morgan (270-273) has studied in great detail numerous cases of the same kind, which he calls "linkage" and "crossing over" of characters.

Regarding the explanations offered of these phenomena, we need only state that Morgan's hypothesis is an attempt further to utilise cytological data, and assumes that the characters follow the distribution of the chromatin material during meiosis. Bateson and Punnett, on the other hand, neglect the cytological facts entirely and assume that all such partially coupled distributions of characters depend upon the particular succession of periclinal and anticlinal divisions which is supposed by them to take place in the embryo. Not only has this assumption no facts in its support, but it ignores the many facts which indicate that the redistributions of characters usually take place during meiosis, and moreover, in such animals as the Insects the conception cannot possibly be applied. For in the insect embryo the blastoderm is formed by the migration of free nuclei to the periphery of the egg, and certain of these nuclei are then set apart to form the germ cells. The nuclei and their chromosomes are the only structures which are common both to the insect embryo and the plant embryo, and it is reasonable, if not necessary, to suppose that the chromosomes are the vehicles concerned in this as in other cases. Everything goes to show that the basis of sound advance lies in the further correlation of cytological with external structure, and not in the production

of *a priori* hypotheses which neglect or run contrary to the known facts of structure. From these considerations it will, we think, be clear that the chromosomes furnish a parallel, and therefore a highly probable basis, not only for the distribution of ordinary Mendelian character-differences but also for the various complications of Mendelian behaviour which are now known to occur.

2.—*Mutation in Relation to other Evolutionary Factors*

When we look about us for evidence of actual species-origin now going on in natural conditions, we find numerous instances of recurring mutations; but in the nature of the case we can scarcely expect to see new species appear before our eyes through the effects of natural selection (because of the time element), and still less can we hope to see direct evidence of orthogenesis. Experimental evolution therefore has its limitations, and a philosophical view of evolution must include in its purview the whole realm of palæontological succession. But in the present book we are dealing only with mutations. That new wild varieties and species do originate through mutation, both in animals and plants, there can no longer be the slightest doubt. Several such instances were given in the table on p. 309, but we wish here to refer in particular to two striking cases described by Bateson (18) in an extremely interesting and valuable chapter on variation and locality. We select these because they illustrate so well the only method we know by which new varieties or species actually appear in nature.

The first case is the well-known one of melanism in British Lepidoptera. In *Amphidasys betularia* the totally black variety *doubledayaria* appeared in the vicinity of Manchester about 1850. It afterwards spread through the district, and in the 'eighties appeared on the Continent, reaching Berlin in 1903. It is now the prevalent form in

Lancashire and other counties, and in some localities it has entirely replaced the original species. Some thirty species in all have given rise to similar melanic varieties (306A), and less conspicuous cases have occurred in the Noctuidæ and the Micro-Lepidoptera. In the species mentioned the melanic variety seems to have appeared sporadically as a marked mutation, though it has since occasionally given rise to paler or otherwise intermediate forms. In some other species there has been a progressive darkening in colour, apparently through a series of mutations or steps. The new character is, at least in some cases, a dominant in crosses, which accounts for its spreading. There may also be some connection between the smoky industrial surroundings and the development of these melanic mutations. If such is the case, it shows that in some unknown way there is a relation or a response between the environment and the particular type of mutation developed; but this is improbable. If the melanism is adaptive there seems to be no evidence that it has been selected among other kinds of mutations, but selection, which evidently favours the new variety, has been directly between the mutation and the parent species. This is all very illuminating from the point of view of the mutation theory.

The other instance is a black variety of one of the Sugar-birds, *Cæreba* (*Certhiola*) *saccharina*, found in certain of the West Indies. The species is marked with yellow and white, while the variety *atrata* is pure black. They were named from specimens collected in St. Vincent about thirty-five years ago. The variety was already at that time commoner than the type, which has since become almost if not quite extinct, while the variety has taken its place. If, as appears certain, the black is dominant, then the recessive is less tenacious than would be the case in a freely intercrossing Mendelian population. This could be accounted for by birds of similar colour always mating together. That this is also a case of repeated mutations

is made highly probable by the fact that in two groups of islands off the coast of Venezuela, black forms of closely related species have been found, which must have originated independently.

It is thus abundantly clear that mutations appear in wild species and gradually supplant their parent forms. The cause of such definite germinal changes is, however, still a mystery. Natural Selection may or may not be called upon to adjudicate between the old and the new form. If not, then the new character is innocuous and both will continue to exist side by side, but in the above cases selection seems clearly to have been at work. In the main, Natural Selection appears to be a conservative factor, maintaining each species in its own ecological niche, confining it within certain limits, and keeping it at its best level of efficiency through the competition of its own members. The equilibrium thus maintained is a moving one, in which all the species of an area react more or less upon each other. Variations, either gradual or sudden, in any species, or an environmental change, as in climate, disturbs this equilibrium with the result that new adjustments are made and new variations may survive. Selection thus only comes into operation as a modifying factor when some new variation or some environmental change has taken place, although, like gravitation, it is ever present, as a conservative factor eliminating the weaker.

Orthogenesis may be searched for in two ways, (1) by comparison of the members of any existing family of species, (2) by examination of the phylogenies of extinct groups or comparison with their living members. In this way, what are believed to be orthogenetic tendencies have been traced in a number of recent groups, and by palæontologists in a large number of fossil forms. Palæontologists appear to be agreed that many cases of this kind have occurred in the larger sweeps of the fossil record. Although their

existence is not open to doubt, their explanation is usually obscure. They hold their course despite the vicissitudes of a changing environment, nor can they be regarded in many cases as stages in the perfecting or usefulness of any organ. Natural Selection therefore seems inadequate as a constant directive agency, and they appear to be independent of its influence. It would appear that something within the organism is responsible for such unswerving progress in a given direction as appears to be repeated over and over again in the palæontological record.

Finally, it may be observed that evolutionary thought has become so manifold as to be almost co-extensive with biology itself. It has become questionable whether we can properly speak of evolutionary factors and compare them with each other, for the conditions and forces that make for diversity are themselves so diverse as to be incommensurable. Natural Selection and mutation, for example, cannot be equated in terms of each other, but they are to some extent complementary phenomena in the process of speciation. The evidence, so far as we have it, shows that evolution proceeds, in many cases at least, by small steps; and that variations are not indefinite or equally in all directions, but are either definite or orthogenetic and frequently discontinuous.

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