# THE   MUTATION   FACTOR   IN   EVOLUTION

# THE
# MUTATION FACTOR
# IN EVOLUTION

## WITH PARTICULAR REFERENCE
## TO OENOTHERA

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SOMETIME LEC PURER IN HIOLOGY, ST. THOMAS'S HOSPITAL.
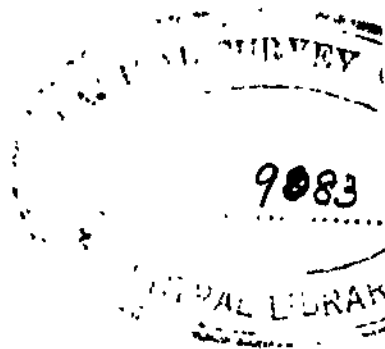LECTURER *IS* CYTOLOGY. BEDFORD COLLEGE, UNIVKKSITY OK LONDON.
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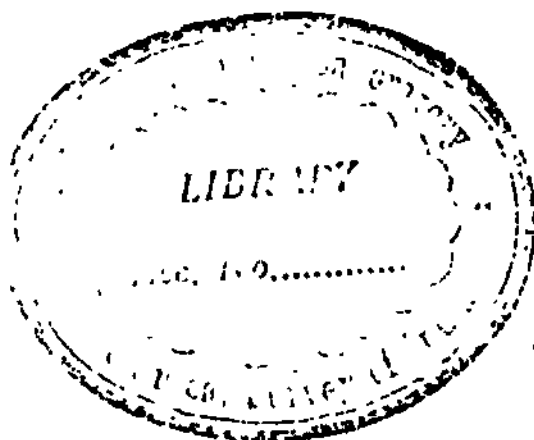
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# PREFACE

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 Mendeliams, 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. Lainarckiana* has the same right as any other North American species to rank as an endemic element of th« 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 pro-cesses 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 T 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.K.S., and Dr. 0. 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, 6i, 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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# LIST OF ILLUSTRATIONS

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.

<div style="text-align: right">

JOHX KEATS : Early Poem,
(181'5 or earlier).

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# THE MUTATION FACTOR IN EVOLUTION

## WITH PARTICULAR REFERENCE TO OENOTHERA

### CHAPTER T

### IXTROIHTTION

### *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 \vhile variability leads immediately to diversity, heredity is the conservative factor which preserves, and so accumulates, the differences gained. Regarding the ultimate naturè 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 Ueniendously 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 complemental 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 Eed 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 tKe 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. Lamarckiniia* 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]*!*[1] and (2) What is the relation betwqpn 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.

Eegarding 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

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[1] Since this was written, tho 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.   Tt should be remembered that crossing in nature is a common phenomenon, and that many wild species are hybrid in this sense.   So true ia»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 *Eropkila 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 Hieraciuin 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.  Oe. *grandiflora,* Solander.
2.  Oe. *Lamarckiana,* Ser.
2a.  „          var. *cruciata,* Hort.
3.  Oe. *biennis,* Linn.
3a.  „ var. *sulphurea,* de Vries.
3b.  „ var. *cruciata,* de Vries.
      = var. *leptomeres,* Bartlett.
4.  *Oe. cruciata,* Nutt.
5.  *Oe. muricata,* Linn.
5a.  „ var. *canescens,* B. L. Robinson.
5b.  „ var. *parviflora* n. var.
6.  *Oe. Tracyi,* Bartlett.
7.  Oe. *argillicola,* Mackenzie.
8.  *Oe. Jamesii,* T. & G.
9.  Oe. *macrosceles,* A. Gray.
10.  Oe. *macro8vphon9* Wooton and Standley.
11.  Oe. *Drummondii,* Hook.
12.  Oe. *Hooheri,* T. & G.
12a.  „ var. *irrigua* (Wooton and Standley), Gates n. comb.
12b.  „ var. *Hewetti,* Cockerell.
12c.  „ var. *semiglabra* n. var.
12d.  Oe. *Hooheri* var. *angustifolia* n. var.
12e.  „ var. *parviflora* n. var.
13.  Oe. *Simsiana,* Ser.
14.  Oe. *MacBrideae* (Nelson), Heller.
15.  Oe. *ornata* (Nelson), Rydberg.
16.  Oe. *angu8ti88ima,* Gates.
17.  Oe. *nutans,* Atkinson and Bartlett.
18.  Oe. *pycnocarpa,* Atkinson and Bartlett.
19.  Oe. *canoviren8,* Steele.
20.  Oe. *rhombipetala,* Nutt.
21.  Oe. *Oakesiana* (Robbins), S. Watson.
22.  Oe. *strigosa* (Rydb.), Mack. and Bush.
23.  Oe. *cheradophila,* Bartlett.
24.  Oe. *heterophylla,* Spach.
25.  Oe. *procera,* Wooton and Standley.
26.  Oe. *depress\*!,* Greene.
27.  Oe. *Heribaudi,* Lévl.
28.  Oe. *parviflora,* Linn.

Oe. *longissima,* Rydberg.
Oe. *hirsutissinia* (A. Gray), Rydberg.
Oe. *sicbulifera,* Rydberg.
Oe. *Cockerelli,* Bartlett, *in litt.*
*Oe. Miller8i9* de Vries, *in litt.*
*Oe. jranciscana,* Bartlett.
Oe. *venusta,* Bartlett.
  „ var. *grisea,* Bartlett.
Oe. *8tenomere8,* Bartlett.
*Oe. stenopetala,* Bicknell.
*Oe. atroviren89* Shull and Bartlett.
Oe. *venosa,* Shull and Bartlett.
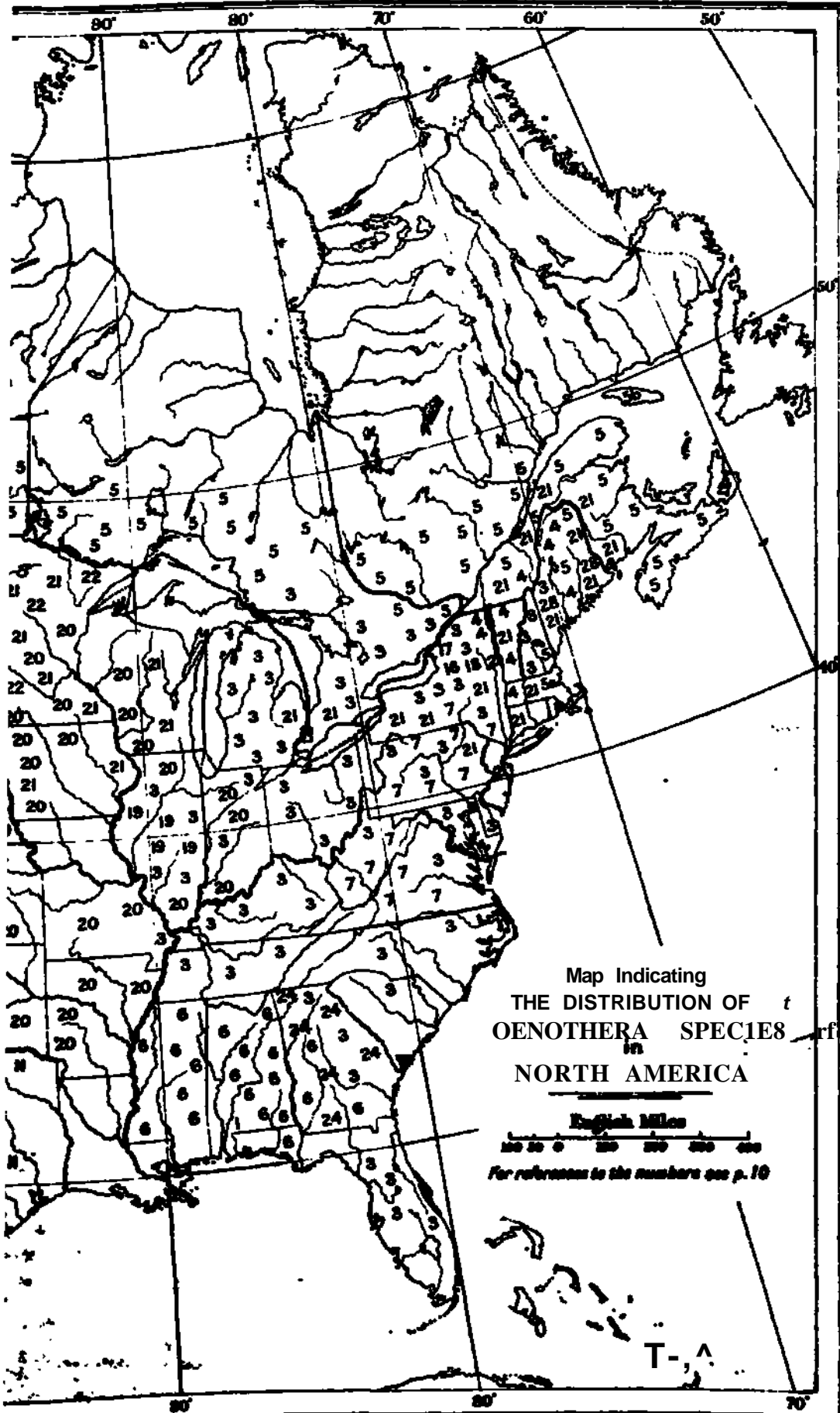
Map Indicating
THE DISTRIBUTION OF
OENOTHERA SPECIES
in
NORTH AMERICA

English Miles

*For references to the numbers see p. 10*

# CHAPTER II

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, Eussia, 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

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[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. Z winger *(Theatrum Boianiciwi,* p. 974) speaks of Ocnothera 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, then-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. Ilookeri,* T. and (I., 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, *Lusltanica* (see p. 67) indicates that he thought it came from there.   Parkinson, in the *Theatrum* (1640), refers to *Oe. bknnis* and two species of Epilobium as wild along roads and the borders of fields.   Hence it was probably naturalised in England between 1629 *(Paradisua)* and 1640.   Zanichelli *(Istoria delle piante de\* lidl 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 Veg. 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 Oanclolle's famous *Ofoymphle boUtnique raisonnée,* 1855.

In England, Watson in his *Cybele Britanm'ca,* 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, ami these m* .shown on the accompanying map. In thiamap i-lut ranges indicated are of cotuse only approximate, and *0e. himnix* iw coumdejced in an inclusive sense,

### 1. *Qe. ffrmtflifttnt.* **Sdandtiv.**   (Fig. !.)

Exsiccata.—1, Burtrttm^ |»Uiui-. " ec i]Uwt»d in CwoKoifc, Florida and Georgin, 177,1 «," fpt, tO, $ ^jux-imriiv t\ y|- .il, \M**\* jUnmt 3Ji iiuti.. hypanthium

tips, >iM'iiH*ftii hmp luitw *>n nt-'iu. tmtVl taper-tin[1] In NWh   2. Ait,
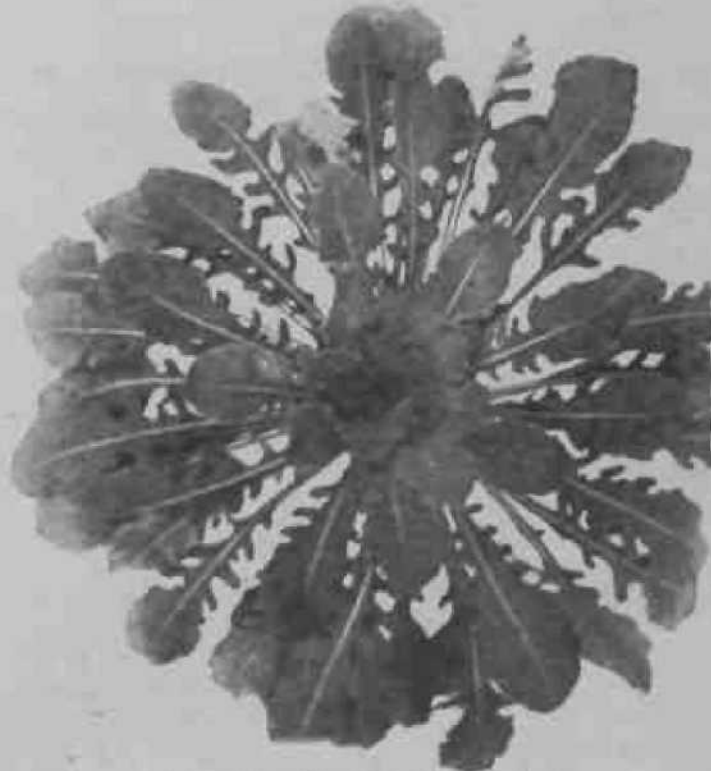


Oe. grandiflora race.

Hort. Kew, (B. &taa).  ♣ (to. if*«t*vWfiM, I'Jiwf*  R. Vjicente, Madeira, Lowe, 181)2 {*' quits n v...'"). 4. H<rW. D^riclufT, 1'tilliw (pntote 42 mm., hy kiintliiuni 4s itiin..^ rout, in (fiamotot hiufs stout, glabrous, a very lujuiniitit rJ i  5. Col iK*/ii l/ni^e. 1831 (cyh; r-llort, flowers smaller, bin! come 18 mm.). I *'J>itaun ls*i$> . 1829. T. Jurtftn des ... Chap ... Herb. Lindley (Cambridge), Hortus ... nu" (apparently a small-flowered rtiiety of *)« QtTjai\jl#r&, bud e*«»*» H ft:; V. \V»-t*- urtniud uciu" St. Botolph's ... Colchester, 1881 (buds stout and perhaps squarish, sep T'. r.vl as m mm. rubriacrvis).

N iw known to be imligenowj only in Dixie Landing, *mi **one** t)i Un other lpcaiitie** in AbUnw, **though there**

arc records under the name *(k. gramlijlora* from Ontario, where it is said to be common on good soil (Macoun, *Cat. Canadian Plants),* **Michigan *(Cat. Wlieeler 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." [i] Barton gives an excellent figure of the plant, and describes its variability. He also quotes the statement of Elliott[2] 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 ˋContinent. 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.

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[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. *(k. Lcmarciciana^ Spring*.*. (Fig. 2)*

Exsiccata.—1. Switzerland. Mus. Henslow,     James
Dalton (1820-40), the exact counterpart df ~~~~~     Garden
Edw. Leed     Hort.
Kew, 1883.     *ubrinervis*),
pet     Uxbridge,
England, 1907 (buds with red stripes). 6. ~~~~~ in ~~~gate, Boulanger,
1907 (B. Mus.). 7. St. Anne's~~~~Sea, Lancash~ 1907. 8. *Ibid.*
(petals ^-*uivrti.*, *tub* ^0^^ 77_A; *l. (rubr~* · _r * ^ · _h     10. St. Cast,
Britta~ hybrids = *Lamarckiana × biennis.*
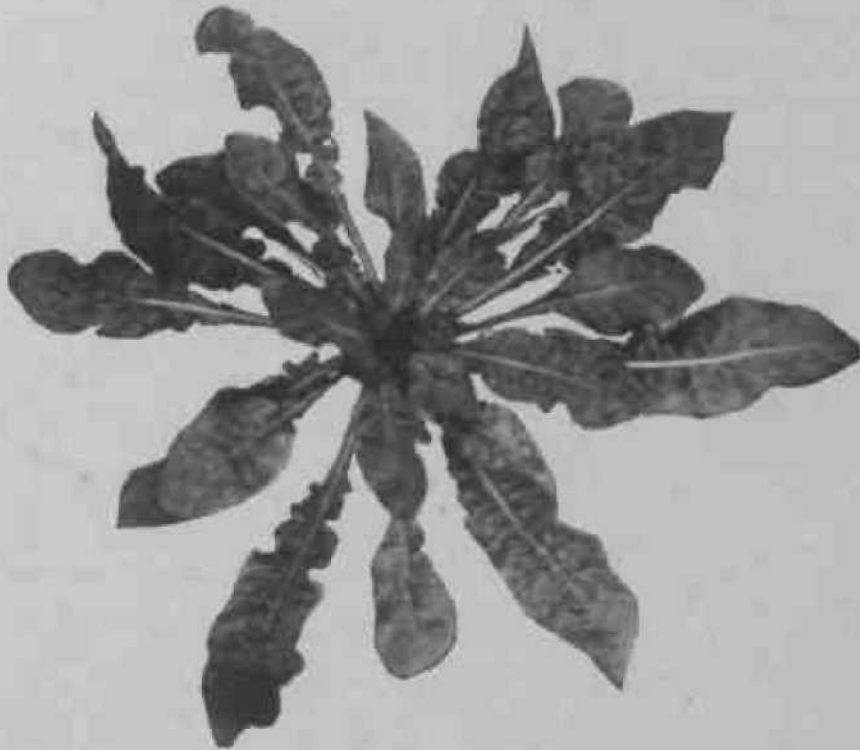


FIG. 2.—*Oe. Lamarckiana*, Ser., de Vries's race.

This species ~~~~~ naturalised and in
cultivation, and was ~~~~~ _v ^· posed by some to have
originated in gardens. Thi~ be discussed in the next
chapter.

*Oe. Lamarckiana* is the common
English ^s_f rdens ^evcr -V«here. and lu» been oxtensivoly
natura taed on the Lancashire coast for morethan a ceatuw.
A spe
Switze~~~~~ »^b^o« 1820, appeals 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 *Kur/lish Botany* (Vol. 22, p|. 1534) in 1800. Again, Smith's *Flora Britannica,* 1800, contains no Oenotheras, but the *English Flora,* 1824, refers to the Liverpool plants. Hudson's *Flora Aiu/hca,* three editions of which appeared respectively in 1762, 1778, and 1798, likewise makes no mention of Oenqthera. It is, therefore, probable that *Oe. Lamarck-iana* 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. Tjamarckiana* var. *enieiata*

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. Uennis₉* Linnaeus. (Fig. 3)

Exsiccata.—1. " A Hortus Siccus by Mr. George, London," fol. 459, *Lysimachia siliquosa latifolia virginḿna magno florq* (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** °nly, 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** [1]**&mm.). 6. Flower, fol. 98. ("Sept.")** petals **18 mm., hypanthiuro** [28] mm. 7. Herb. Sherard, *Onagra latifolia,* **Inst. E. H. *Lysirn.*** *lutea comic.* C.B. Pin., *Lysim. lutea comic, non papposa* **Virg.**

major, *Lysim.* **V\f\*f, ttttffit, iijr** is latioribus, floribus luteis, majoribus **Uftt** AM., Ukij, Hut, bti^ (petal* estimated about 25 mm.).  8. Herb. Sii.-mrd, 771 (petals **S6tmo<).  0.** Herb. l>u Htiis, Onagra latifolia, etc. **in.** Hwb. Mpcison {Fiji. 3).  It. Piuki:, et. Thesaurus Botanicus, 1661, tot 75.  12. *lUvb.* -Slunof, Vat 22, fol. *r,l* (' Planta Coll. by Mr. Scott in J'jiri- ''.•  \'.l *UMt,* SitXiijc. Vol. *.Hiit. M. II.*5 (Uvedale, H(•»*>. Raya iiLiin).  H. Hfpl>. S)<>an(^ Vol. /»'', fol. * mid **Vol** ^m, fol. !•* (colI, **by CgqxUQ from** thi- **Kln^i** Cinrdcn, Mont^ her).  15. **Hrr+***
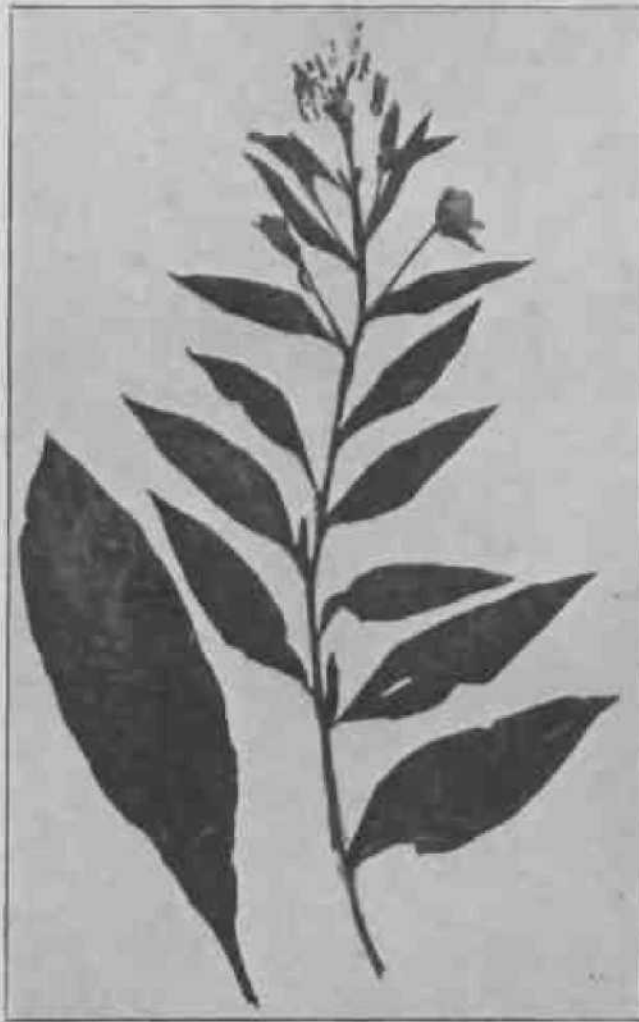


Fig. 3.— *Lysimachia lutea corniculata non papp.vi., Virginiana major.* Morison **II**-erb. = Oe. biennis Linn.

Sloane\ **Vn|, Ui», loL LM:. tBftnirto*** f*ulL>.  |0, Herb. **StoMW,** VitJ, **4Q.** foh **23 ["Plant*** (Jutlit^yd **dbmrt ti** ne Year 1660''].  17. **Serb,** altvioe, **VoL** i:Ji*. ftil, 11 (n.itln>i.i. i &( Man. I Hi hess o| Knmfnrt. v*wy iuxurimii **Hfwmmwn^** porAl-* ^IIUII,.I. is. H^rb. **Stout*,** Vol. 321. foL St» (Tiyrb. iJoorhiuivEiuiiiiu i.  [9. **H«rf,** Slo mft, VoK 333, fol. |Jj (*' ttiirdcn Plants *nt\ Wkrwtti* «;jiih<-j>^| **mid** XIUUMI by Dr. I ve dale '' *i,* Uu. *nwjrrr htifoKa* T. *'Mr*_x* ,It. Mi.s.) H^rt.. i*tiff. (st^nw lobes **10 mm,).  21.** O M^^J *iatiJoUa,* Totirn, ClidM.^ Harden ;

1052), 17.13. 22. (IK»lma Garden (No. 2878), 1779, another race, petals 14 mm., leaves short with broad, cuneato base. _ *IS. Hortus Hyemalis* (petals 15 mm.). No. 68 (Hill's *Hüt.*, p. 398). 24. Linn. Soc. ..... 26. Entre St. Jean et Landeron, 25. Hort. Kew (Brit. Mus.), 1781. 1811 (petals 18 mm.). 28. 1834 (petals 22 mm.). 27. Suffolk coast, ...al). 29. Crosby, near Liver- Mrs. J. Turner, 1806 (upper leaves .... cont pool, 1825. 30. Near Woodb .... =C. ii. 31. Herb. Rottlerianum, East Indies UJL ££ . 33. Woodbridge, Crosby Warren, near Liverpool, 1837 p e total ee Suffolk, 1829 (petals 15-20 mm.). 34. Gerd, near magner y- — 1824, Mus. Henslow. 35. Banks of the Rhine, M« Henriene «^, mouU. Sands, Rev. W. R. Crotch (petals 22 mm.). 37 Lake o 39. Near Townsend. mm.). 41, 13. Bot-

Hamburg, Herb. Auswald. 41 H a g e *£%£** TM*^ Herb. Mus. Tirolensi. 44. Near St. ^^f80,,,8, . 1887 (I)· 45. Near Berne, ^ - ^ ^ ^ Z S i S ^ g 2! Albm, 48. Bords du Lac, sous Lausanne, 1879. 4J J» uliar new g e g Herb. Hook. 50. Jacksonville, Florida, 1894 (a pec r sules near Oe. *Kennis,* having petals 15mm.tong, J J J S.. J with very very short (14 mm.) and stout). 51. Oregon BO ..KK, eculiar narrow leaves, 10 mm). 52. Georgeville, Quebec. |«w^P 11 mm } bud cone 13 mm.). 53. Acton (new London), 1907 petaU 1909 (b ^ 54 S. Kensington, 1907. 55. ^ T ^ ^ S S T ^ 24 mm). cone 12 mm). 56. Heidelberg, 1829. •>/. n»«" w

If Bartlett's delimitation of Oe. 'to**^ ^J d, and there is no doubt that it should be, *» * ^ J which has been common in HoUand sincere toe of Liru^us, and is now frequently debated as the "Europkn *bmnu*," should be *^»J**££ the species. This particular race whi h ...s pr( America, is now, the fcrt Oenothera to be brought from occur there, like Oe. lamrctona, no longer known to Herbarium though de Vries found a specimen m ^ rr eared to be of the University of Minnesota which close £ £t £ identical with it On account * t and for other reasons, it is certain hat * £ ? ? £ £ has not been modified during the three centuries ol d» cultivation and naturalisation. . . TTnlland

It seems to have been first naturalised in HoUand, where it wa, already common in the time of^Lnnams,

•

1737.    This type, which bore the original name *Ly-simachia hUm rorniculata* 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 Linnaeus. 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* x *Oe. biennis sulphurea* gives *sulphurea*, and *Oe. biennis sulphurea* x *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 x Oe. biennis sulphurea* **the ordinary deep yellow is** fully dominant so that it alone appears, both in Fj and F.[2]

### 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. naneUa*$_t$ 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. Tjamarckiana* has originated in cultivation."

[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. *fasiopetala*), and Bicknell (24A) *Oe. stenopetala* from Xantucket. 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 Geoige, 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)

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

**I-R.H.**   *Ljftkn,*   <*uuju#i.* ttnwxfabm. ***oornioulaia,*** if- **B**, I V . *Ly\*im. tonic liitm rtannd,* **minor AM wyt&tijolia,** Mor. H. R. **Bhw.** At/j»rm. *lutea* oo««r, *rtfin pttpiwm Virg\* mimr,* H, Ox. 77JJ ([jetnln **9-lfrmm,, stem-hteW** 22-23 mm. widfl).   3.   772,, Jnrgnr JICHVDI^ **(petalu** 19 jnnt. T) »\*\*d vf-ry imrrou- ]₍rtv\*i\* **(tfr-12 ttim.** vritJo).   **4. Herit.** Slu-mni 77-1. *l>etaU* Jfiinm.. *wiry* it-S nttii.   **ft Bach. Slow\*.** Vol. **:m», faj, Ma fleavftj dtttTOWt IS nmn.,** hi iff «on\*» 7 nun.), fl. (<imrm|{|.< \*:oin
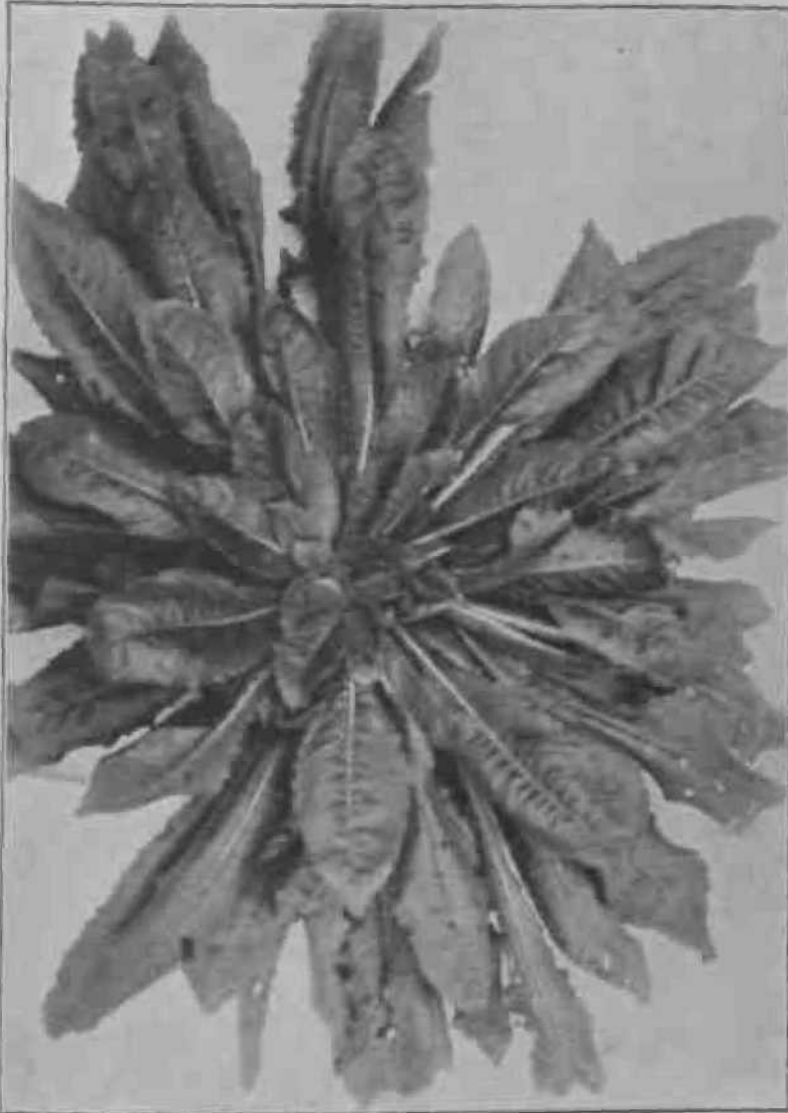


Fig. 4. — *Oe. muricata,* broad-leaved form
(fr\*i. Middleton, Nova Scotia).

(Georgia}₍ **u**'. \. Turner. 1769 : **bud** cone 10 mm., leaves narrow (10-12 mm.), stem **nd:** Indian name, Outa kenoka = " red stalked. st«nd Furaight.[1]\*   **7.** findpon't **B«y. Bknkt. 1771** fprtah 10 oun.ᵣ leave\* narrow, **10-11 nu»< nwi.**   **B** Hart- 'lotting.. **Murray, 1782** fpee\*l\* 15 mm., **H** lds ne«,rlv ylrtbroits, sttj'Je slww u» in ^r. mut bcfijj^f\*). "- **CoJumbtfl** n m , **new** Uu< sw.   **D.** Douglas 1&25.   **10.** Plain\* o[ **JW** River, **I).** DougL₅₅, 1827.   **II- Unn. Soc. Hert.** (bud c«tic 11 nwn.J.

*VX Ctftbmm* Uod. m 13. Ruggisberg, 1830 (?) [bud .-•«.- 20 mm., ntaia **muvteaio**}. U. **Nmr** f reiburg, 1849. 15. **Kudton's B** **(hud iwmr L^tnntH IDBTI** narrow). **I'** •'- > HI\IT, **Ihmjiin***. III (petals 15 mm.). a (very narrow leaves). 18. Hamburg, 1842 (narrow leaves, petals 1+mm.).
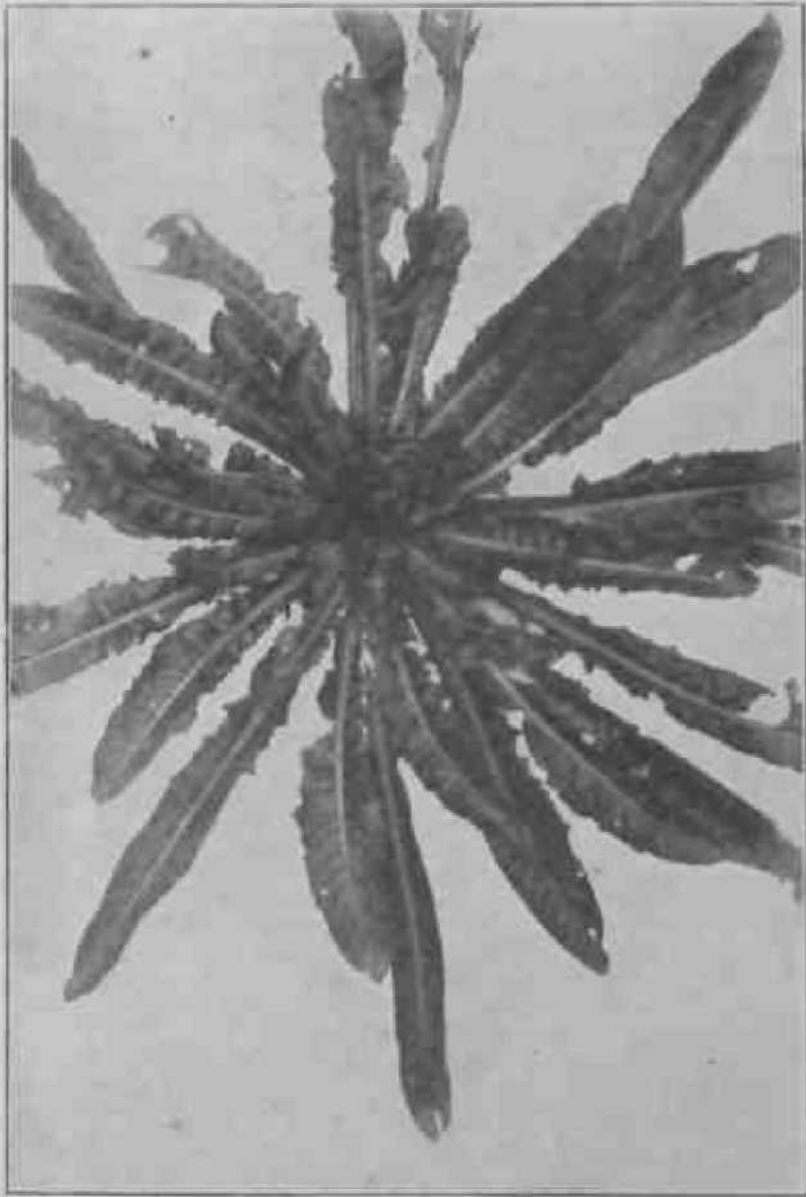


FIG. 5.— *O. muricata,* ft-11 row leaved form (fr. Winnipeg).

**10. (Julmar. Fnmrr. IM!** leaves v ny wmww, | mm,). ill), **Hotetnn** (petals **I-irun** . *| **IJ-rl** o *in* M — llr A **I^Vflnbdi, Hiltm. tftAl** (leaves \ *rty* **hattint,** V nu<. 22. St. Tron U f Jtttly., ISti.'i ^ttiivit' ftmnu). *2U, I>* er', Demidoff, Pallas, several specimens, petals 2-,— |u mm., le •tvew Jr. 9 mm. A K|«> ; fi^t probably liybrirh ^irtthi* × *muricata.* **24. Bitolta nf Klbtf, I»*M*. Sft. Bea Hi.inlrurg, 18M** (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. Chatel, bord de la Moselle, 1885 ; forma *Mosellana* H. Waldner in litt. 32. Miilhausen 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 ty$es 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 northwestward. 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. *jxtrviflora* 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**

races 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), Miilhausen in Alsace; Colmar, France (1841). According to the Eev. 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 cornicuhta 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. Iongi88ima,* 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 leavas, 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 papillae.

## 11. *Oe. Drumtnondii,* 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. Ufrons,* 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 Fucgo, Guatemala, 1873.  7. Santa Cruz, California, 1884 (named *Oe. Lamarckianci*).  Bodega, California, Barclay.  9. San Bernardino, 1890.  10. Santa *F6,* New Mexico, 1897.  11. Parrott, S. Colorado, 1898.  12. Near Varrott, 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 *HooJceri* 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 papilla) 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 papilla).

(4) Conspicuous red papillae 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.

*Oemthera 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. HooJceri* 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. *Mr-sutissimi,* Gray, which was the name formerly used to

designate all forms of *Oe. HuokwL* The specimen lias 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 papillae 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. MacBrideas.*

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

Exsiccata.—1. Lindley Herb., Douglas, British Columbia, 1826-7. 2. California, Douglas, 1833. 3. Nova California, D. Douglas, 1833. 4. New Mexico, 1847 (petals 30 mm.). 5. W. "Jexas 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 spocipH, *Oe. f rmic inert na,* liartlett, and *Ov. remutta,* Kurt let t> (15), segregates frmn *Or. llookcri\** are described from California.

*Or. hirsidiss'nn<i,* liydh., -*Or. hirnnin* var. *hh'sutiss//////,* (Jrii$_t$\, lias I wen considered a synonym of *Or. HooLrri,* T. and (J., hut· lias shorter sepal tips (2 mm. instead of 4 nun.) and very Jong and loose pubescence on leaves and ealvx Xew Mexico and Colorado.

### 13. *Or. Sunsiaita* Seringe

Exsiccata. -1. Mexico Valley, Schmitz, 1855 (?) (petals 25 imn.$_t$ leaves rather narrow).

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

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

### 14. *Oe. Macliride<t(>* (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 papilla\*, petals44 mm. long, and base of stigma lobes usually some distance above the anthers.[1]

### 15. *Oe.ornata* (Nelson) Kydberg (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 (fcllectae Padua/' 1665, fol. 78, *Lysirn. lutea corniculata, Lysim. Virginiana.* 3. Herb. Moris., *Ly8im. 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 ") *Lyshnachia Virginiana* (bud cones 8 mm.).

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[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. hiennis* 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

Exaiccata.—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 x 3 mm.), acute, inflorescence long and dense, petals rhombic-ovate.

•JL  *h\  *OakesifBta* (Bobbins), S. Watson (Fig- 7}

Occur* from the St. John River, Kew Brunswick, and Queltec to MaeaachasettB, Rhode bhuul. Oatmecticut, NVw Sotkj *and* westward to South Dakota, Minneaoto and Colorado, K< ✱✱✱> leaves -v liimotric-ailv jmmate-veiiied, devoid t>f ted, with *a* broad, white midrih: pube-spence soft-»ppreaaed ; sepal tips spreading; seeds large.
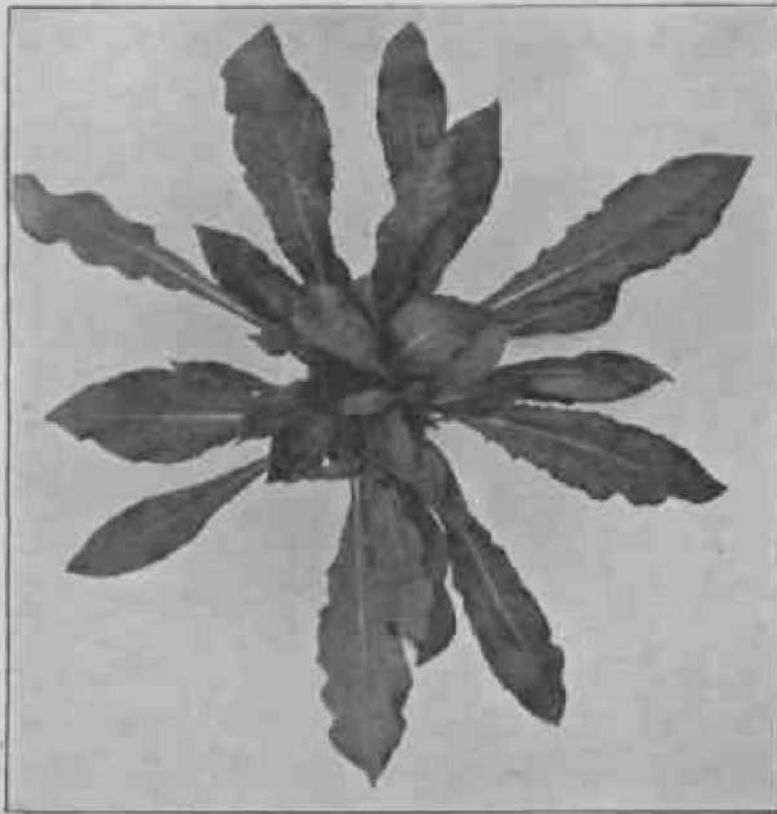


FIG. 7.—**>'. *Ortkrmnrut.*

This species has a wide range, though the western form (which f luive grown from St. Paul, Minnesota, and also from seeds eent I>y hi. Elrast A* Be^cy from Horseshoe Rnnch, Kntes Park, Colorado, at iui altitude of 8.300 feet) *tUWtvs* fiom tbe Eastern plant as descnbcil by Vail, in certain particulars. The flowers *HM* larger, petwls 20 x 23 mm. (instead of 13 15 x £S n IHUL). ami the loaves differ some.,vhat in shape (cf. Fig, 7 with *VI*15, MacDougal, Vail and Shull.. 11IU7),

## 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 floweft (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. *subuhta,* Rydb., — *Oe. subulifera,* Rydb., has the sepals abruptly contracted into long subulate tips.

## *Oe. Snbidifera,* Rydberg

Exsiocatum.—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. rhomUpetala,* 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, Pl. 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 Oenotherd.*

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-polK-nated (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 curtail-ment 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** Onagraceae.

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 iii 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 larvae 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 Bovidae, 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.

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

But it when any of theiie species are taken into **culture** tl • y may *ho* grown aa an mm fa by I *wg* inn ing them **Kffder** *glass*. With **different cooditiona^)f** culture, the hubit uiul **development** of th« plants **vary enormously,** ft nil it is possible



FtK   H.—*fh<. liht* in tri<|*ioJ conditions.
ormed.

even to trantsfiirin stj).....f ih'Mii into perennialjt.  Cultural condition^ of couree, hruig out -ninny elmiaeters wliich would raieJy or never Imve a dttUOfB to <levelop under the more rigorous eowiitiuna of **cofnpetition** 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 OP 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 anv structural modification. The physiological difference, in rate of development, may have been impressed on the species by continuous

TABLE T.—*Early*

| Date. | Place. | Name. | Author. |
|---|---|---|---|
| 1014 | Padua? | **Seeds from Virginia ..  ..** | — |
| 1019 | Basil | *Lysimachia lulea corniculuta[1]* i | C. Bauhin. . . . . . |
| 1027 \ | Venice | *Hyoscyamus Virginianus-"*. , | Alpino  . . . . . . |
| 1028 | Koine | *Lysimachia Americana[1]"* .. | Coluinna in Hernandez |
| 1029 | London | *Lya'nnavhia lutea siliquosa Virginiana\** | Parkinson. . . . . . |
| 1040 | London | *Lyxitnnrhin httvn sili(/no.sa Viryiniana* I | Parkinson. . . . . . |
| 1000 | — | *A Hera foL lotion'bus flor. hit. majoribus* x | — |
| 1009 , | London | *Lys'nnachia cornicukita minor lutea ('(incident\*is* I | Morison  . . . . . |
| 1080 | Oxford | *Lysimnchia lutea corniculata non pappo&a Viryiniana nuijor* | Morison  . . . . . |
|  |  | *Lysimachia lutea corniculata non papposa V'mjiniana minor* | Morison  . . . . . |
| 1080 | Oxford | *Lysimachia Viryiniana lati-folia lutea corniculata* \ | Morison  . . . . . |
| 1080 | Oxford | *Lysimachia Viryiniana an-(justifolia corniculata* | Morison  . . . . . |
| 1080 | London | *Lysinmchia lutea Viryiniana* i | Ray  . . . . . . |
| 1080 | London | *Lysimachia V"mjiniana al-/era, foliia kitioribus, flori-bus luteis, majoribus* | Ray  .. ^ . . . . . |
| 1094 ! | Paris | *Onagra latijolia.* . . . . ., | Tournefort. . . . . |
| 1094 | Paris | *Onagra angustifolia* .. .. | Tournefort. . . . . |
| 1094 . | Paris | *Onagra angustifolia^ caule rubro, flore minori* \ | Tournefort. . . . . |
| 1700 | Paris | *Onagra lalifolia9 floribus amplis* | Tournefort. . . . . |
| 1714 | Paris | *Lysimachia latifolia9spicata, lutea Lusitanica* | Barrelier  . . . . . |
| 1714 | Paris | *Lysimachia angustifolia^ spi-cnta, lutea Lusitanica* I | Barrelier  . . . . . |
| 1714 · | Paris | *Lysimachia lutea, cornicu-lata latifolia Lusitanica* | Barrelier  . . . . . |
| 1757 | London | *Oenothera foliis lanceolatis, dentatis, caule hispido* j | Miller. . . . . . . |
| 1757 ! | London | *Oenothera foliis ovato-lanceo-latis plan is* | Miller .. .. .. .. |

[1] **Seeds from Padua.**      :' **Seeds from an English physician, Dr. More.**

*references to Oenothera.*

| Work. | | Identity of Species. |
|---|---|---|
| Pinax, pp. 245, 520 .. | Description .. .. | *Oe. biennis*, L. |
| De Plantis Exoticis .. | Description and plate | *Oe. biennis*, L. ?. |
| Nova Plant., Anim. et Miner. Mexicanorum | Description and plate | *Oe. biennis*, L. ? |
| Paradisus. . . . . | Description and plate | *Oe. biennis*, L. |
| Thoiitriim Motanicum . | Description and plate | *Oe. biennis*, L. |
| Cat. Altdorflinus .. | Name. . . . . | Luxuriant *biennis* ? |
| Hort. Rpg. Blesensis .. | Description .. .. | *Oe. muricata*, L. |
| Plant. Hist. Univ. Oxon., ii. | Description .. .. | *Oe. biennis*, L. |
| Plant. Hist. Univ. Oxon., ii. | Description .. .. | *Oe. angustissima*, Gates |
| Plant. Hist. Univ. Oxon., ii. | Plate Sect. 3, t. 11, Fig. 7. | *Oe. biennis*, L. |
| Plant. Hist. Univ. Oxon., ii. | Sect. 3, t. 11, Fig. 8. | *Oe. angustissima* |
| Historia Plantarum, i. | Description .. .. | *Oe. biennis$_y$* L. |
| Historia Plantarum, i. | Description .. .. | ? |
| Klém. de Botanique .. | Listed .. .. .. | *Oe. biennis*, L. |
| KJ6m. de Botanique .. | Listed .. .. .. | *Oe. angristissima*, Gates |
| Kiém. de Botanique .. | Listed .. .. .. | *Oe. muricata*, L., narrow-leaved race |
| Institutiones Rei Herbariae | Listed .. .. .. | ? |
| Plantae per Gall., Hisp. et Italiam observatae | Plate 989 .. .. | *Oe. biennis* race |
| Plantae per Gall., Hisp. et Italiam observatae | Plate 990 .. .. | *Oe. angustissima* |
| Plantae per Gall., Hisp. et Italiam observatae | Plate 1232 .. .. | " Luxuriant *biennis* " ? |
| Figures of plants described in the *Gardener's Dictionary*, ii. | Plate 189, Fig. 1 .. | *Oe. muricata*, L. |
| Figures of plants described in the *Gardener's Dictionary*, ii. | Plate 189, Fig. 2 .. | *Oe. biennis*, 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 Linnams'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. Tjamarckiana* 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.

Eeferring now to the history of the Oenotheraain 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 Bauhiti 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 de- < tailed 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-l"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 Linnaeus, 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
excedentiq"* 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 \ an inch to
\\ 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 *Ik Pttmiii* fittJ&JW 0027), luul nlso published a figure (see Fig. «) of &n Oeiiotliem ante **the** B&HH *Hyoscyamus Virginianus.* from ficwltt obtaine<l from an English pliy-
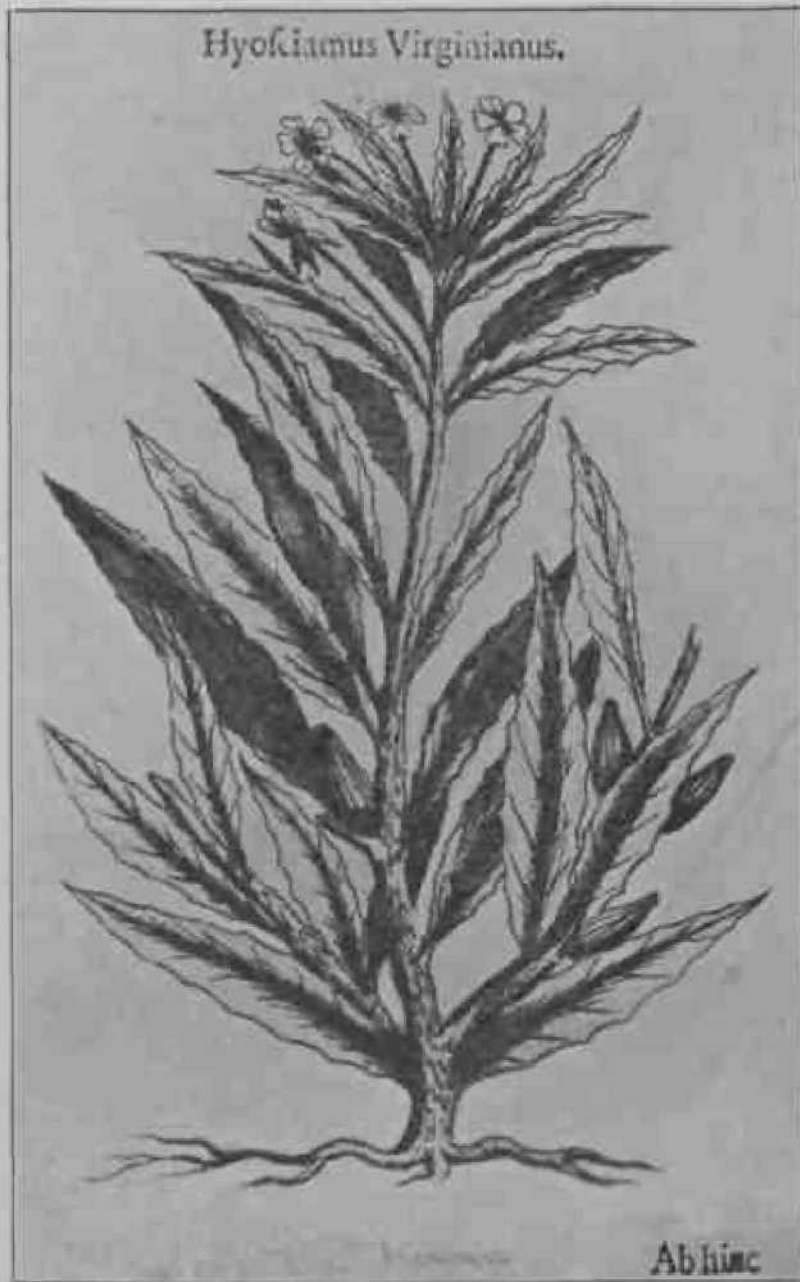


Fm. 9.—H... *win«m\* T...giniamus.* Alpin's *De Pl. Enot.*, p. 324.

=i<-ian, Dr. **Wtottt,** Thta i» prrhap\* tlifc wrnio plant, but these drawing, **KID <••• nodi ta** In\* jtif much SCTvice in detcrniiuijirr **dotsSfl** od Btxactnte or **even** matters of relati[1]

size. Colmiina (1628), in the *Nova Plunlamw. I Imcdium MrxicanortpfHj* of ETetnandes, described &nd figured what was probably a different *rm-e* of *Q& biennis* or Cfe, momoA^ under the name *Lysimachia AmerictmtL* Mis rather inricciiratye h'guio represents a plant: with narrow leaves atvd muerciDiite petals. (See Pig. 10)*

Ooranle's Herbnl in Iii33 copies Parkinson's figure



*Lysymachia hera cormulata langfol limmmia*

‼ L. Hi. LHKT- *Lysimachia* Hernandez, *Nova. Plant.,*
*Anim. et Miner. Mex.,* p. 882.
Hi..NT. I-i_s. 1232, *et*
*Jam observatae.*

(‖>. 475) and records several additional observations in his description. The plant ifi tall and with " many branches of an overwome colour, imd a little hairie." The leaves are somewhat sinuate and the midribs whitish* The capsules grow to lie [(c] *ome 2 inches long₁ being thicker below, and sharpen at the top_t and somewhat twined[1] —an inaccurate description.

Morison, in his *Rwfots Regius ffiesensis* **(1669), was** one of the first to recognise vnnotw forms.   In ;ntdition to *bi/mnachitj* **kttea** *t'ornicuhta* of Bauhtn, he **listed another** species which **was a43ad** to the London Garden between 1655 and 1*160.   Thia is named *Lt/mnacJtia armicuhta minor lufrn Cftnadenais, and* was probably the scconcl



*Fu,.* **LI.** *-Lilt* mnachia *\utiia tt/rtur»Luia* non pappous Virginiaoa minor  orison Herl.. — Ce. angustissima.

Oenothura sjweied to be introduced hitti Kurope.   It was **evidently a race <f De,** *(mgustiaswruh* **(iatcs.**

The evidence for this ideutin'cation ia found in anoth*r valuiibli? Bpecimen in the BConsoo HetWrium *td* Oxford (we Fig. MJ.  On this specimen is writivn *m* the hand of Bobart, [ik] **tysHtnaehia** *lulm co-rmculata iion jxijrjmv Virginiana minor.* Moris. *H_t* (>j;.27i, *Lysitnachia siliquasa*

I *Minium Ttatb'iuutttL* Park/* Somi afterwards (for it **w** in the same ink), Boliait, evidently through **some** misapprehension, changed the; word " minor " to " mujur.[1]* The **dot** *oven* tin* **origina]** *i* **can** \>e |>hinlv **Ken,** In 188tt the Rev. (.Ittrnaey **mtfttcaJiit-ed** tin* ' I [n] and **"No. 7"**. **which** ahonhl have been No. 8. It w **pbviona** that Morison us*;d th« **tends Vttgmiaiifl said Ctoftdepids** interchangeably und that \hv *Lvtimachw* /«/*•« *comicuJata* imd X*ysimachia
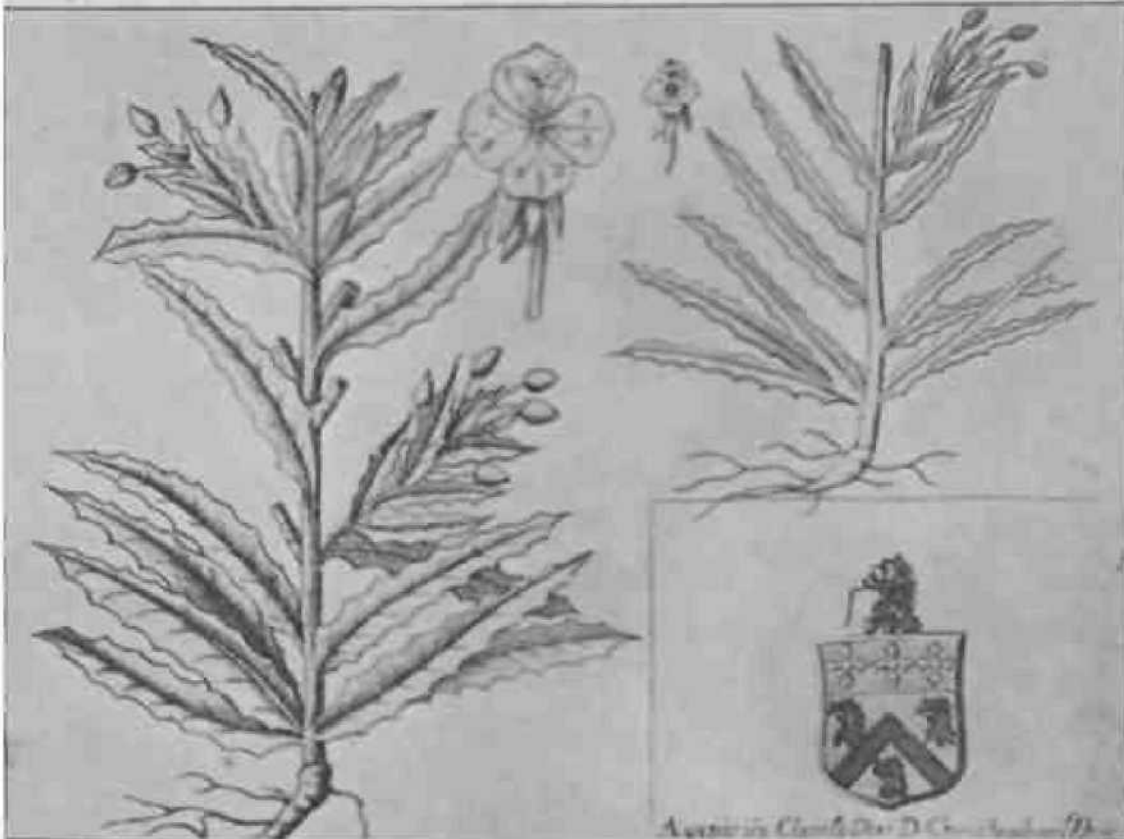


Fi». IS —1 LEFT, *Lysimachia Virginiana latifidia, lutea, corniculata,* Morison, Hist. Pl. Univ. Oxon., = Oe. biennis.
HiGHT, *Lysim. Virginiana angulifidia, corniculata = Oe. angustissima.*

*corniculata* **mmor** *hxtm Canadttmt* <"t *nmjtuttjfttlia oi* I he *Hortus Blesensis* wen[1] th,Q BUUfl r6»pftCtiv«l)' . J *Lysimachia lutea* **cornwttiatfi** *turn papjKtm Yiftfiuwtut major* and *Lysimachia luka cwnicuktfa n<m pappota Vinjiniana minc>r* erf tlir? *Hint, hsaiu* The tliinl '" *LvMnmohm* ' of the *Uitit. Bles., Ijifaim. Ittlea jhtn: tfltdtoso,* **Park. Get.j ^** 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 angystifolm, 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 papillae, 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
Linnaeus, 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 Eobert 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 corni-*
*culata* **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 repre-
sented 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

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[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 (6) *altera fol. latioribus flor. lut. 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 Altdorjina* 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, fioribus 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 ; fioribus 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, ./lore minori* **Fluk. 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, =0e.** *angustissima*[9] though there is no specimen to prove this.

The last species listed by Kay is *Lysimachia lutea corni-culata, flare sulphureo,* Hort. Lugd. Bat., recently shown by Bartlett to be *Oe. biennis* var. *sulphurea,* de Vries.

**The view that *fysim. Virginiana altera>foliis htioribus, floribus luteis majoribus,* may have been merely a more** luxuriant form of *Lysimachia lutea corniculata* was sug-gested 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 neces-sarily 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 Her-barium 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, Jlore minare SchoL But. 44.

" *Onagra angustifolia, caule rubro, jlore minore.* LR,H. 302. 772s."

As shown by Fig. 13, the flowers are extremely small, the bud rone 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 (14-10 mm.), margin distinctly repand-denti-culate, pointsratheT broad. This agrees with Yail's description of **0e.** •*parmftora,* L., in practically all particulars except the remark-ably short ovaries, **which** measure only 4 mm. instead of 8 OT 9 **mm.** in length.

There are two small specimens of this species in Plukenet's col-lection. 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. Plukenei's figure in the *Alma-gettom {1 <3%)* was probably drawn from **this** specimen. He further re-marks (p. 235):—" Hujus plantae siliqua in comic**atam** non extenditur,[1'] **from** which it may be inferred that the plants failed to set seeds though the **flowers** are self-pollinating.

FIG. 13.—*Lysimachia lutea, angustifolia,* i'*intiuhi***no,**^ **mtftore,** MUI'IKD]] Herb., = ()e. *parviflora,* L.

The pre-Linnean polynomial, *Lysimackia Intea angusti-folia Virginianu fort' miwre,* \$ therefore clearly identified by these specimens and figures, as *Oe. parvifiora,* L. *Onctgra angustifolia> caute rubro, ftwe minore* of Tournefort, was in sonie 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 Tourne-**fort'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  x  4*1 cm. wide, repand-denticulate ;  stem-leaves 21-23 mm. wide; flowers small (petals 9-10 mm.).  It is to be con-sidered as a broad-leaved type of *Oe. muricata,* L.

The next specimen (see Fig. 14) bears only the number $772_2$, 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.  x  $3^{\#}1$ cm. and 24 cm.  x  $3^f4$ 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 sperinutn i⊳ the **l)u** Bms **ooHeotiqp** at **Oxford, which** belongs to **the** iypr pi **Gte,** *mttriftikt,* **b&fttd** the following label : " *Omym* **a^guMifdUa^** *CQtlU* *rubm$_t$* *flat\* mitxote.* TournK. **302"** nml **"5VttDl** Mr. **Stoncatroet"** The sheet bears a knig, IUITFOW. rosette-lcai **about** '24 om. long, 4 cm, greatest **wHth,** with **probably ned** iniilribs. The **Stem** bears **Conspicuous** long hairH, arising from red papillæ ;



Pin, U\* — H«Hk. Morison.
muricata, L.

the shoot in in fruir. so the flowers tire late ones and are very snmll (length of laid cone 5 mm), length of hy pa nth mm 14 mm.$_t$ sepal tips **noi** in contat-L. The above **polynomia]** tlier^furft in M>me eoacs refera to ruc^ps **of** tfe. *muricahi,* L., and such spe^itneixs as this show that races existed which were intennedifi&G Imtwecn *Oe. murioata* and *Oe. uujmlmima* **in** width of leaf and size of **flower.** The

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

Before Tournefort's *InstUutimes* (1700) the following species were therefore known, as shown by herbarium specimens chiefly at Oxford and in the British Museum :— (1) *Oe. bimnis,* (2) *Oe. angustissima,* (3) *Oe. parvijkra,* (4)-'0B. *muricaki*; 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 *Lysimackia V%rginiana aUera, folus latioribus, floribus hdeis majonbus,* 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 *hamu* always applied to it ?

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

Onagra latifolia. *T/ysimachia lutea* comicwZoto, C.B. Pin.

Onagra angustifolia. *Lysimachia angustifolia Canademis corniculata,* H.R.P.

Onagra angustifolia caule rubro, flore minori.

In his Institutiones Rei Herbaria* (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 dilutiore. *Lysimachia corni-culata non papposa, Virginiana major, flore sulphureo,* H.L. Bat.

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

(4) Onagra angustifolia.  *Lysimachia angustifolia, Cana-densis, 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* (" Euro-pean *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.*

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[1] **One of the specimens in the British Museum, marked** *Onagra latifolia flore dilutiore,* **Tourn., and believed to be the plant referred to by Linnaeus 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. parvifiora, 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.* **PI MO nhoir\* p\*rttcukHy** tti-ll the long ami loose iiitl--i- •••• '•.. . . . . . Icavi\*, **and the** euiitrgiiuite and plicate **p«tftlfl pi** Q\* *mgu\*ti\*$rma,* the flowers being evidently **«jnfX5 BmaD 0- tfun\*)** as in Monisou's race, I fonnerty, **bftfore** fM *(mgtutitwma* had been rediscovered and described, regarded thia iigiire aa Teferring to a narrow-leaved rare of <*k. wuricata.*

BarrelUu-'s third spudeH, represented in Pl$_t$ T23\*2 (Fig.



FIG. 15.—Barrelier, *Plantae per Gall., Hisp. et Ital. observatae.*
FIG. 989 = *Oe. biennis,* or perhaps *Oe. muricata.*
FIG. 990 = *Oe. augustissima.*

11", *y,* ▷M i^ **appawndj?** the **mmrictknifl** \>*hut* \*f Kay aiid the *Cat. Atidoi'jf,* 1 formtriy regarded it as certain that this was a large-flowered species, probably nearest *Oe.* ***Lamarckuma.*** Though that hypothesis is by wo means disproved, yet it docs not now rest on *an* tirm a basis as before. A utitivul eonii>;irinon of the figure with the other two of Barrclier seems to iudfcn-te that ,\\*w.* (lowers 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 Eay (1686) and the figure of Barrelier (1714). As pointed out earlier in this chapter, this figure 1232 may represent merely *Onagra latifolia (Lysim. lutea wrnwulata)* 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$^9$ lidi Veneti)* gives figures of two Oenotheras as follows:

I. *Onagra latifolia,* Tav. 112.

IT. *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 Linnaeus 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 Linnaeus was then familiar. He also recognised the var. *sulphured.* He cited figure 1232 of Barrelier (s^e 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 Linnaeus were apparently** *Lysimachia lutea corniculata nun 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 Linnaeus 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 Eay 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 Linnaeus 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 Dktwmry,* 1768, Miller applied binomial names to five species of Oenothera. Those which concern us are (1) *Oe. bknnis,* taken from Linnaeus, (2) *Oe. angustifolia,* and (3) *Oe. gUbrą.* The second is a synonym for *Oe. muricata,* the name given by Linnaeus 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. grandifbra* 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. BartTam sailed from Philadelphia in 1773 in search of rare and useful plants. He discovered *Oe. grandiftara* 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 Kervensis,* 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 *Dw-tionnaire* under the name *Oe. grandipra,* from plants grown at the Museum d'Histoire Naturelle in Pans. Seringe recognised this species as different from the *grandir jhra* 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

(I2f») lias **recently dtoared up** the mnttar by the important discovery that a **specimen collected** by Miuhaiix in Extern Nortli America about the end of the eighteenth century, and now iii the Paris herbarium, is identical with *(k, Ijnwttrvkuttm.* **Bet\*,** aa now known from hi»



FIG. 16. —*Oe. Lamarckiana,* specimen collected by **Midtuitut id Korth** America. From a photograph Blaringhom.

cultures *ntv\* froHl Uiiioasliire. The upper part of tbia specimen, from a phot^igraj>h kindly supplied by Prof. L. Bhmnghom (sec 34]$_t$ is ^liuwn in Fig. 16, It apparently leaves *uo* **doubt** that f^. *Lamavahiana ti&* we now lctww it originally grew wild in North Ameriuji, 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

a! Mu'liaiLx. As is #eJJ known, the cultures of tie. Ytu·s are d•sc·>-nd«l from deeds originally derive! from Met·srs. Carter and r....**pany** in **London** in \\*mt* ami tuituraliised at KilvfirsLinu Tkcee **seeds** w«rp, suppos^l to hnvc beei
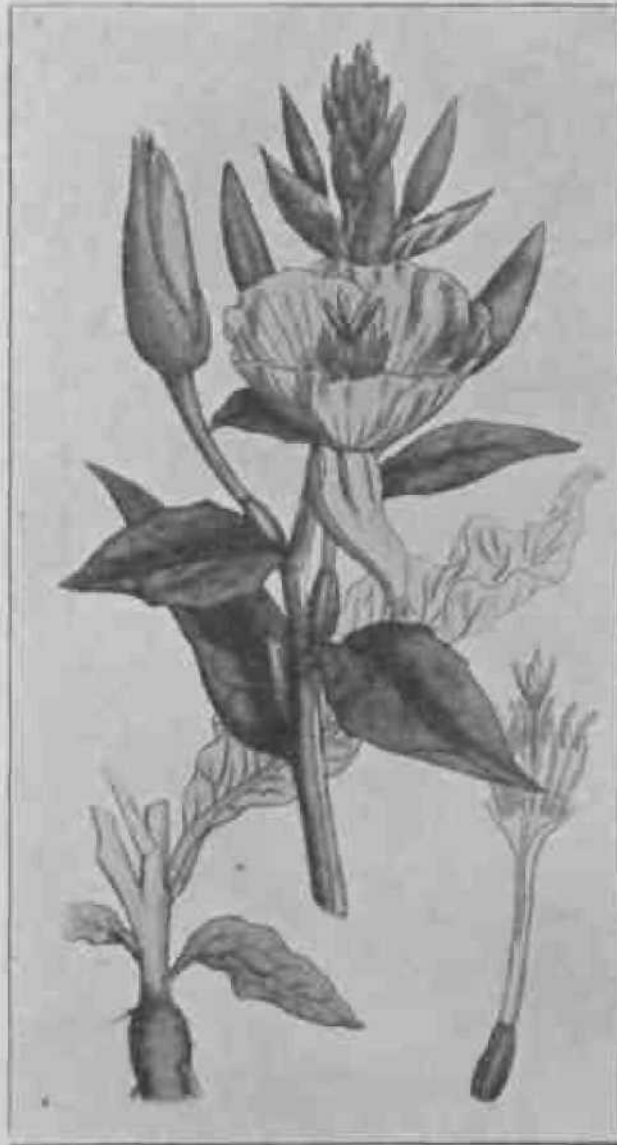
Fig. 17.
Sowerby's English Botiiinj, VuJ. ±1
pl. 1534. 1806.
Probably = Oe. Lamarckiana.

introduced fri>m Texan. But it is much more **probab)**e, as Dnvis j*njt";estjn, tluit they wore derived, from **some** **naturalised locality in** Kokand, **presumably** tlie Lancashire eoasfc. **Ah. F*: A. Gftrdlicicr, 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 htifolia, floribus amplis,* of Tournefort (1700) and corresponds to the second species described by Eay 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.    Barretter'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 thajb *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. muktitaeniata,*** 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 uf these mutants tire, however, nut described, atul it is not stated ivhutlier they arc **reversions towards the parental** spucies or variations in other directions. Jt is possible that irregularities in chromosome distribution **may explain some** of these Hpoimlic variations in *Lcptino-tarm, us in Oenothttra.*

Any study of t:lie histury of *On. Ijamarckiana n\*ust take into account the fact that, like other wild **spe‹8es,**
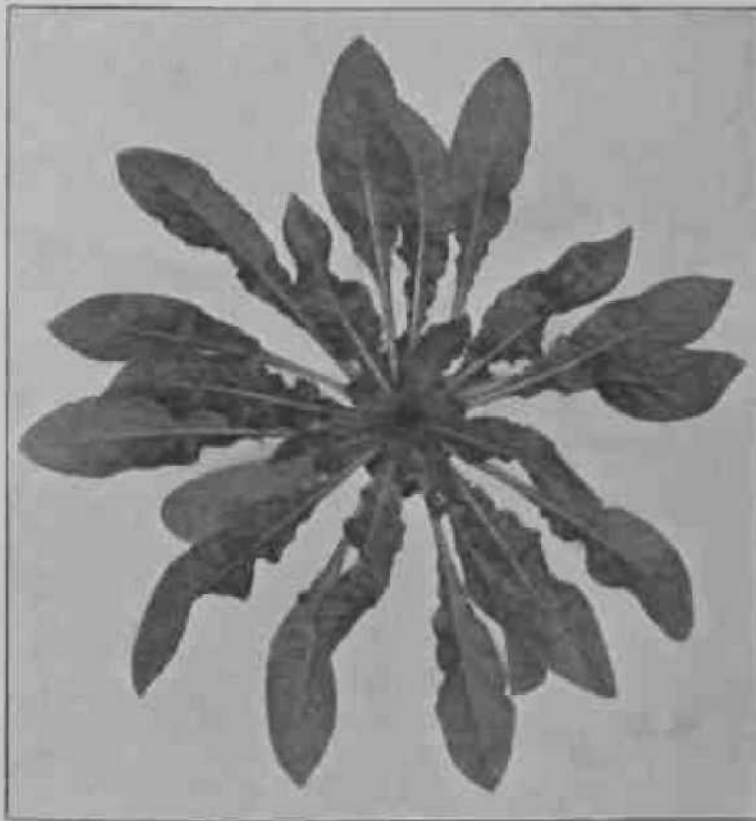


Fig. ia—*l'. Lamarckiana*, race from **tilt** JH1‹‹ of Wight.

such &a Oe_f *gmndiftora\** it **coutainfl** a number of **independent** rac(is or **elementary** species. The strain atudieci *hy* de Vries is only one of several which are known to exist. We a\*e not now speaking of **the** mutants, but of fche various known raves from different sources, which must be c-laajjed with Oe, *Ijttnarcfriana* in the stricb sense anil yet which differ ffrom 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



FNJ. 19.—Isle of Wight race of *Oe. Ldmarckiuna.*

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-Njlsson 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 iu *Omatihmi Lamarck iuna,* and is the sole bads for his sweeping Mendciiuti hypothesis of mutation.

(3) The race already mention^ which Heribert-Kllsaon (1S4) obtained from a gawlen in Almaröd. in Southern Sweden, in 1907 (Fig, 20), *is* not identical ivith the Isle of Wight race, though both show the same heterozygous condition with regard to one character. It differs from the *iMrnarckiatia* of de *Vnm* in the fulJawtng features,
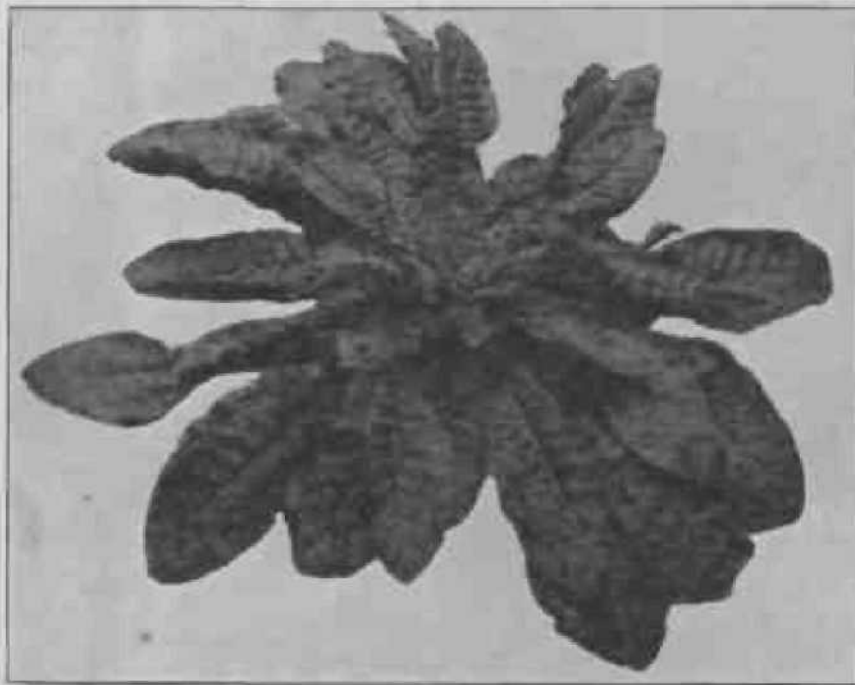


Fɪɢ. 20.—*Oe. Lamarckiana,* race from Sweden. Cf. Figs. 2
•nd 18. Fntro a photograph by Heribert-Nilsson.

according to Ilcribart-Nilfisou : *[a)* It is less strongly bieuiual. (6) The rosettes lire not so large and have fewer leaves, *(c)* The sepals arc coloured with, brownjsh-rpti jugment. *(d)* The fniits have fotu: deep red lines of pigment. It U greatly to bo hoped tbnt Bwediah bot«nifU will *race *Htm* history and source of this race by lucftitt of early records and op^imens. Fig. *21* represents a narrower-leaved vatituit corresponding to *rubrincrvis.*

Obsem tit ins of the I Jen other as in English gardens

show that thfire arc **various** mees of *Lantattikiana* which seed themselves from year to year. Some of these have much-crinkled leaver find conm near the race of de Vries's experiments; others, such as the lale of Wight- **race,** are l crinkled, ami still others **which** are but little crinkled have few long hairs on their buds, are distinctly *gratuiijtom\**

Another riuie (4j of *htmarckiuHa,* derived from ft privAte nlea in St. Louia, Mo. (145), differs quantitatively from the race o[ de **Vries** in *many* features wheu grown r the same conditions (sec Fig. 22). In fcbis **rftce** the
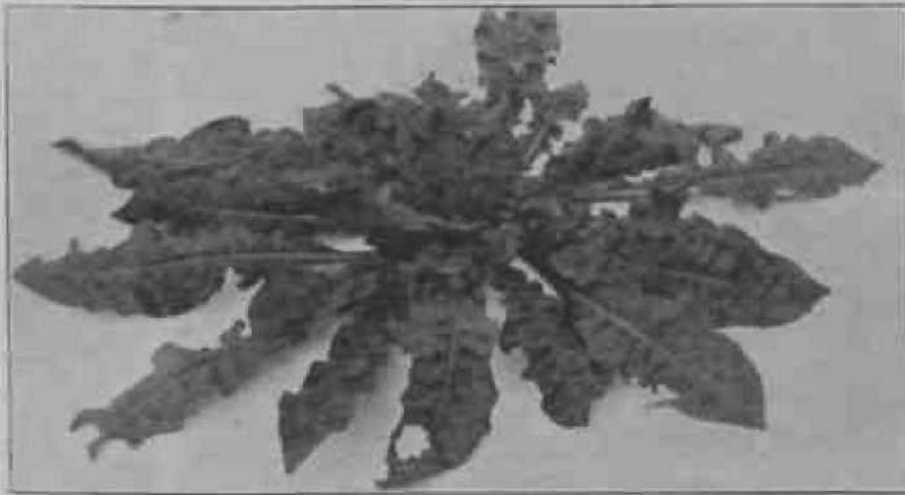


Fin. ifli—(><:, A-<»tiiiv£tituH *fawn Wm&en\** Narrower-leaved i,'U-mT[-n n-winJiliiii (A unit. IMIMIJMIU pr«pnt n photograph by Heribert-Nilsso

rewsettes are much larger with decidedly bToader, rathur more critikJed leaves. The stem-leavea vary from ovftte, tapering at both e-nds, ami potiolate, to acdaiie with broad and **anrate** base; and the buda have fewer long hairs. Thfl geutti-sil aspect of this race is hence quite different from any of the others. This rae« produced a dwarf and a narrow-leaved mutant in cultures.

Of these four races, all **except** the last stand between the *Qe. Lawarckiana,* Ser.$_f$ of de Vries'a cultures and *Qe. grawtijfora,* Sol Ami er, in variou» feature*. The Itw acc«ntuatea certain features of de Vries's race, such as

**a**

the ea nk ling ol t h B 1«I vw, i • i • cnnes neu ror *grandi-Jont* iEL h&Ytug li-- bitiry imil*-.

<sup>F</sup>11i' **Ocmot&eca*** *in* cultivation m botanical gardens include a niimhtrr uf **raoea** bt^on^ng to *Lamarckianft,* under such names **aaftt** *f'imnu ami* **Oft** ws *Itgrandijhra.* **T&e$e QIQ often** vary variable, and have obviously **oncb**-gone **croe&ng. Sometiinas** they **alee coltiviitcd** under garden names such **as O*f.** *^rijthroarpaht* **and OR** *hungarica,*



ffttl, fiS, - »*- *Lamarckiana,* race from a garden in St. Louis, Mo.

**and** they often show **mfttationa aimilai to** ULOM **of** the de **Vriae series.**

It is tints clciir that Oe. *iMinarckiana,* like other species, contains n nitnitwf of elomeutAry Hpecics *and* races differing **Erom** each t>th<?r in vitrying degreta. It **doa** not seem pr.,1,jtl.lt= that th<?^e raoe-a httve originntct] **itMlfperu** ently **through** hybrid syntticsiis. They may be **merely** forms produced by crossing at **different** titties and **under djffen** nt conditions, ui *om* original type eiidemii: *Ut* N< rth 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 ate 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 land of diversity which is usually found in an interbreeding population of forms belonging to one Linnsean 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 *Lamarciciana,* 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 *Mutationstheorie* 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 40-50[1] 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,

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

Put, 'SX  -Young seedlings of Oe. *Lamarckiana*.
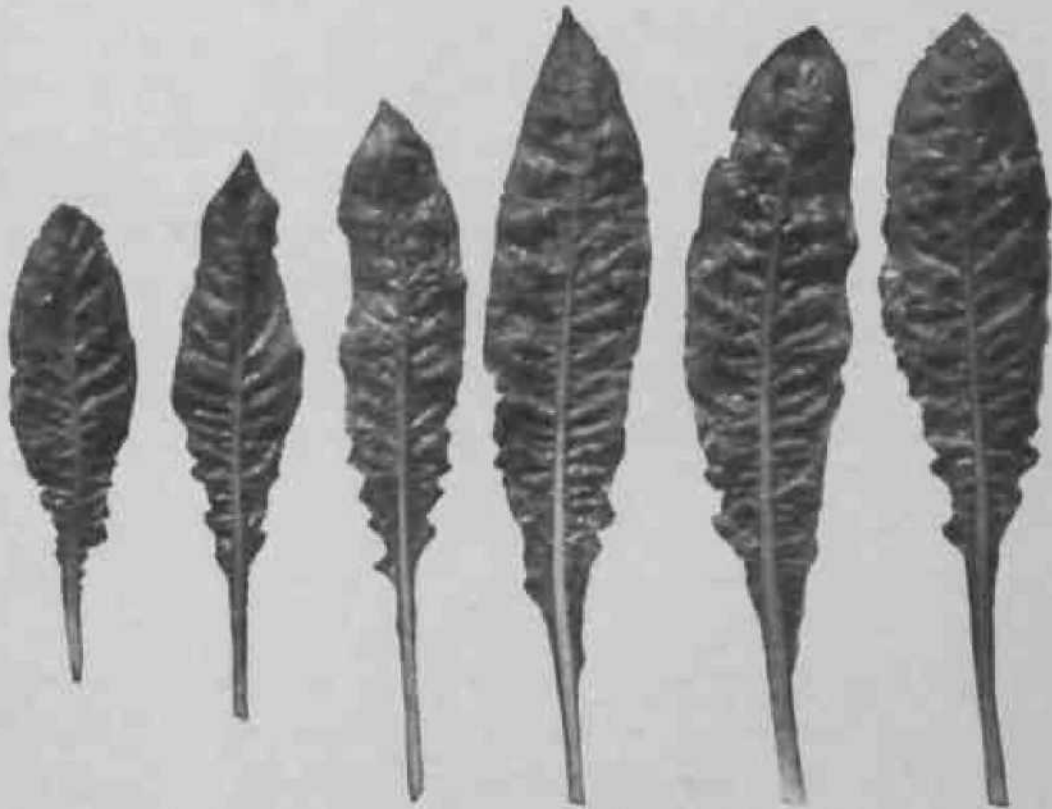


FIG. 1H. —Ot. *Ltttwrtkinna, nolvetixl* leaves *tr''t»* Hmtut*.* rutotUta, showing range fluctuation.

ovary 10-11 mm, long, fl"5 mm. in diameter, sepals yellowish-greea m- with fine redtlfch lines near their Imtder. Fruits 15 34 mnj, m length, There appear ʞ lie two types of hr.niriimg. Siine indmthldls form a ring ol ijtiisal sthoota wliith uiwi- some con ɑ Wrame akaO8i vertical. Tln'\ roUtivelv tote. Otheis do not



Fig. 25.—*Oe. Lamarckiana*, full-gro*iKU* plant.

form *n* m»g of basal brow baSi and flower somewhat earlier. The**c differences do not aeem U> fo« inherited,

Thft frequency uf the c ^octtrrcnce of mutants from *(k\* Lamarckiana* and tln-ir relative viulnlity are matters of much interest. De Vrie\* has given his rateruůve nssulte in T/^ *Mutation Tf>-ory,* VtiL l$_t$ pp. i>24 d \*^$_M$ so they need only be aumnuirisetL 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 |
|---|---|---|---|---|
| *Lamarckiana* .. .. | 53,000 | — | 10,000 | — |
| *oblonga* .. .. .. | 350 | 0·66 | 69 | 0·65 |
| *lata* .. .. .. .. | 229 | 0·43 | 168 | 1·58 |
| *nanella* .. .. .. | 158 | 0·3 | 111 | 1·05 |
| *albida* .. .. .. | 56 | 0·105 | 255 | ·240 |
| *rubrinervis* .. .. | 32 | 0·06 | 1 | 0·009 |
| *scintillans.* . .. .. | 8 | 0·015 | 1 | 0·009 |
| *gigas* .. .. .. | 1 | 0·0019 | 0 | |
| *elliptica* .. . .. | 0 | | 7 | 0·066 |
| *leptocarpa.* . .. .. | 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 sojj—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. |
|---|---|---|
| *Oe. albida* .. .. .. | 64 | 95 |
| *Oe. oblonga* .. .. .. | 9 | 30 |
| *Oe. rubrinervis* .. .. .. | 1 | 0 |
| *Oe. nanella* .. .. .. | 0 | 55 |
| *Oe. lata.* . . .. . . .. | 61 | 54 |
| | 135 | 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 Ilaage and Schmidt of Erfurt, and found that they contained 1 *rubrinervis,* 1 *oblonga,* and 3 *nanella$_y$* a total of 0*25 per cent. MacDougal (253) grew 3,500 seedlings from seeds of de Vilmorin. They contained 14 *nanella,* 3 *scinlillans,* 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 *!ata,* 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$_y$* 3 *subovata,* and in addition seven new mutants,

making about 8 per cent, of mutations in all, This included 5 *ffhjus* **individuals,** or 0**25 per cent., a **greatly** increased frequency for r/i//o*.  The considerable increase* in the number of **mutations** is attributed to the higher percentage of **germination,** and **particularly to** the first that the mutated **seeds** probably survived the high
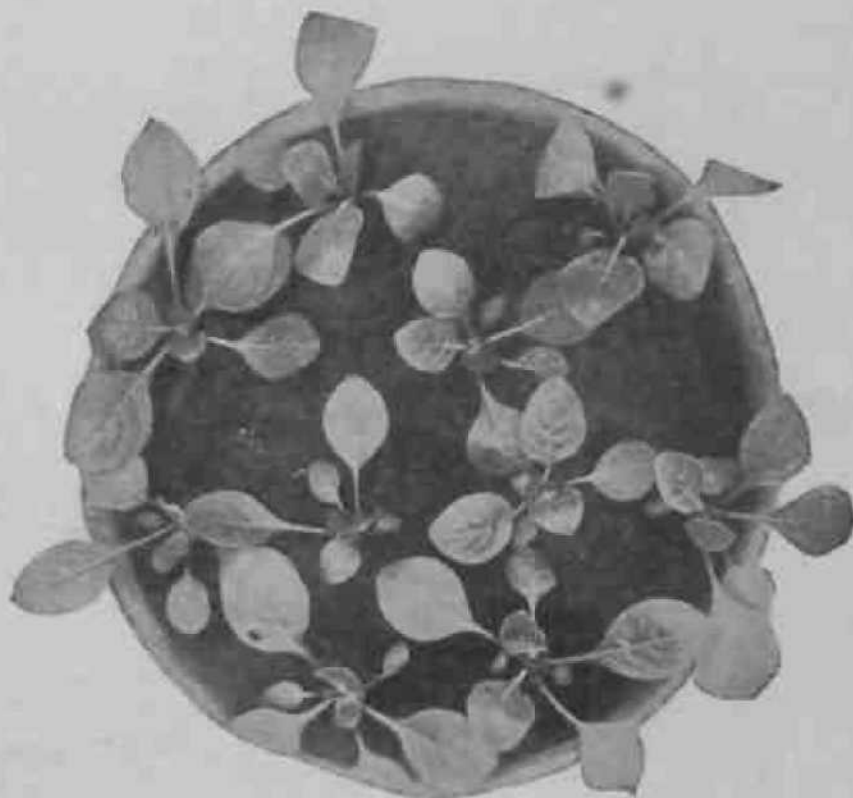


**Flu, 88*—(h,** brevistylis, young * sedlings.

**temperatures** experienced in transport to Java **better** than the normal setds.

*Oe, bremstylis,* de Vries.  |Figs. 2C$_t$ 37, 28, 29).

Rosette-leaves similar to thosg of *Lamarckwna,* **but** rather **broader** and with very obtuse, **rounded** tips.  The **bracts** are also broader and more rounded than in *La\* niarckinm,* and the sepal tips very short;  the style only reaches to the top of the coiolhi tiibe$_t$ and **the** stigma is miftshiipen.  The ovaries arc almost wholly sterile.  This may be because pollen fails to germinftte on ibe **stigma,** but the Ovary may also be **abnormal)** For peculiarly
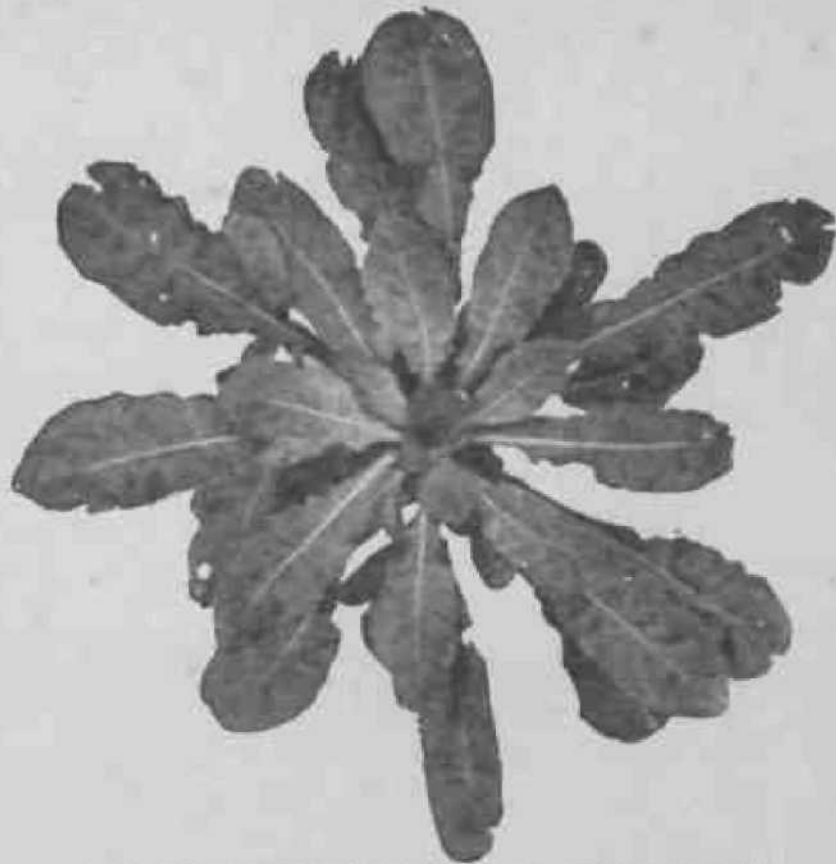
Km.i 7 -<. *brevistylis*, rosette (*cf.* Fig. 2, p. 15).
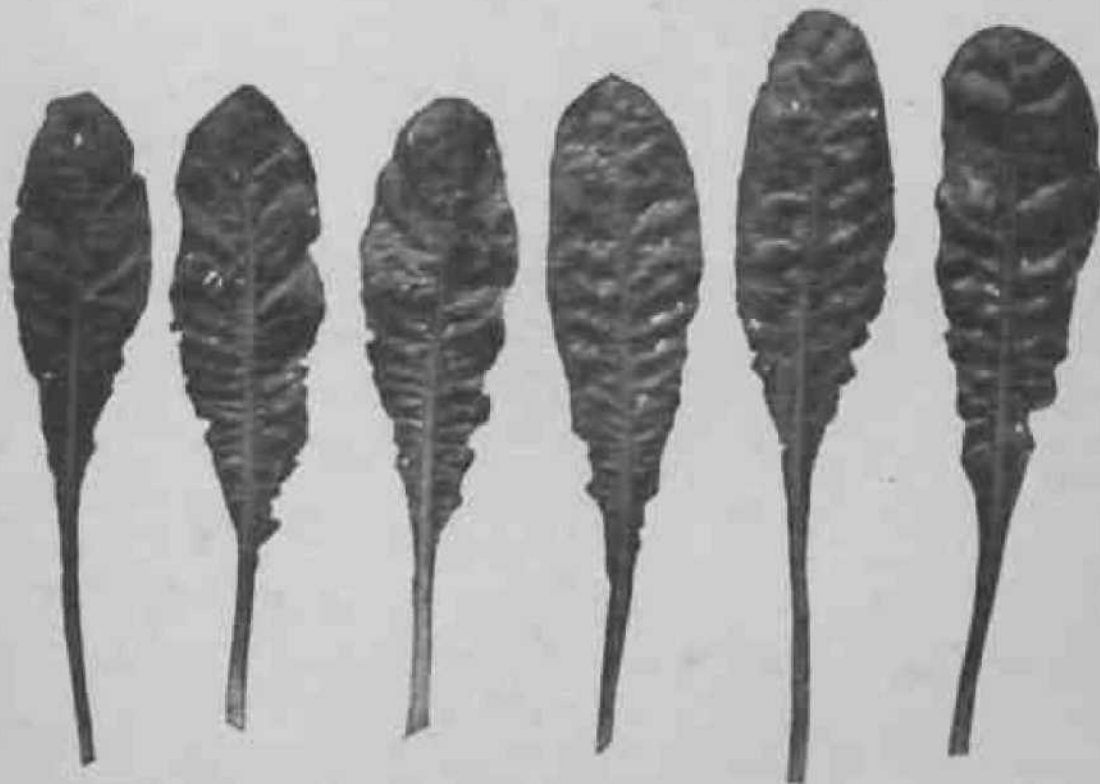


**Flu. SS.—Or,** *hrtriiAytui* **\*\*lected re it\* »e l««ire« dhowjpg nmge of Ilnutimtieifi <</. Fig. iM. p. 8fl).**

developed and of rcourise **fanetianless** stormira **frequently**
occur on the inner face of the ovaty wall, where they
seldom or never occur in the other forms examine].

This type was origiimlly found growing wild with
*Lamarckiana* at Hilversmn by de Wies, but lias since Wen
**obtained** by Scbouten in **commercial** seeds, so it lias
**very** probably originated as a mutant. It producer
plenty of pollen, though very few .seeds can **be** obtained
fri>m it, but **de** Vriea succeedetl in uelling five **plants**
These in 18JI8 yielded 175 plants all *brcvialytis.* **showing**
that it breads true. *Brevktylis* is usually propagated
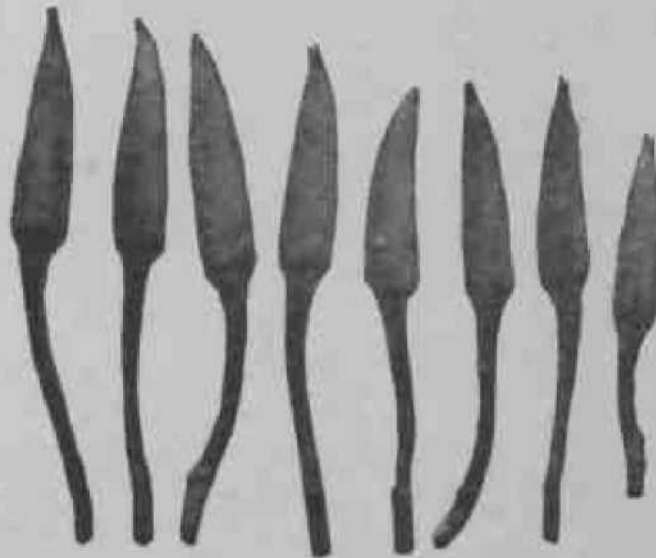


Fic, 29. — Oe. breviatytis, buds showing short
sepal tips.

by OTOlsng iu polkn with *taman kiana.* In this way
it is **shown to** lie probably **8 ample MendeKan** recessive,
though t. lie *re vx\* \*\*»M*-times **tetble** **departures from**
the expected **ratios.** *lAtmawkiana* and *brevtstyU\** ;-lmuld
thus give 25 pet **cent,** *brevitrtytia* **in i\** and **the heterosygoua**
*Lawtrckiamts* of the B\ otos>ac<i back with *brevisto/ti\**
should give 50 per cent, of each type. A paukct of seeds
from de Vries, whirl) hatl beun crossed back in this way
for several generations, gdve, in 1009, 56 *fjimarckiana*
and 32 **bremstyliA,** Ijesidea 3 *laia* and I *rubrinerm* (?). Two
f the *Lamarckiattas* were selfed and |iroduccd *Latnarchiuna*

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 *Lavnarchiana* x *brevistylis* x *brevistylis* obtained 39 *Lainarckiana* and 30 *brevistylis,* or 43*5 per cent. *brevistylis.* Of the 39 *Lamarclciana* plants, one differed from the rest in having cordate petals of cartilaginous texture, thus resembling a certain form of *Icevifolia.* Its style was also shorter, and the stigma finger-shaped. This plant was selfed and gave in 1907 the following offspring :—

| | | | | |
|---|---|---|---|---|
| *brevistylis.* | . . . . . . . . . | .20 | plants. | 31-75 *J.* |
| *Lamarckiana.* | . . . . . . . . | .37 | „ | 58-73 „ |
| *Icevifolia.* | . . . . . . . . . | .3 | „ | 4-76 ^| |
| *Icpvifolia-brevislylis.* | . . . . . . | .2 | „ | 3-18 > 9-5% |
| *lawifolia nanella* (dwarf *Icevifolia*) | .. | 1 | „ | 1-59 J |
| | | — | | |
| | | **G3** | | |

The *Iwvifolia-brevistylis* plant Schouten (333) considers to be a mutant combination, produced by the union of germ cells one of which has mutated into *Icevifolia* 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 *Icevifolia* 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 in-florescence, *(d)* in form and texture of the petals. It agreed more nearly with *brevistylis* in (a) the bracts, (6) 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* x *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 *Iceyifolia* pollen, for the percentage of mutants is ordinarily not above 5 per cent.

Of the *brevistylis* plants referred to above in *Oe. Lamarckiana* x *brevistylis,* two showed chloranthy, 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:—

| | | |
|---|---|---|
| *brevistylis* .. .. .. .. .. | 123 plants. | 50 % |
| *Lamarckiana* .. .. .. .. | 47 „ | 19·11 „ |
| *rubrinervis* .. .. .. .. .. | 74 „ | 30·08 „ |
| *Icevifolia* .. .. .. .. .. | 1 ·, | 0·41 |
| *rubrinerv is -brev istyl is* .. .. | 1 » | 0·41 „ |
| | 240 | |

***Laniarckiana, rubrinervis* and *Itevifolia* 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.*

*bred&lylis.* Hence it was essentially a short-styled *rubri-*
Bemts. Schouten considers the plant a combination-mutant
and not a hybrid, %.<?., that it came from a germ cell of
*brcvistylis* which had mutated into *rubrhitr&i&i* crossed
with onft which had **remained normal\*** But it is not
clear that a combination-mutant derived from germ
eel I a which had mutated respectively into *rubrinervis*
and *brevistylh'* would be a different product from an
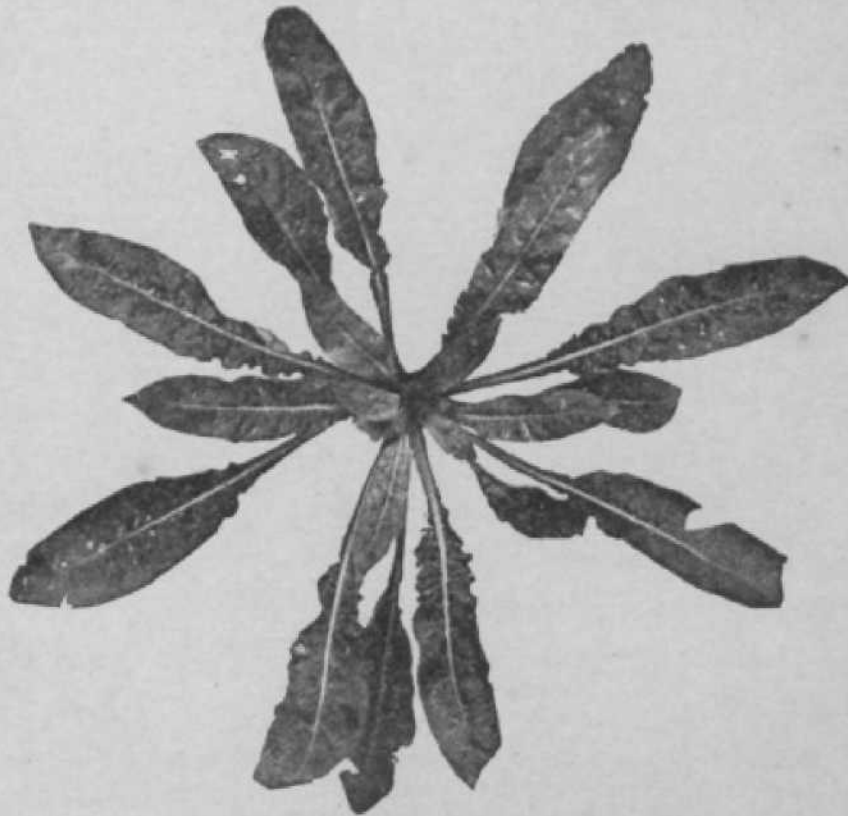


Fm. *SHI,—Oe, Xavifoiia,,* roeette.

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, w<
think, clear and will be referred to ugain later,

*Oe. lemfolia* de Vries (Figa. 30, 31).

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

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

Fin. SI.—Oe, *Uxvifdia*, mature plant.
*(rf.* **Fig. 86,** |». **87.**

The exact status and **origin of** this form remain some-what obscure. It was also discovered by do Vries ai Hilversum, but neveT appeared as a mutant in his **cultoree,** though it has since occurred in the **experiment** of Schouten, md forms more or lees resembling it have also appeared

H

in our own cultures. We have found tin's typo to he 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 *Icevifolia* should
be so relegated. From his description it would seem
that the mean type of his *Icevifolia* differed somewhat
from that of de Vries.

Schouten (333) states that he obtained *Icevifolia* as a
**mutant (1) from *gigas,* (2) from *LamárcMana* x *Lamarcic-
iana brevistylis.*** It is probable, however, that the first
was one of the narrow-leaved forms of *gigas.* In 1906
he grew 260 plants of *Icevifolia,* which were all like the
parent except three. Of these, two were *Icevifolia nanella,
i.e.,* dwarfs having the same symptoms of sickness as
*nanella,* but like *Icevifolia* in the form and colour of their
leaves and petals. The third was *Icevifolia-salicifolia.*
It had smaller leaves than *Icevifolia.* 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 *Icevifolia* pollen. The offspring
proved to be

| | |
|---|---|
| *Icevifolia.* . . . . | 22 |
| *scintillans.* . . . . | 6 |
| *loevijolia-salicifolia* .. | 1 |
| **unknown.** . . . . | 1 |
| | —— |
| | **30** |

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

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

Foliage greyish-green in colour, leaves somewhat nar-
rower 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.

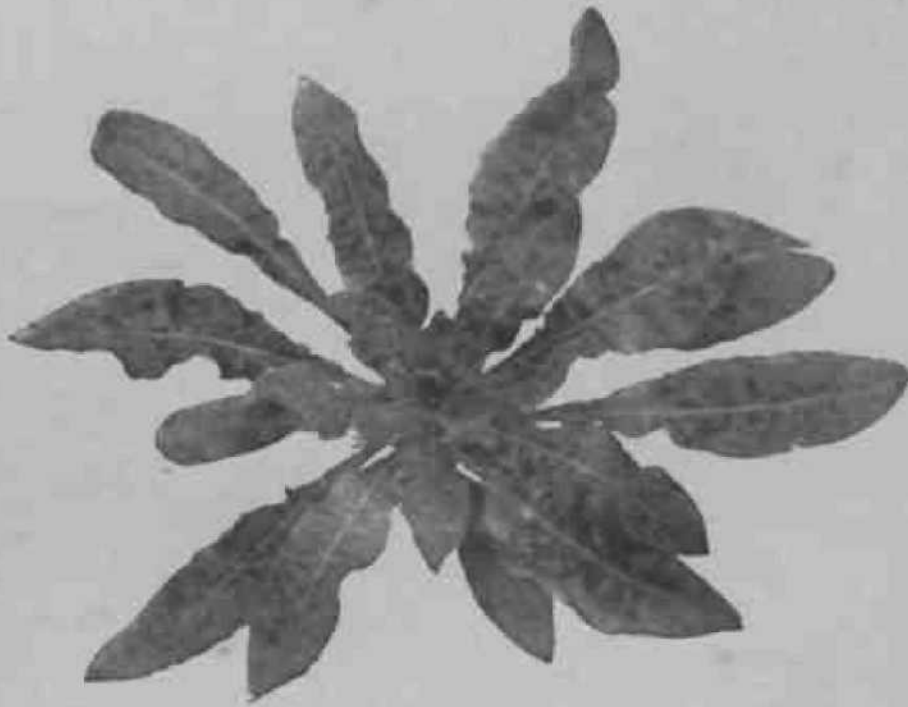Fig. 32.—*ik,* unit. rubricalyx, seedlings.
(*f*. Pig*. Mi and 26.)



Fig. 31.—*Or, mut. rubricalyx* fiflf, 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 *rubrinervis.* | Percent |
|---|---|---|---|---|
| *Lamarckiana* family | /1890,1895, 1896,1897 | 33,800 | 32 | 0094 |
| Branch of same .. | 1895-6 | 10,000 | 9 | 009 |
| *Oe. laevifolia* .. .. | 1889 & 1894 | — | (4) | — |
| *Oe. lata* . . . . . | 1900 | 2,000 | 3 | 015 |
| *Oe. oblonga* .. | 1897 | 45 | 1 | — |
| *Lamarckiana* x *nanella* | 1897 | 1,051 | 2 | 0-19 |
| *lata* x *nanella* .. .. | 1895, 1900 | 222 | 2 | 0-90 |
| *Lamarckiana* from the field .. .. | 1889 | — | (1) | — |
| Total .. .. | .. .. .. | 47,118 | 49 | 0·104 |
| *Lamarckiana,* biennial culture.. .. | 1897 | 164 | 2 | 1-22 |
| *Oe. lata* mutant .. | 1896 | 326 | 4 | 1-23 |
| *Lata* x *Lamarckiana* | 1898, 1900 | 750 | 2 | 0-27 |
| *lata* x *brevistylis* .. | 1896 | 266 | 1 | 0-38 |
| *nanella* x *brevistylis* . | 1895 | 270 | Γ | 0-37 |
| *scintillans* x *nanella* | 1898 | 95 | | 1·05 |
| *Lamarckiana* (*from Lamarckiana* x *scintillans*) .. .. | 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, |
|---|---|---|
| *rubrinervis* .. .. | 1,097 | 95-89 |
| *rubrinervis* with " *gigas-huitx* " .. | 6 | 0-52 |
| *Oe. blanda* .. .. | 36 | 3·14 |
| *loevifelia* .. .. .. | 4 | 0-35 |
| *rubrinervis-lota*.. .. | 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. |
|---|---|---|
| *Lamarckiana.* . . . . . | 0 | 1 |
| *rubrinervis* . . . . . . | 310 | 40 |
| *Isamarckiana lata* .. .. | | |
| *rubrinervis lata.* . . . . . | 3§H'2% | $1 -.14.00/ |
| *candelabriformis* .. .. | 1 | 0 |
| *rubrinervisscintillans* ? .. | 1 | 1 |
| **unknown.** . . . . . . . | 4 | 0 |
| | 348 | 49 |

*Oe. candelabriformis,* 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.

I)e Vries (425) has recently recognised under the name *mbrobusta* a form of *rubrinervis* which differs in being less brittle, ft produces about 20 per cent, of the brittle *rubrinervis* in its offspring, fn crosses with other mutants *rubrinervis* produces an K, containing from 27 per cent, to 80 per cent; *subrobusta.*

*Oe.* mut. *rubricalyx,* (iates (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. Tt 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 those Oeno-thcraj* have been in cultivation.

*Oc.* **tnnt*** *rthficatyx* originated in a pun.' culture of *Oi •* mut. *rubrwwrvis* at the University of Chicago in 1907. Four **rubrmervia** individual o£ the previous generation wlied gave 112 odfopri&g, all of which **wedm** like the parent except the *rubrieah/nr* mufcunt and two sin*im*what doubtful rosettes.   The origin of thin nuitant i* thei^fot^ accurately
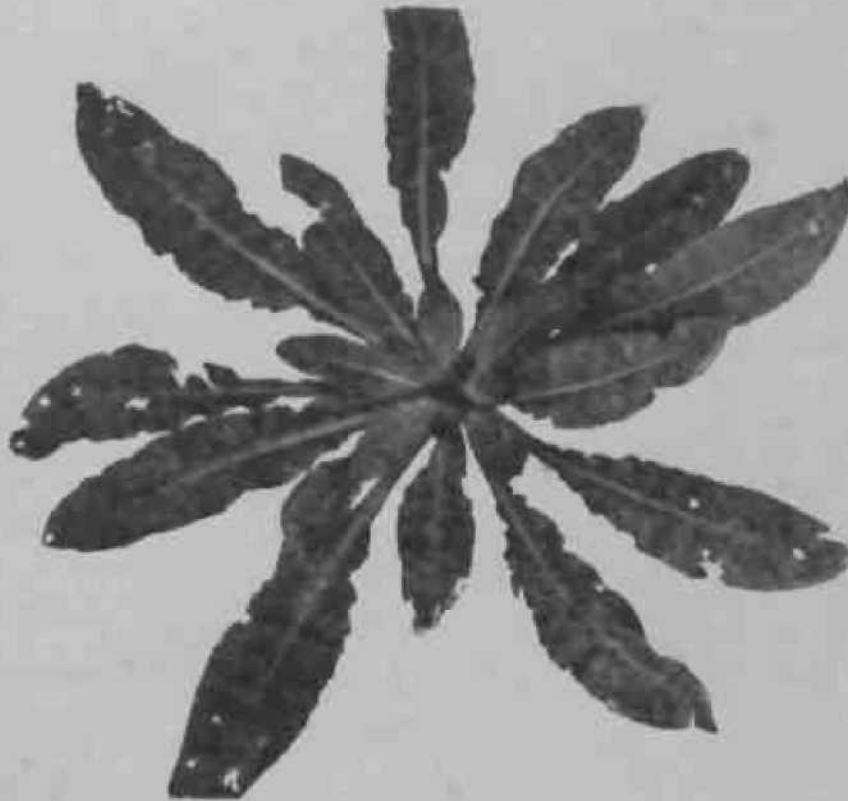


FIG. 34.   /^. **mitt**. *rubricalyx, rosette.*

loiotvn.   Fortunately the writer happened to be making a sptKrijk] study of **the variability** in **pigmentation of** *the* **bud*** **in** the very culture of *rubrinmrit* in **which the** *rwvum* appeared. The range of **variation** in the **ruifftwrpis popula-tion** numbering in all more tlum 1,0()0 pUintswas found to be **absolutely continuous,** while a marked gap separated the **oxtreme** »f pigmentation in *rubrmenHS* from **that ol** tho *rubrimhjf* **individual.**   The **offEspring of** the *tubricalyx* plant, moreover, **showed** no **tendency t«** regrese towards

*rubrinervis.*    **Instead** they split into **two sharply** distinct **daases** belonging **rMpectnrelr to m . . ,** *tmd rubrinervis.* The **number** \*if -oirvivors i i th«- first u\*neration of offspring **wag** *UH>* small **to** tk—ermini\* **n mtio(ll** *rubricalyv,*[1]1 *rubri-nvnm,* hut **thTceaf tb&te** *ntbrimtyn* **plaattsseHwl ptve** iu the

V i . 35. — "•. **mat.** *rubricalyx,* hiU gri<wii **plant,**

second **gonemtiofi tin** ratios respectivoty of **10:5, U:6** and **33 : II.   These four mtu\* mok\* A t->tnJ of tl8** *rubricalyx*

*to* 23 *rubriturri.\*.* whidi is n very close e approariniatiofl t o a 3; 1 ratio,[1]

It is thus dear that the original *rubricalyx* mutant *mi* hcteroayguu.-s having originated through the union of a iiormtil germ cell with it mutated gprai cell posaesaing the new dominant character, The tliflereBce beti.....D *tvbti-(vihfr* and *tttbrinervi\** w I bits =» simple onohybrid difference according to Micwdeli&H methods of utterpretation. It is not neMssary «u suppone tlmi *nthricahp* luii acquired
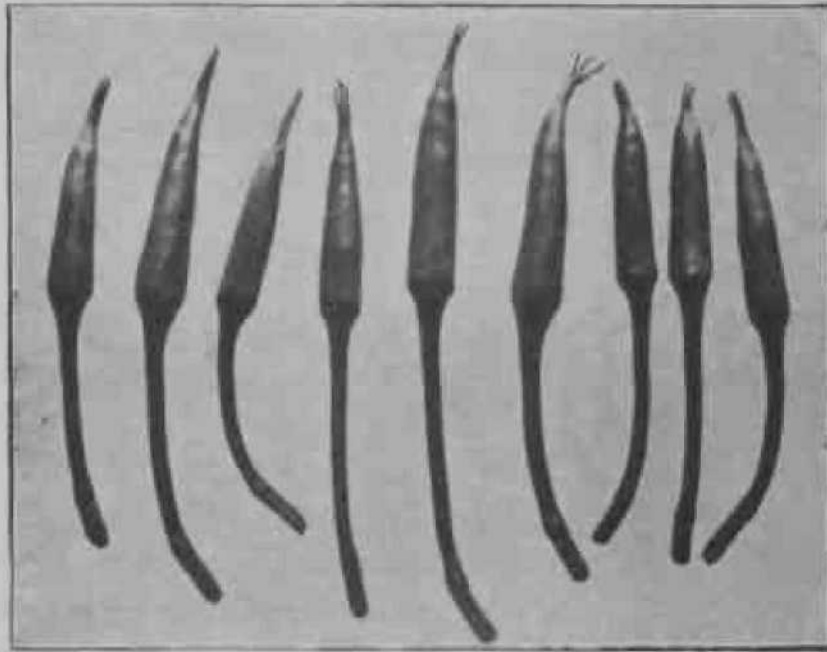


FIG. 36.—Oe. mut. rubricalyx, buds.

an.additional unit Wtni^ut^r, exoepi a» u mattea *oi* corn eni- once in dt^oTibing tl« i os•wug expenm«nto. fn reality, oil it is possible to i\ - i ri .3 *i,* |(.n i < nJ.ir L'^'ini roll inulri- weut a germimil thjuipe (»f such n nature th&1 in develop- riK-nt the resulting orgaDism produced mi enormousfy in- creased quantity *at* anthoey&niDu

Th&t *rubrimhjj* originated from tsuch ;i getruinal rhiutgc (\*n one rel]v and nut from gradual accumulation, through

---

[1] li i- in\*essary to i|it|\*httrtiw Utc fin t iluit l»v tin [H^tiliiliiv rim «ny >*i* thnw ratios (exnopi pwttafW II: I whiHt In too wiuitt |« 1« considered JJ> il-M'lff !« BQQitinWK] a^ (5i l.

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* x *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* x *rubricalyx,* in an F, 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 arc indistinguishable from homozygotes except in the deeper red of the latter, and even this

**can only** b& determined by doae **inspection** in i-ertain r.ases.
The **200** pl.iins grown in **this** family in **1912** were remark-
ably uniform in every*feature, with **the** ea ception of two
plants, **one** of whitrti was **somewhat aberrant in fo]**iage
**and die otbec waa** small having **furrow-shaped leaves**
willi **white** midribs.    **The Heeda feom this pure racen**ere
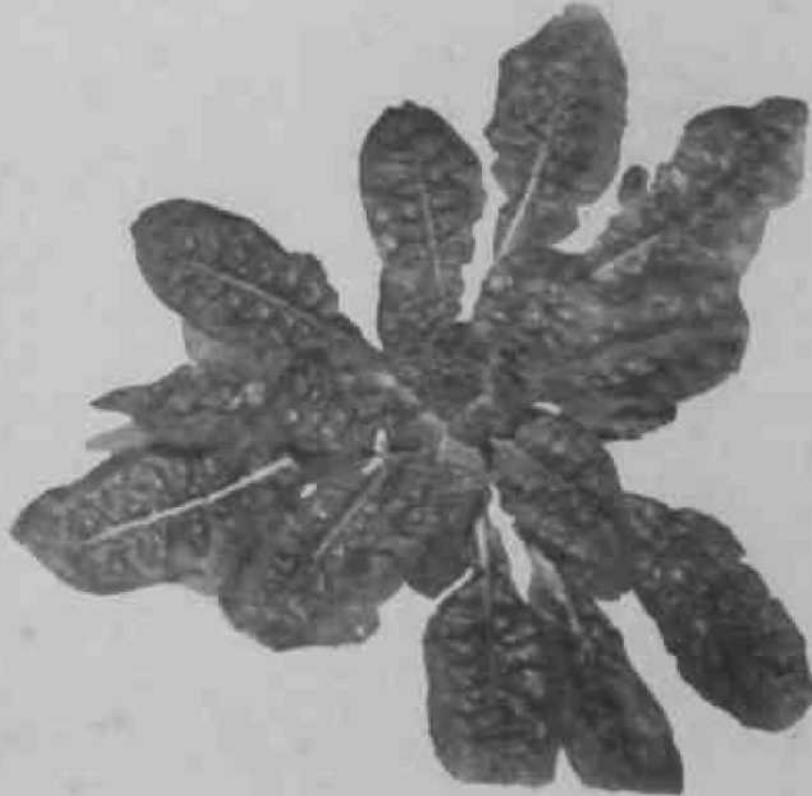
Fia. 37. — .. mut. *lata,* rosette (*cf.* Fig. 2, v- •5).

**acquired by Messrs, Button Hud** 8ona_t who are selling
it umU'r the name " Afterglow."

*OL\* nmt. *ltit<a,* **de Vidflft.** (Kig*. :*7, Hrt.)

**Rosette leaves** ^Imrtor ami **more crinkiod th\*n** iu *Oe.*
*Lamarckiana,* **the |nts being uMfca** ftod top; **tihe** up s of
**tlK- I.** osette [eaves **are** .lnu.t<i< ristic <l!y **very broad and**
**wranded, ili<- Imwa** >twti leaves l«^{1}ir^ **atoo bluat-peanted,**
the upper ones **obtttW.** Tln^- 1in»;i-l. obt«a« «r rou.ru led
points aro much more **exaggeratod Uwffl in &n** vistylis,

SI ml the foiitige ia **also** lighter greeu. The steim of *lata* are short and usually more or less decumbent, with irregular **branches** the t*>p**of** a sten>often hanging over to one -side. The buds me ptx-ulkirly stunt and I mrrel-shaped, usually **with** u prr.it nision tir herniu on *one* wide due to the • 'hplicig **of** iht- **petalu** within. The wpitk rai^ly **if** ever -how any **coloration.** The **stigma** iw **peculiailj** tll-^litipi-n **and kand-flhajwd, often** with a tendency to **confluence of** the **tabes, but pollen germinatafl on it readily.**
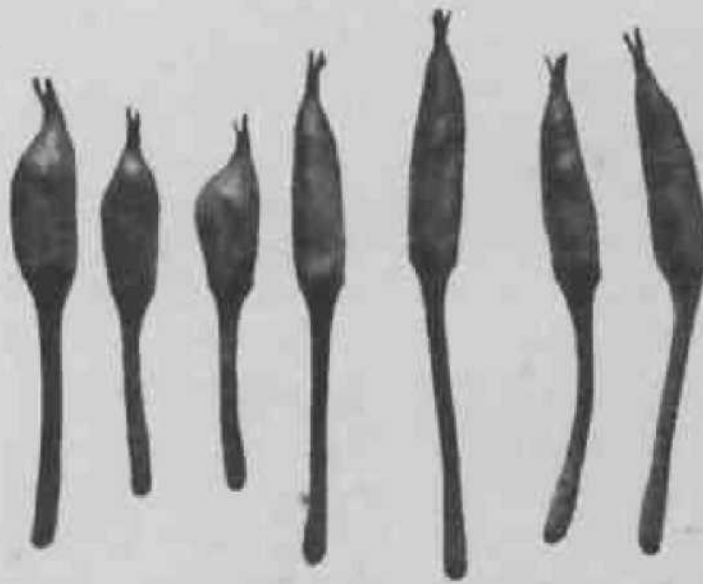
FIG. ;»*.– Tliruir hiuin CW *thv* left, "r. *htn,* ik- Vrii»:
four buds Mi (hu ri^lit. *lit. *rmiltitn,* I i ates.

Tin: t'Upsules are short uticl thick, containing relatively few seeds, and the pollen *la* wholly or almoat: wholly sterile. ТПОНС rcrnarkablp **peculiarities** are associated with the presence of 13 instead of 14 chromosome** (see **Chapter** VI).

*Qi\* **rant** ?a/* hns occiirretl a number of times in my cultures, and when derived from the *LavtarGktam* of de Vries'a culture* **it** appeara to beren^rkablyconirtfliit in ap|warain:e. Table VI Hiimmnriscs its occurrence in the **experiments** of *t\o* Vrira. It wua *ftm ft dmt* mtttnnt to *h ha* rccogmsed- iu 1887.

**TABLK VI.**

**Mutations of *lata* from *Lamarckiana*.**

|  | Year. | Total. | lata. | % lata. |
|---|---|---|---|---|
| **I.—From *Oe. Lamarckiana.*** | | | | |
| *Lamarck,* family .. .. | 1888-90 | 25,000 | 8 | 003 |
| »» »> . . . . . . | 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 | 50 |
| ***11.*—From crosses.** | | | | |
| *Lamarck,* x *nanella* .. .. | 1897-99 | 8,283 | 22 | 0-3 |
| *Lamarck,* x *gigas* .. .. | 1899 | 100 | 2 | 20 |
| *Lamarck,* x *biennis* .. .. | 1900 | 80 | 1 | 1-0 |
| *Lamarck,* (from crosses) .. | 1896 | 4,600 | 7 | 0-2 |
| **III.—From other families.** | | | | |
| *Lamarck,* from *Icevifolia* .. | 1889 | 400 | 3 | 0-8 |
| *lasvifolia* . . . . . . . . | 1894 | 1,500 | 2 | 0·1 |
| *rubrinervis.* . . . . . . . | 1894 | 96 | 2 | 20 |
| *sdntillan8.* . . . . . . . | 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. | lata. |
|---|---|---|
| From *Oe. Lamarckiana.* . . . . . | 117 | 2 |
| „ *Oe. Lamarckiana* x *brevistylis* | 92 | 3 |
| „ *Oe. rubrinervis* . . . . . . | 96 | 1 |
| „ *Oe. rubrinervis* x *nanella* .. | 42 | 1 |
| „ *Oe. rvbrinervis* x *Lamarckiana* (from *lata* x *Lamarckiana)* | 64 | 1 |
| | 411 | 8 = 1.95?» |

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 *semihta* 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 01 per cent, to 1'8 per cuent., 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., 17 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 off-spring 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 *ktUi* offspring in *latu* x *Ijamarclciana* 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* x *biennis* yielded 53 per cent, *lata* in 258 plants, while *lata* x *biennis cmciata* 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-hke* 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 *semilatu* was different from mine, and since it bred true it probably**

This **mutant** stands **midway** between *tola *mJ* **l&mm** *timu** hs **leaves** urn **moro** pointed aiid rather Je^i rnnfctad than those of *luUi,* the stem is erect and taller than fa/n, though shorter than *ljamarckiavw.* The **buda** ara Ices stout and more, aquarian than *luUt_t* and it produces a **considerftble** quantity of polten.

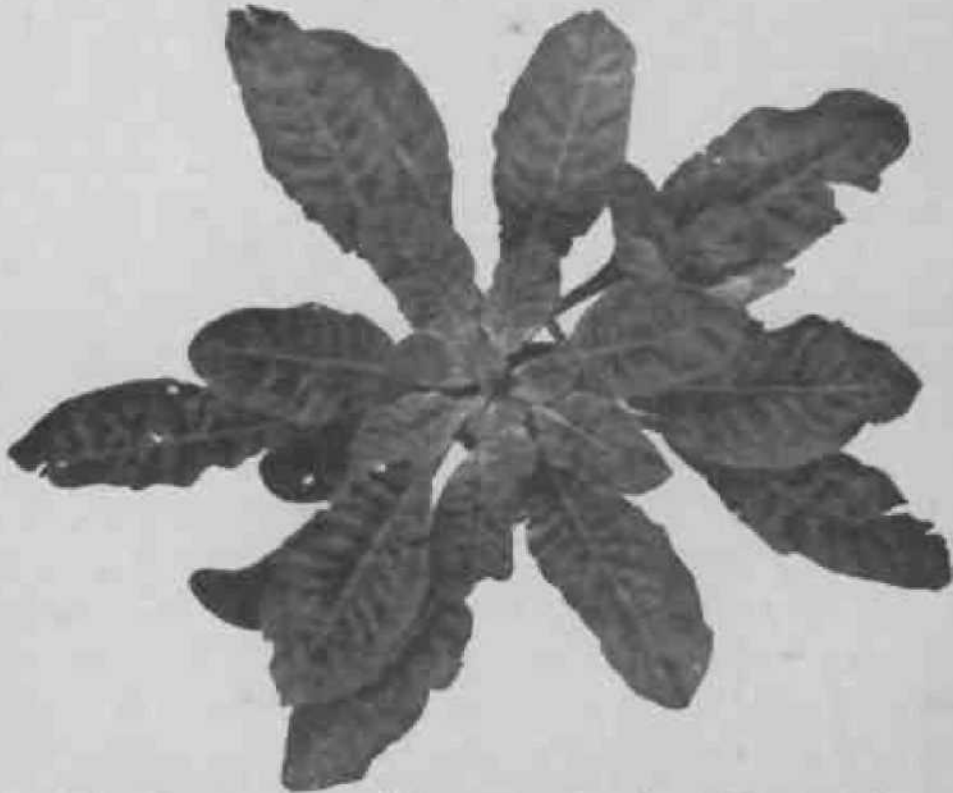**In cultures of da Vrlw'a** rare **of** *lAimarel-iaua.* **temilata**



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

ha& only appcwml in families of *Utht* pollinated by *La* mn-eckmna.* Like *fata* it hns 15 chromosomes, but the nature of the **minor dxCNtastuwu between** *lata* **and** *semilata* i^ at present **obectftfe** Tlii^ will be discussed in the next luwl 10 cliroui'»*jinn. iL JUB> th^rcftm[1] have resembled more osely the form Ju*rt* **dcfCtQwd la** "•- *hn**i*ns* (p, JIT*, However* the *netnilaia ttl tU-* Vrn s was D>i-i^i from liU cultures hm «K», mid has since bec •Yj |«»H»4 -.ii *wt* I m w iw.Tfirtjdrrrd it desirable name *semilata* in I ho ftpnM? in which I tiuvo used it, ^h|K'^inMy »« tliln ruunp exactly CXIJTVM*'* *the* n?1utifntilii|) of rhin form to *toia.* It will, **tbartforo*** understood \.\\ii\ tlit' *semiluta* of dif Witt's A/*tiUHUtunthntr.r.* \n UUifchtW miutant wlik-li probably luiit 1T chromosomes.

chapter. Tho mule **sterility** of **fcito, s*ini** \\w small **numbfti** of needs it, products, **wftttf** at. first **supposed** to **be due** fcot **h** **pMnace** of tin* fKld HtroimwoiHt'; **but** in *$em&ota.* **where,** **OOJ** • to !•>.;•-•'-mtiim. an **extra cliromo«omo** WHS alsi. **aid, the** storility **h&a been largely,** tlkmgli **no<** wholly overcon .

**I**De Vries lias only **obtained** *mmktia* **three** (amen.. and **way>** from **&^tt** x *Lamw&ian* a. **When derived** from **»Jthet wrtirtf^. ##/f** mid *wmitcUa* form **a variable Kou** 
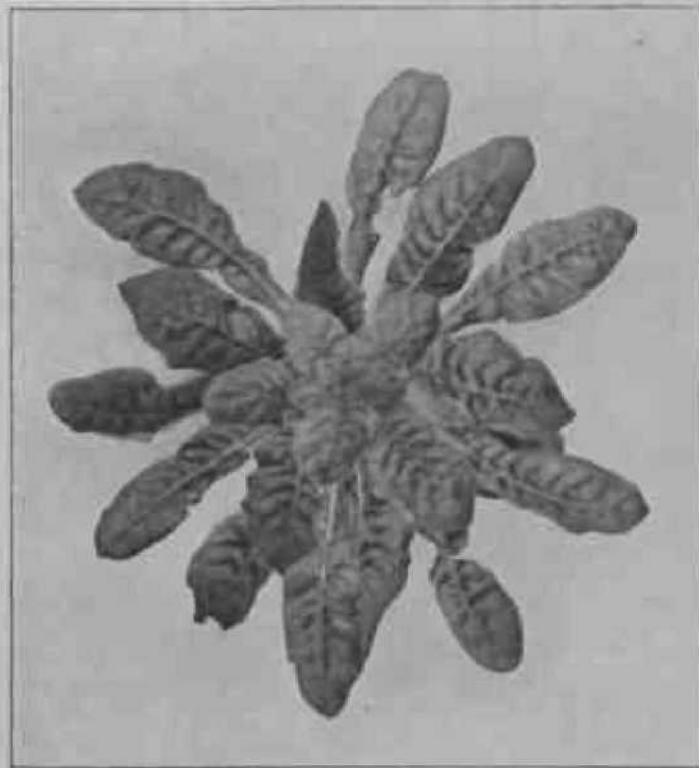


Fig. 4u. —*Oe.* n ut. sem .fr</.i frotn ^wedish race.

**grading into each fithor po that ii us iinpoatdbtc bo draw B sharp liin* bctwecti tlicni.**

" ^*iwilftfil* " ijt el assec. by *\*U' ^'|•i^^'^* iis ;| constant species **on thfl biuiB "I**[1] **ilu- MI(»vvii^ Kjpmitne»nt. hi ia»7** tin **Me]f-fQitUJ!«hl Mif0tln MI -I** *mmltiitt* plant **ytnidni STK** imli- vidujtU **o!** wl»ir|» :t we# *tmvrtht.* :\ *iota,* aut! **II«*** nnnamijer W 

**In a culture of 75** plant- iimii *lata* x *Lamaroktatta* were

ained «3 *himarckiatm¡l hla, *lfata nane&a* (^),2 ssmtfeto, 1 *lavifulia.* and 3 aberrant roeettea, L* of wMofa were prul> ;il»]y *frmildttt.* One of these four *scmitotas selicd* produced 10 vorv variable rosettes, about U *oi* wliioh were jretnt/afa, the remaintter foraiing n continuous ncri&s nmning to



Fig. 41.—Oe. mut. semilata grandiflora, three branches from a ma ... nt.

*Lmutrvhmta.* Three which afterwurds bloomed wcie *semilata.* One t^f these soif-pollrnAted guve three offispriiig, two of which wiTf /^/<* ftMUid by Miss S. Thoinas to have ir» chroirio^juii-s and iho third a slightly modified *Lamarckmua* having 14 olirotDOSODies. The modilicfltioTus consisted *i.iu\y* in having nearly timotith Ifittves, dome ol

obtained **03** *Lttfl>arckittmA fatu,llata nandUi \*)s2* semilata,
1 *lawfulia, m\d* 3 abermnt rosettes. 2 of **which** were prub-
ILJIV *srmtUttn.* OHO uf ilie^ four *svmilatas* setfed d t
10 **vety** v;id;ible rosettes about 1J of which were semilata,
the remaiTider forming a **continuous** series nmnmg to



branches from *n* mnhip* plant.

*Lamatckiana.* Three which **afterwards** bloomed were
*semilQta.* *Quu* of theiic self-pollinated gave three ofispriug,
two of which wore *hta* found by Miss N. Thomas to have
15 chromosome mid the third a slightly imidified *IM-*
*niarckuma* lutvij^ U **dhmmosomfitt.** The uiodiGtiatiot^
consisted **only** *m* **bftviug** uuariy »in*joth leaver w>nw ut

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 *Latnarckiana.* 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 Zato-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 *LamarcJciana* 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 x *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 *nibrinervis-like* parent, for ordinary *lata* never shows red pigment in any part. Another culture, containing 79 plants from open-pollinated seeds of a *lata-]ike* 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 Zata-like plant** having slender, weak steins, 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 wo found (153) 15 in every case. •

In addition to these cases, t.wo 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 *semilala* mutations **which occurred in the $F_2$ of *Or,, grandị flora* x *rubricalyx,*** and its reciprocal. These mutations, among others, occurred in a total offspring of 2,794 plants from these crosses, in 11)12. One F.j family from *gramliflora* x *rubricalyx,* numbering 82 plants, contained a mutant *sanilata 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-Yike* foliage modified to show the peculiarities of *semilata* (Fig. 41). Another mutant of the same kind **appeared in an $V_2$ family of *rubricalyx* x *grandijlora*** numbering 80 plants.

In a third F.j 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 . (i-chromosome distribution in one pollen mother-coll, for two pollen grains having eight chromosomes each would result from such a lreterotypic 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 dates 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-Niksoc in Sweden, The culture contained 7ft plants, IUV\*\* <f wliirii bad fota like foliage and jr. ohiomosomoa TliN pliini v<iy prohiiltly hm) Hi chromoewes, though fchey lmvo not IOMI counted and the offspring have noi been grown.**
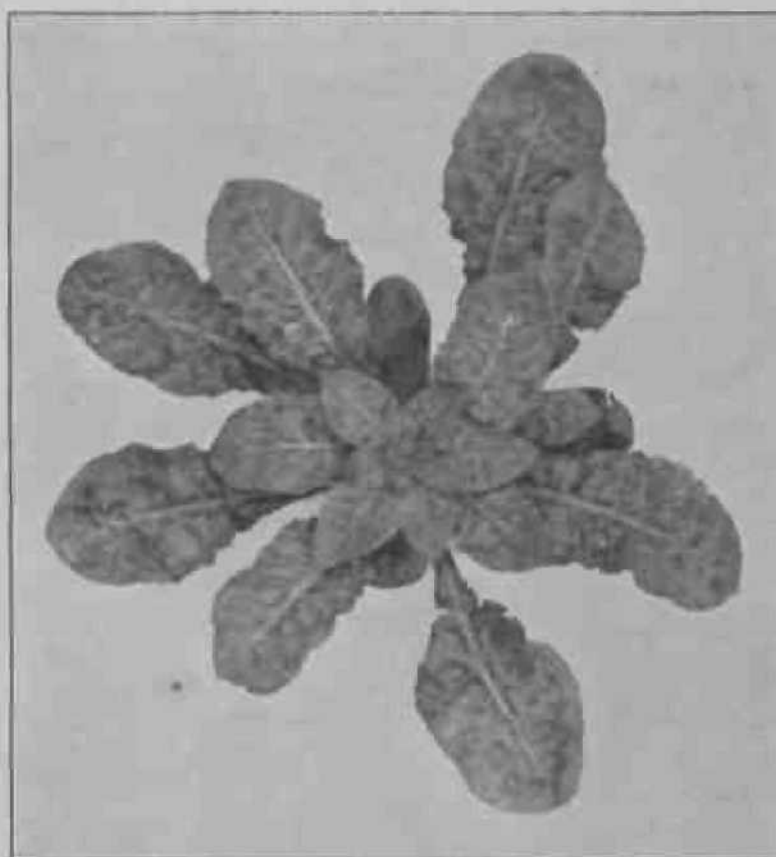


Fi. 2.— . mut. lntescens

*Oe. taut, yiifat;.* dc Vries. (Figfl. \*S 55.)

j:.r-:.-n«»-Itviws Imnklly lauooolatQ with obtoae or rouncled tiji to nearly orbicular. m<jt> crinkled (hon in *[jamnrckimw,* p<\*tiolt\s shorter. The stem-loavee also arc larger, broader, thicker, more obtuse, ami uior\*\* mnkl^tl thun in *Idtimrckiana.* An exact comparison of the pubescence has not been juadff, but the leaves appear more pu!>csccnt and the individual hairs are probably larger. Tho plants develop

ni>M *d&yAy* md *&rv* henee more strongly bienuial thm the other derivatives of *Lamarckimat$_t$* ajuj (lie BOWPHJ are more .susceptible to frost. The stem is much stoutor tliaii in *IjctmaTchittna* (aixonliiig to de Vriwt, often 10 mm. in <Hfimct«r, instead of 5-tt irnii.) fchoti^b it is not talier* This appears to be becaiiije the upper internodea are botb



li.:. *AX Or.* unit. ^ V * '•'»'tte, Palermo ru•'.

shorter and leas mnaetoxw than in *Lutnarckiftna.* Comparative measurements of two lyjHrul tndividuflifl, both having a rinp d haisal bafcncheB, WBOT O£ ft^lowB, tingi^w belot.ing to the Italian race:

| | Lamarckiana | gigas. |
|---|---|---|
| Tota J JnighT . | 93 cm. | 87 cm. |
| Distnice of flrrt i^p»i from g : n | »tl cm, | 67 cm. |
| Length of •tem from capsules 1 to i | •17 I mm. | 50 mm. |
| " " " I to 10 | 120 mm. | 90–113mm. |

The petals of *{/if/as* are about 50 mm. in length and
(*() mm. broad, truncate or slightly emarginatc ; bud cone
40 45 nun. in length and 14 1ʹ5 mm. in diameter at
(lie base ; liypantliium 40 43 nun. long, about 4*5 nun.
in diameter; ovary 14 nun. long, somewhat flattened,
about 0 x 5 mm. in diameter; sepal tips 5*5-8 mm.
long, coloration of sepals as in *Lainarckiana.* 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 rela-
tion to *Ijamarckiana,* 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 Bovidse 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 *hrevistylis* and *cruciala* the origin of which has
rarely occurred in breeding experiments.  The history of
the first *gigas* imitation was carefully recorded by Pro-
fessor do 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* x *hirlella.*  Neither of these
plants matured, and it is probable that they were poly-
ploid mutants but different from *gigas.*  A mutant
resembling *gigas* also appeared once in MacDougal's
cultures of *Lamarckiana* (1907), and three times in Schou-
ten's studies from commercial seed..  In addition, we have
described a tetraploid (4#) 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 aa in Hf\* Amsterdam** raue, and **included also three ^^w** *tumdia* **rosetta** . The **remaining\*** seecis wt'rc sown at **tlf\*- John tunes Horticultural** Institution, Mertxju, in 191 % and **produced** 12 **plants,** all i>f which bloomed **and** were **identical** with *gtgas* of de Vries



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

in every stage of their ontogeny (.see Figs- 43, 14). Nine of these belonged to the typical broad-leaved *i/ttfos,* one was more Sender and probably corre«pt™<tal *onga,* having **nearly smooth** leaves, oblong, with a nearly smooth nuirgia. Another differed from the **tope in having smaller** leaves **which** wore more doeply

crinkled, and narrow strips of red on the budy. **though I** he **rosette** was typical.   The last plant was **distinctly sinalki** in iill it* parts, **having** petals as long ihmigh **broader** tbau in *Lawutwkhftu.*   It- was fouud to **hiive** 75 per **cent** 4-lobed pollen grains. 23 per cent, with three lobes and 2 per uent-ᴛ **with** more than four lobes.   Its chromosomes hii\*e been found to V 27, while typical plants were exiiniincd and found to have 28 chromosomes.



Fig. 1& — "     ill          1 frrmt 8w*<3iMii mots«( *it\*. I m* arekiana (>. I Fig. *;*

It appears that in all the giant races of Oenotherti **the** flowers tend *to* remain attached longer than in other furnw.   In one individual of this culture the absciss kyer between hypantimim and ovary was completely lackingₜ so that the laded flowers remained **permanently** attached to the plant, even weeks after blooming.   This feature was exiubit^ed to *t\* less extent in two other **plants.**

Another and different race of *giga\** has appeared iu

Heribert-Nilsson's cultures of the Swedish *Lamarckiana* (see Figs. ... IT). It has been found by Miss K. TJhomas to have 27 or 28 chromosomes.[1]
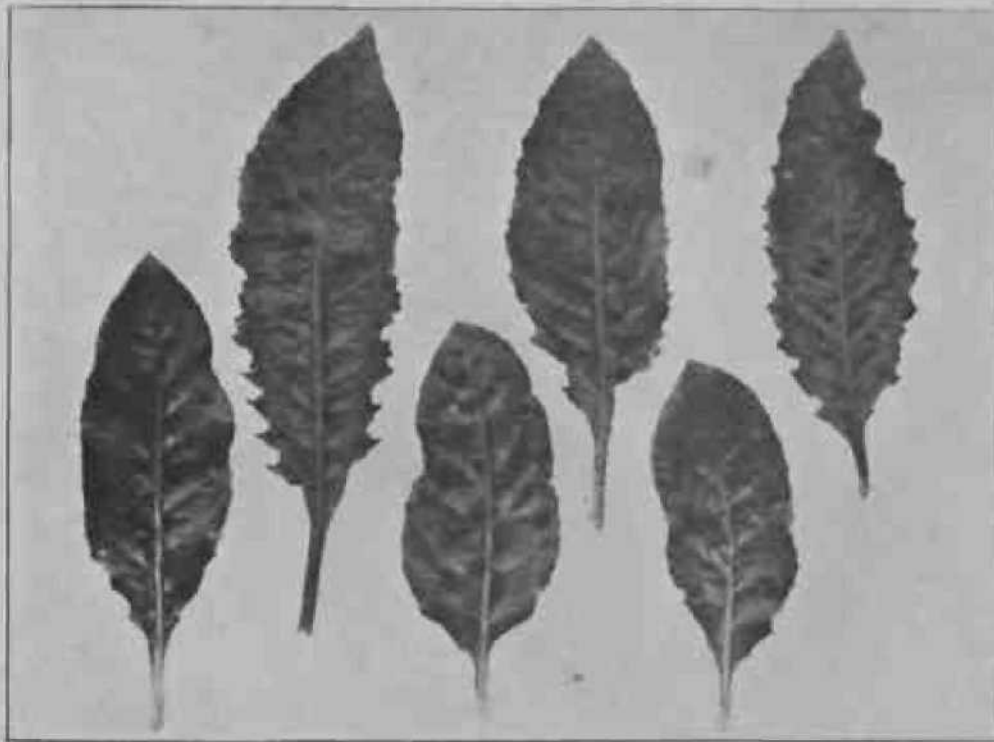
Stomps (1922) has estimated the frequency of mutatiaD-coefficient in *gigas* as nine in a milli ... M*000B per cent., but the limits of the estimate is rather sensitive. It



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

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

[1] I have details from Miss Thomas of the meiotic divisions, enable us to determine *the* number of precinpJ) 28.

*Wm.*  17-—  Fpgwrr rwr.  three•U!*u-l«i%¹t« fwmi  Swedish *gigux.*
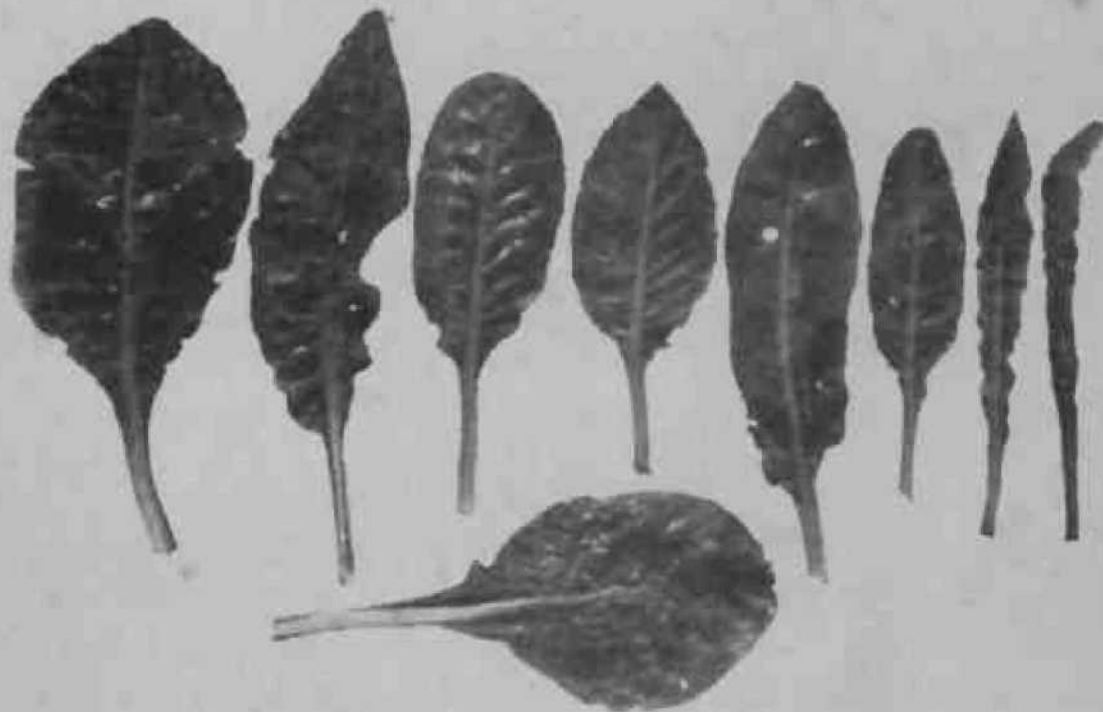Uiwut  r''vr_T  UtfM!  frtetU'lddv«  from  Palttftuo *yiyttiL*



FIG. 48.—Leaves **linn mature i.mjUi-ftiii** **-. mut. *gigux,*
showing range of **Vftii.it inii** uiTshape.

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

In **its** offspring, *rjigas* is the most variable of all the mutants, though it apparently neveT **reverts** to *Lantarekiana.* 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 *gtgas* except one dwarf plant, (*jigas tianella* (Fig. 54). In 190U we grew a family of 434 plants from *ffigas,* constituting the sixth generation



Fiu. 4y,— *O\*\** uiut, *gi&av,* « rutlier u m w - leaved **rosette.**

from tW 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. Fry in the four **which** blooniRd pure *mefe* WЄre **obtained,** an. I from liieac 48 plants wunj raised in 1910.
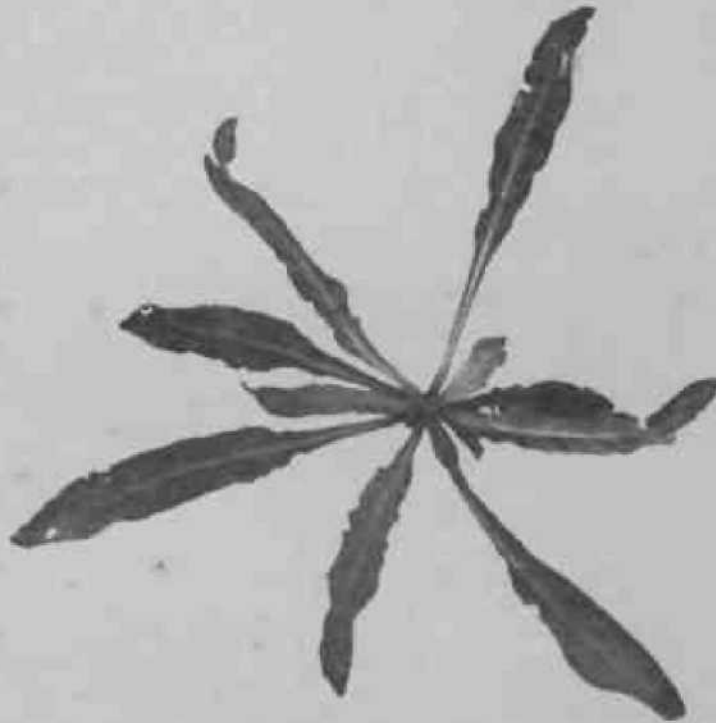


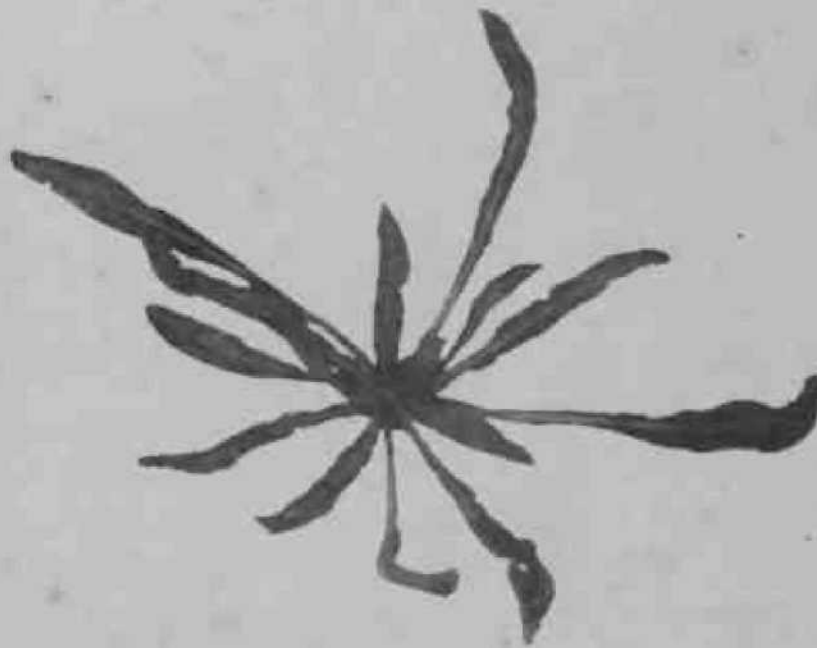FIG. ;"M — '.h. mui *gigas*, a **vt-c)** narrow-leaved **rowtte.**



FIG. 6L—*i^. mut. *gigas*, a linear-leaved rosette.

These numbers were *not* krge enungli to tot- tli»- mluu- tance of the **parented** differenced in **foliage**. Tlunrgh the

**ofepring tended bo resemble** their **parent, occasional** rosettes **departed** from thiw **rul&** It iipixwirrt **probable that** the **distribution of the** $t^{\wedge 1}$ **meiotio** ohromoHomes **is concerned in** iliis **remarlcable range** <f vurialnlity.

**In fchfl** *i* ulturos *of gitja\** **also appeared** a large |rt»rcpnt*ige til' dwarfs (/i#^,v *uufuitti).* TIIPHO do **Hot** h&V« this fnli.ige t\\ *nittirUit* l>ut Site m<*Pf'ly injjiiaTun* //"/'^ usuallv of «1.- broad-l••a\M'<l type < Kij^. r>4). Out <*f :wi» plants, »>!•<•



hu, 6S1. — r#, mill. *gigas,* narrow-leaved n**:te.

l»t cootained 4*28 per cent., another S-TU P<M cent.j while a **third** lot **of** oiiiy **10 plants contained** 10''9 ]<>r cent. */«/«« *ntnttlhr* **It is therefore evident** tLat CIAIJT nnil ilwiiilisin **in Oenothera** an* *wut vUv* **two extm&e** a **sin^c pcricis, bui** i\ro *\w-* t<> **ehangna** »»f **quita tliwp^ kinds,** fiirinrisni in **iteuotUtum i- ;i rowtM ol orD gianti** :iji]i;irrntfv flJwttpJ ;trt-i»iiipiHiii'.l liv U t ra]i|i>«ly, ivhllt< ilwjjriisni (srr *wtt/i'lhf.* p. I*U) appears to IM- itm **hk of- iaterncidea accompanied** Uy dceveaHe **in** *the*

size of cell- M well   In *giijM natteUa* or imniubuni *jj*
plants the fcetraploirt cbromotfomc-nimibei is probably
retudned, and then? in pTobably u very marked ilecreatie In
the -i/»- of tin[1] cellw. n<rouipani«*l by………spending diminu-
tion in lite volume <f *muM* and chromosomes.   This will



FIG. 55.—Adult stage of the plant shown in Fig. 52.

be tin intei'etfting suitjeel i-»r future investigation, l)n!
the fiMs already known m&lra it clew tlta? (jiaatism
itdil il\v.irfi.sm tti Oenntbel i n • due t*) vny »li>nm>i an,J
divcrtw gornrrimil ctutti^s. imil thai dw^irfwrn siIJM I-
imposed iipun guintisJii b»y no menu* etmyes tctutn fci the
original ry|i<. Cross les between *gigm* -iml *uaiwUa,* wliich

K

**have** so far been **made** without **peat** success, **would** **probably** contribute **fco** an **usdes'standing** of this subject.

In 1906 Schoutojn (333) grew **a1 Amsterdam** about 1.200 *ffigas* hum s<*m& of de Vines, Some of their iloweis wwe a** much *us* 10 cm, in diameter, and thi? plants showed the usual wide range of variability in foliage, the culture containing also 2 per cent, *ipgas nanetla** Six foliage **types** were distinguished, in addi-t ion to the type form, individual* **belonging** to these typ^s **were** seUetl, but theLt offspring **were in** no e^kse uniform, each group bring* according ^> Schouten, **M VAhabk***
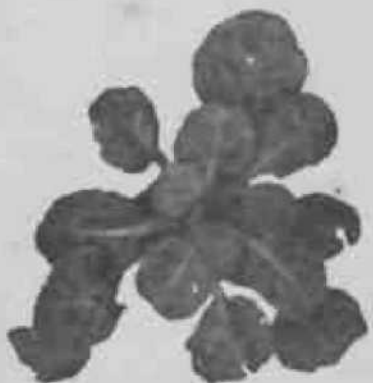


F1.. .%
Oc. mut. *gigas n'ttrrltit.*

as the whole culture. The seven .families contained abfm ],IH)O plants as **foUows:** —

|  |  |  |  |  |
|---|---|---|---|---|
| 945 | *gigas* | .. | .. | 07-03% |
| IS | *gigas nuudta* | .. | | 1 S7 |
| I | *gigas* IotaK. | .. | | |
| 1 | *lævifolia* 7 | .. | | =2-o:% |

The froquency of the *gigas mmdUt* varied from 07-4 p&r cent, to **L4*8** per cent The family containing tin? hist percentage Schouten thinks **came** from *a* plant **which** was produced *hy* the union of :» *giffM* germ cell with a *gigus nmeUa* **germ cell. The** *ijigux lotto* **resiiinbled** *loUt* in having roundeii leaf tips nud buda, and in its male sterility. Did it, perhaps, have 2l) chromosomes ?

ttchouten's iOOfi culture contained also two plar*ts* called ⟨yV/*ts argenf&Xj* in which the leaves, especially of the rosette, were covered with silvery pubedcezwe. **One** of these was male-sterile and was pollinated from **typical** *fftga**. It yielded 37 oft&pring, all of *whkir* **except one** were typical **f^f/fttrwithout** the *argeniea* character. Schout>.*n* therefore oonaidors this feature as a **non-mhet^ed cxtteme** variant, though it is conceivable thut the **cAa/actet** may have been inherited but rece&ive.

The original Swedish giant mutation **appeared** in i»07, iu \*i* culture of about 30 plants of the Swwlish *fjannarckkma* (see p. 123) grown by **Heribert-NIIdaon at** Lund (162). From seeds sent by him.*we grew in *VJV2* ;i family ol 36 plants (see **Pigs,** \:> 17} whkh **wen\* aniforra except** for **two** or three individuals, **one** uf which **agreed aJmosi** with the typical r/i*p» of di \'ii-. The typical pkuate differ from the Amsterdam and Palermo races ol *gigas* mainly in the fallowing **partkolaj** : (1) when **half** developed tlie rosettes were in- distinguishable from those of Kilenno, but their later leav^a ate larger, with mor<' jagged teeth at the baae of **the** blade.

**(2)** The **stem-leaves have** con- spieuoufc red midribs, itud tin? midribs uu◁ **petiolefl** arc also pink on their ventrul surfautj. (3) The Hfceni-le-aves are **longer, Ifats crinkled, often** nearly amontlu jind thpii[1] n.irgm is naoie cou- **(fpicatbtusly pepftndrdeatate, often •with** JiigHo d teeth◁ »rar 111*- ham*. **(4)** Tin- **basal** brunches ure more epreadiiig, the **stam~brancheg**



Fio. 55.—.: mut. oiu< buds. (*f.* **Pigs** Jt), :Vi; mi-l 38* (same sen .

tnote mimeroiis ii.nd i>ftt*u with sccondnry branthcsj **the whole plan\* being** larger and **more** inmhy. (5) Th« **flowers are considerably l^rget (petals** (to x 7» mm., ovary L8 mm.), and **the** *iu\\\$* hitii> **on** the **buds arc lodge**r, more **miM◁ ious, and** train larger papillae. **(0) The c**apsules **arc expanded .it the** *hm* to **a brotid** attachineiit, they urc also mut'li **longer** (3fi **S9uun.)nndc<jntatinjiiaii^** seeds, iho **plants elinwmg much** l^s sterility **than the** *pigas* f>f ◁le Vriei*, **both in anthem** and **bvaim** (7) The **dovelon**ment **W4H slightly dower,** liw **plantu remaining rotofti**es.

Heribert Nilssem (lHlj gives u» extended a(ft;»juat **o;**

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 nuinber 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 *Jjamarckiana* 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 *Ijamarckiana.* 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 *Or. hla,* 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 *ffif/as,* 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 x 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. l)e 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 3# 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 (ieerts (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 *semigiyas* some reversions to *Lamarckiana*
with 14 chromosomes, some plants with numbers inter-
mediate 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 *Lanuarckiana,* petals
usually about 25 ˙x 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 *Lamarch-
iana,* 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 dwarf ness 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 *uaudla* 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.y., rubrinervis* or *lala,* 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 $F_t$ 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* x *nanella* and the $F_t$ contained 77 plants, about 25 of which were *Tjamarckiana* (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* x *nanella* yields both parent types in $F_t$ and both breed true, in mut. *rubrinervis* x *nanella* the dwarf character behaves as a recessive, reappearing for the first time in

*Y.u* The Mendelian presence-absence hypothesis completely fails to explain why splitting should occur in F, in one case and in $F_2$ in the other. The hypothesis of dc 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 dc 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* x *biennis* (though not in the reciprocal) both tails and dwarfs appear in F,. 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 876 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 1B87 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 *Immrclziana* 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. | Nanella. | Per cent. |
|---|---|---|---|
| *Lamarckiana* family, 1889-1899 | 53,000 | 158 | 0-3 |
| A branch of same, ] 895 .. | 10,000 | 111 | 1·1 |
| *Loevifolia* family, 1889 .. .. | 400 | 12 | 3·0 |
| *Lamarckiana* x *nanella* ·· ·· | 1,063 | 5 | 0-47 |
| *lata* x *nanella* .. .. .. | 1,693 | 12 | 0-71 |
| ≫ ·· .. .. | 390 | 6 | 1-54 |
| *lata* x *brevistylis* .. .. .. | 1,026 | 3 | 0-29 |
| 0. 8*cintillans*, 1897-8 ·· ·· | 1,654 | 15 | 0·9 |
| A biennal cult. 1897 .. .. | 1,529 | 9 | 0-6 |
| Cult, of plants with variegatccl' leaves, 1899. . . · | 1,972 | 9 | 0-5 |
| *Lamarckiana* x *biennis*, 1900 ·· | 80 | 1 | 1·0 |
| *lata* x *biennis*, 1899 .. .. | 299 | 2 | 0-7 |
| *Lamarckiana* x *brevistylis*, 1898. · | 293 | 5 | 1-7 |
| *Lamarckiana* x *yigas*, 1899 ·· | 100 | 2 | 2·0 |
| *Lamarckiana* x *scintillans*, 1899 | 112 | 1 | 1·0 |
| *lata* x *Lamarckiana*, 1900 ·· | 2,000 | 3 | 0-2 |
| *lata* x *Lamarckiana*, 1895-1900. · | 2,387 | 26 | 1·1 |
| *lata* x *brevistylis*, 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 *nandla,* as well as the F$_3$ (547 p]ants)~Hnd 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,* **nanelh-oblonga, nanella-albida, nanella dliptica,** 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 x nanella* and in *lata* x *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 unmargined 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., T7 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,  mid  35  individuals  occurred  in  the  cultures  of  MnrDougnl,  constituting  a  frequency  of  1'25  per  cent.   That,  *obfow/a*  breeds  true  was  shown  by  de  Vries  in  18!M,  when  lie  obtained  as  the  offspring  of  seven  *oblonyas,*  1,083  plants,  all  of  which  were  *oblonya,*  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  *oblonya*  self-pollinated  contained  3  *albida,*  1  *dliptica*  and  1  *rabrinervis;*  and  in  another  case  305  offspring  of  *oblow/a*  included  0  *mbrinervis.*

*( )e.* mut. *albida,* de Vries.

This  very  delicate  form  seems  to  have  been  brought  to  maturity  only  in  the  cultures  of  de  Vries  and  MacDougal.  ft  is  pale  green  or  whitish-grey,  and  rather  brittle.   The  rosettes  resemble  *oblowja*  in  leaf-shape.   The  stem  is  zigzag  but  stout,  the  height  not  exceeding  a  metre,  the  **flowers  arc,  paler  and  smaller  than  in  *iMwarckiana,*  more**  nearlv  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  *Jjaniarckiana.*

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  retro-gressive  variation,  and  since  it  breeds  true  it  should  be  classed  with  *nandki.*   *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  *La-mmckiana*  introduced  in  Nantucket  City  from  garden  seeds  many  years  before.

Mutations of *albida* from *Lamarckiana.*

| Source. | | Total. | albida. | % albida |
|---|---|---|---|---|
| *Ijimarckhina*family | 1895-9 | i 28,500 | 5(5 | 0-2 |
| *Lamarck,* from crosses .. .. | 1898 | i 4,599 | 2 | 0·05 |
| Lateral branch of *iMmarckiana* family | J 805 | 10,000 | 255 | 2(5 |
| *Oe. lata* .. ..' | 1900 | 2,000 | 42 | 2 ·1 |
| *Oc.lata* .. .. | 189(5-99 | I 751 | 31 | 4-0 |
| Oe. *Lamarck.* bion-nial. . . . . | .1896 | 1(>4 | 15 | 90 |
| *Lamarck, x naaella* | 1897 | 1,341 | 1 | 01 |
| *lata x nanella,* .. | 1895-00 | 1,580 | 15 | 10 |
| fata x *rubrinervis* | 1900 | j 1,844 | 37 | 2 |
| *lata x ficintillans* . | 1900 | (53(5 | 2 | 0-3 |
| *scintillans xnanella* | 1898 | 95 | 3 | 30 |
| *lataxsuaveolens* . | 1900 | j 743 | 13 | 20 |
| Total. . . . . | | > 52,259 | 472 | 0-903 |

*Oe.* mut*. *eUip&ica,* do Vries.

The seedling leaves are recognisable by their long petioles and very narrow blades (0'5-0'7 cm.  x  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 *Tjaniarckiana,* 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.

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

*Oe.* nmt. *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 *Ijamarckiana.* The earlier rosette leaves are oblong-obovate, obtuse or acutish, tapering to u 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 thfr 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 *scintilhns-yio&ucmg* 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 offspling 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** | *Lamarckiana* | ] | *albida* |
| **3** | *sublinearis* | **1** | *gigas* |
| **1** | *lata* | **1** | *obldnga* |
| **1** | *nanella* | **3** | *subovata* |

**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 *spath-ulata, fatua, suhovata.,* and. more recently, *ovata* and *ohovata.* These forms and the various other aberrant individuals which have appeared in the cultures of dc Vries, Mac-Dougal, the author, and others from time to time, serve to show that this type of variability in *Lamarckiaiia* 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 yeneris,* 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. Jt 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. Tjaviarckiana*

WE may now summarise the facts regarding mutation in races of *Oe. Jximarckiana* 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. Ijatnarchiana* is known to have been derived from seeds introduced into commerce in 1850 by Messrs. Carter & Co. (see p. 74). But the origin of the Swedish race of *Ixiynarckiana* which Heribert-Nilsson (184) has studied (see p. 80) and which differs from that of de Vries, is unknown. This race evidentlv 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 *lala*. 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
*semilatd,* 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
*Ijamarckiana.*   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,
spathulate  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 frojn *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  *Lam-
arckiana* with long internodes, (4) in having more squarish

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[1] **The offspring from self -fort ilising two of tho *semilata* wore grown in
1913.   One yielded 11 single plant (Kig. 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, Foi 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 *semikUa* plants (No. I., 6) in culture "-fa" when selfed produced, in 1913, 12 plants, of which nine resembled **Lamarckiana** and three were *semilaUt.* This type is clearly
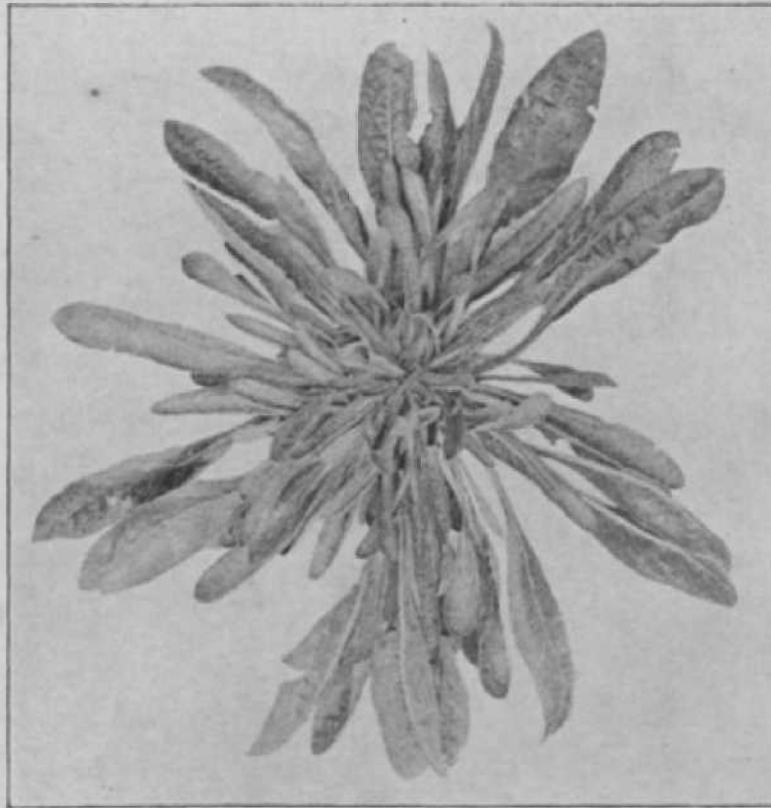


— **Flu, 66,** *0«- tncwmta* **inut. unv, from Swedish M**ee.

shown in Fig. 40, p. I ] 3, which **represents** a plant from another **culture** from this **source** having the .same characters-

The " comb. *2* $^J$ of Heribert-Nilsson resembles *albida,* " comb, 3 " is like **rubrinems,** " comb. 4 " was a rosette, ʿ comb. 5 " was a peculiar plant having the branching habit of **rubrinerviSj** certain leaf-nharacters of *scintillans,* and **buds** and **capsules** like *lata.* It not improbably has a modified **chromosome-number.** ʿ< Sonab. (> " most nearly

resembles the *rubrittrrvi\** oJ -k\* Yties, From soeda >f Heribert-Nilssun we grew 120 plant\* of comb. 6 \* *Lamurck-UtH(l,* riuuit wore one /«"i jniii aiie *ttemilata* (both having 15 chromosomes), about seven belonging k- flu\* *Lttomuvkiana* type, while tin- remaxndex were •i•se "I in the *rubnhsrvi\** type (eumb< <S). The liiiit-i differ Ertnn t.l«- *rubrinatvb* of de Vriert in having nearly srmx>th leaven .nul BomewhAt more ml pigment in the buds, thewpals hn\ing the extreme



Flu. 57- —"r. Mi' I- *rnln,* see md geflr'ation.
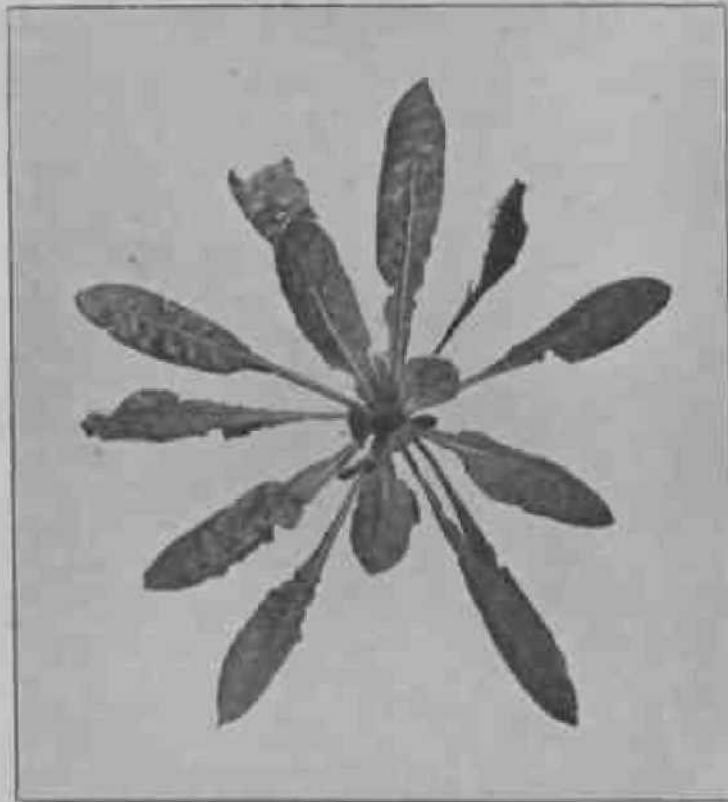
**I**uinount present in *rttbrmervut* (type 7) together with a small amount on tliP hypanthhuB. The quantity oi antho\* cyo!tiin$_t$ however, ui no wety ajjptoaclics that present in *ml'rical m.* Three of those plants, nioroovcr$_P$ had buds like *ffrandi/lora* in shape and pubescence, while in four other here the buds were liJtu typical *mbrinenri\**.

**J** The $^{rI}$ comb. 7 $^M$ of Heribert-Nikson is the giant type already deacribed, while " comK 8 '• i^ almost certain)y

a triploid mutant.   Tn general, it may be said that Heribert-Nilsson's race of *Lamarckicma* shows greater variability than that of do Vries, while the Oenotheras from Birkenlicacl gave indications in our cultures of an even greater variety of forms.   This would seem to show that continued inbreeding in *Oe. ljxmarchimui,* 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. fjamarckiana* is merely a Mendelian heterozygote throwing of? 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, Colander*

*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 \\m wil-l **condition*** 1$ <"ij»:ible *ot* **producing** dwarfs **and \*\*tlier** uhfiTwut ions.

In *runny* from tho .SJIUH- hnjilirv. 1>JLVU obtained four «lis(iii,t **(ypea of *gmtdijtom,*** ami **ftom** one **of these** typos
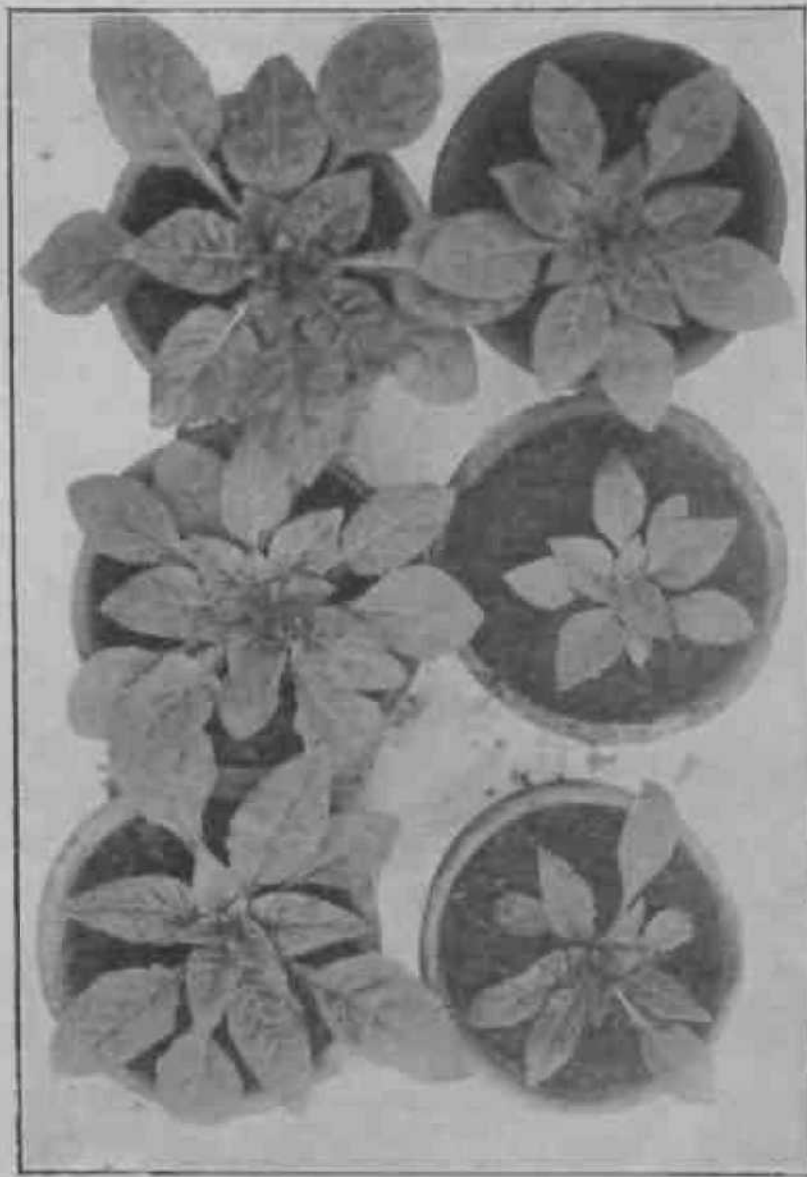


Fic. 58.— *Oe. grandiflora, young rosettes ;* *a* and *b* aberrant.

wkich proved **stable** he **ttffrrwiirtl\* diffcr&ntiatei** thrco straiiw. Tii-ese types d t(Ter«J rhicfly in folinga and in th« colour pattern **of tbett ^p«d».** **Hi- culture,** moreover, co**atained,** iu additiuM **to 127 OP.*ffwndiflom, t'Z th.* Tru\*** yi.

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 *Tjwmarchiana* 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* x *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* atid *Lamarckiana.* Among other variations, this family contained a plant having the peculiarities of Zofo, 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 Oėnotheras, 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 tails 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) " *Lamarckiana "* type. . . . 23 plants
(2) " *rubrinervis "* or red-veined • type
   (Fig. 59). . . . . . 91 plants
(3) *biennis hta,* with pink midribs (Fig. 60) 1. plant
(4) " *Lamarckiana"* type, but with finely
   crinkled leaves .. .. .. .. 1 plant
(5) " *lamfolia "* type. . . . . . 6 plants
   ‾‾
   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 *lota* and the small flowers of *biennis,* as well as 15 chromosomes (see also p. 179). It is, therefore, a precise parallel to *Lamarckiana lota.* Type (4) is not exactly like any known mutant of *Lamarckiana.* Type (5) resembles *lamfolia* in having long, narrow, pointed, furrow-shaped and less crinkled leaves, but its flowers varied greatly in size and had an extensive

Fɪɢ. 59.—*Oe. biennis* % inut* fnjru **Mnririil Iliihiuic*** **iJAitU'n**, red-veined type.
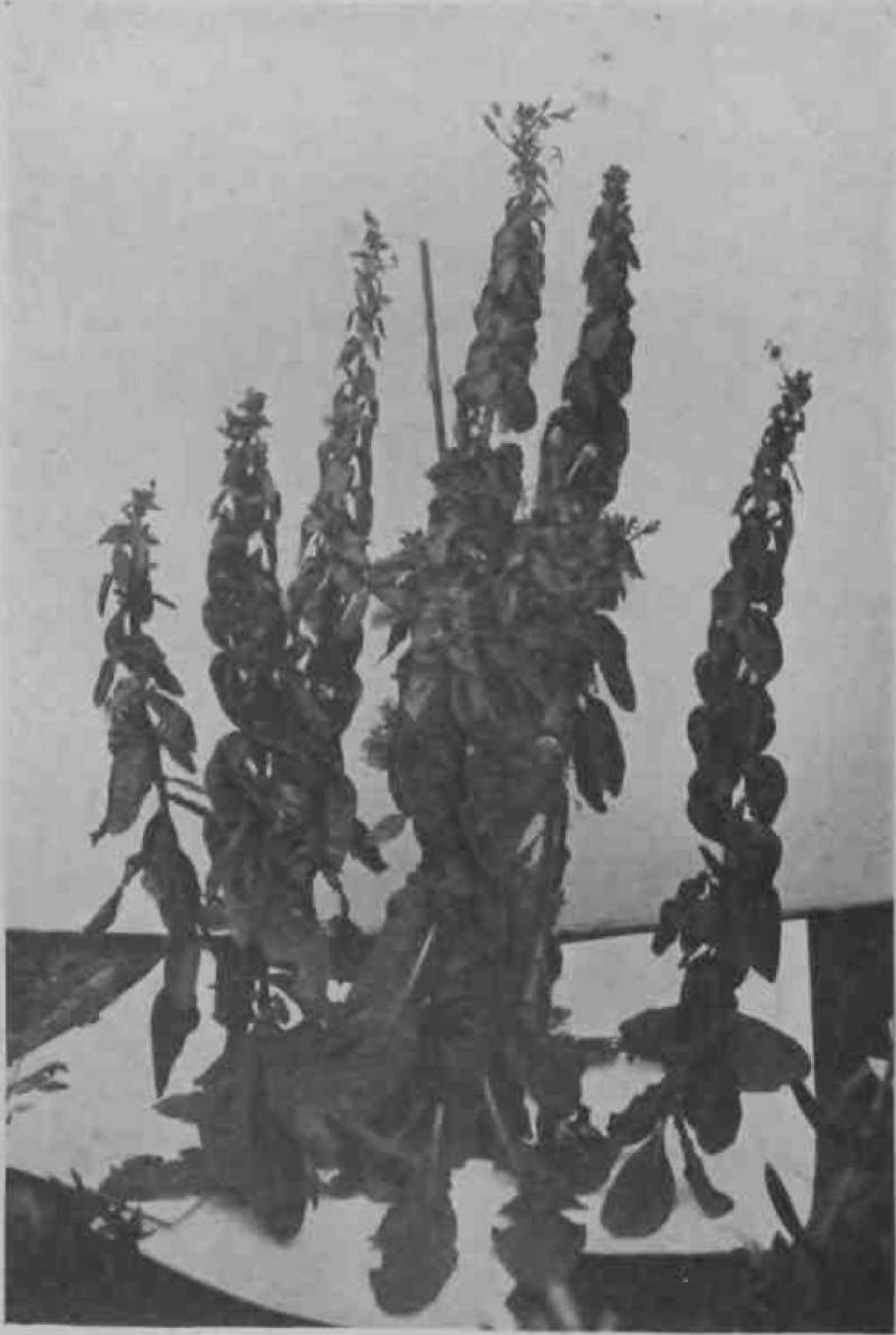
F'", 60.—*ih, biennis mut. •'''*. from MHIIMI *iw:>.-uf-* Kig 59).

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 1)0 rosettes which were exactly like the parent plant. The mature rosettes closely resembled *Ltimarckinwi,* 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 lota* 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 difEerent plants the sizes were as follows :—

### TABLE X.
### Length of Petals in *Oe. biennis Icevifolia.*

| Length of petals. | Number of plants. | LengthL 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 *lota* 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, had the broad petals of *bfimnis,* while the Fo split into the two types.  In addition, in *Oe. biennis* **x *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 à 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* ***cmciata mnclla*, 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. \n 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 $F_a$ culture there was one *biennis nanella,* one *biennis semif/if/as* with 21 chromosomes, and one *sulphured.*   The P\ 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 *Hart. Lugd.-Bat.* under the name *Lysimachia corniculata nan papposa, Viryiniana major, flare sulphureo,* in 1687 (see p. 66). Linnams 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* x *biennis* contained 64 *HooJceri* and six *rubiennis,* one of the latter being a dwarf. (2) *Hookeri* x *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. cruciala,* Nutt., x *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 *salicastnim,* 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. cniciata* x *muricata.* Another type appeared in *Oe. muricata* x *(biennis* x *muricata),* a hybrid race having the features of pure *muricata.* This mutant had small, very narrow

**leaves (9'fi con. wide),** small flowers **and** reddish buds. Do **Vraea'e** Kgiire of if (4-2f>. Fig. Km, p. 303) .shown it **to** have **been, apparently, an exact** paiutiel to a namow-**teaved onitrtnl (seeFig. 61),** which appeared in a **culture** of **(Ot** nrnt. *rubricatys* x *ijmwiijUmi)* x *ymmli-jto'ru* in **1915 (154>.** Tk> family mml>ctr<.l 1S4 plants, iind. this imii-\i> **IUIII** WBS striking!v tliffrnint from **all** tim others. Tht* **chaiaotera** of the **main body** of **liv-**brids **onesponded** with expecration, while the peculi;iritie.s of this plant **ware** wholly unexpected :uid utipr^lkmble. This is, **of coarse,** one **of** \\w **tnaxka of a nmtation in pout** rtuHstinction to **a** livbrid-



..3

Fio. 61.—Mutant occurring in (O<. unit. *Itiit,stltrj* I x *grandiflors)* x *gran...://--in.*

5. -i*Mutations in hybrids*

A **number of** obvious **instanoea** of tmitutions in hybrids have already bwn **mentioned, In** fact they frequently, thongh in>i in',.iii.il.U. ;ini>e^r m races whic i. **have** iijuh'rjroin- **uroawug, [ttdeed,** OIK- *tsttmi* of crossirkg appeal; '> **be** to indute **a** tendency to the UIUTU fr*^\u<MU **production** of jj&iiniual variaiiui>. by disturbing! Uir **balancfi** *at* **oouditionfl** within thft orgtmiaui. In OG **chiding** ihi« **diaptei we ^hall refca: to** onjy uuo more <ase •»I' Jinimtiiiii.s in **hybrids,** fcjeveral other insfcyu^t^ of **a**

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

Numbers of triploid mutants have been obtained by de Vries (425, p. 324 fit.) in crosses between *Lamarckiana, nanella$_y$ rubrinervis, lata,* or *oblonga* as seed parent, and such species as *cruciata, muricata,* or *Millersi* as pollen parent. Jn 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 *Ipomcea 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. |
|---|---|---|
| Oe. *Lamarckiana* x *cruciata* .. .. .. | 6,760 | 15 |
| *Lawk,* derivatives x *cruciata* .. .. | 900 | 10 |
| *Lamarckiana* x (*muricata* x *cruciata*).. | 150 | 2 |
| *Lamarckiana* x *muricata* .. .. .. | 4,850 | ·4 |
| *Lamk.* derivatives x *muricata* .. .. | 1,360 | 4 |
| *Lamk.* derivatives x *Millersi* .. .. | 1,658 | 9 |
| (*Lamarckiana* x *biennis* Chicago) *velu-*<br>*Una* x *Millersi.* . . . . . .. .. | 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

**M**

not exhibited a series of mutations parallel to those of *hwtarcknivti* and *Ennuis*. Kxaininafcum of the pallcn *slums* very few Unl urn ins. probably not im>rc than 10 per cent,, \shi> ii; *LamavckimUi* ami pffob&bjty aW in *hieunis* the petc\*tit\*ge i\* neatvt 30 pet '••nt. The gttwter Erequencj' KI _•• J J *Ytcntet* rhit t IK\* meiottc processes les- beqoeutly go awry. *ft<* *Ihwfa'fi* \|i\x tmt
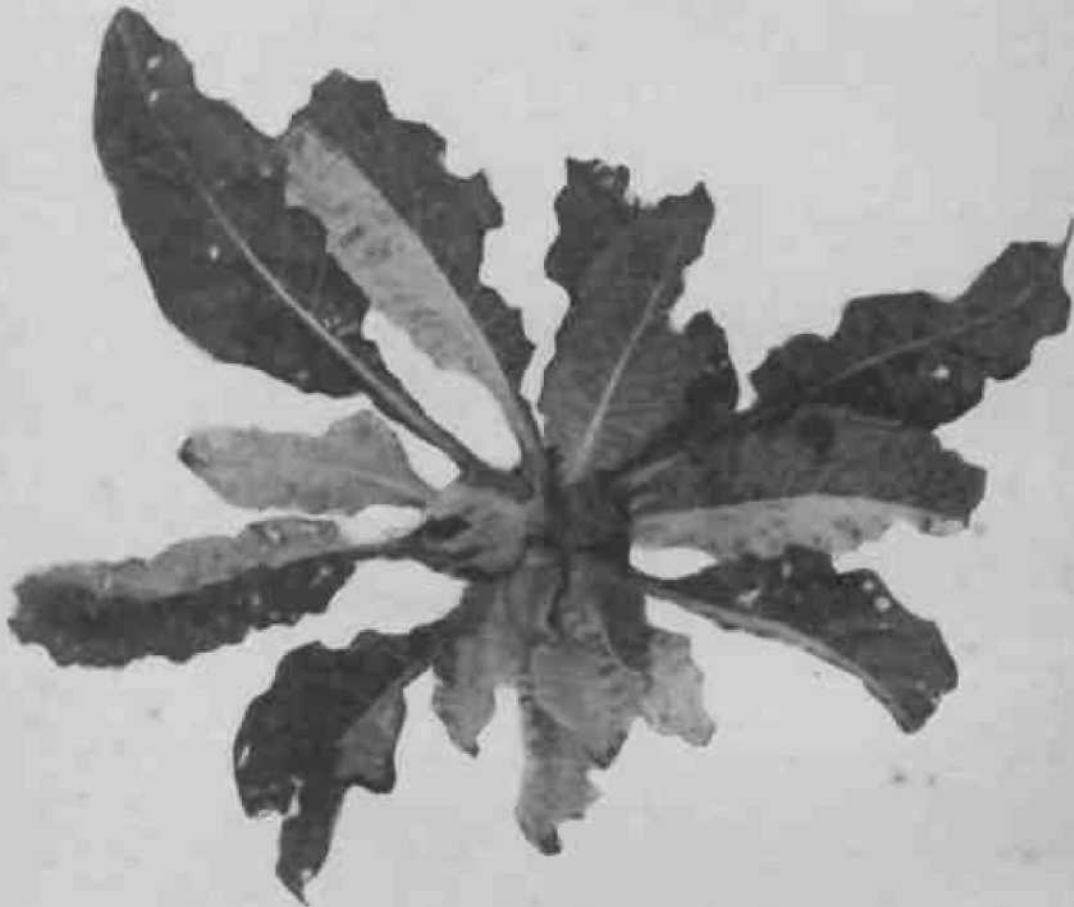


Fig. 62.—Sectorial chimera in a race of Oe. Lamarckiana.

vrt 1«<'JI examined cvfolosuttllv, Imt it jmiv Iw t-liut fcjbo heterotypic chromosomes n.n\* tnoit ••lus«\*lv tm-iml tliau is known to be the ease in Oe. *htwnrvkmm* ami Q& 6t«wi is. aad tfi:H it is theTpfojv less easy for the t&ekrfac tttfihirtt to be tlu-iiwii out of baUnw.

Mtuiv otlier fcypes (^f ovutatimw frequently CKKir in Oetiothera cultures. As instances \* \*i these, mention toay be made first ol a sectoria] chimera (Kig. H2) which appeared

F V. iv! — Virescence in *Oe. multiflora.*

in 1909 in **a culture of 55** *Oe. Lamarekiana* **plants derived** from **Lancashire (133),** One **side of** this rosette **was** white, Jibing devoid of cliloropiasts. 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
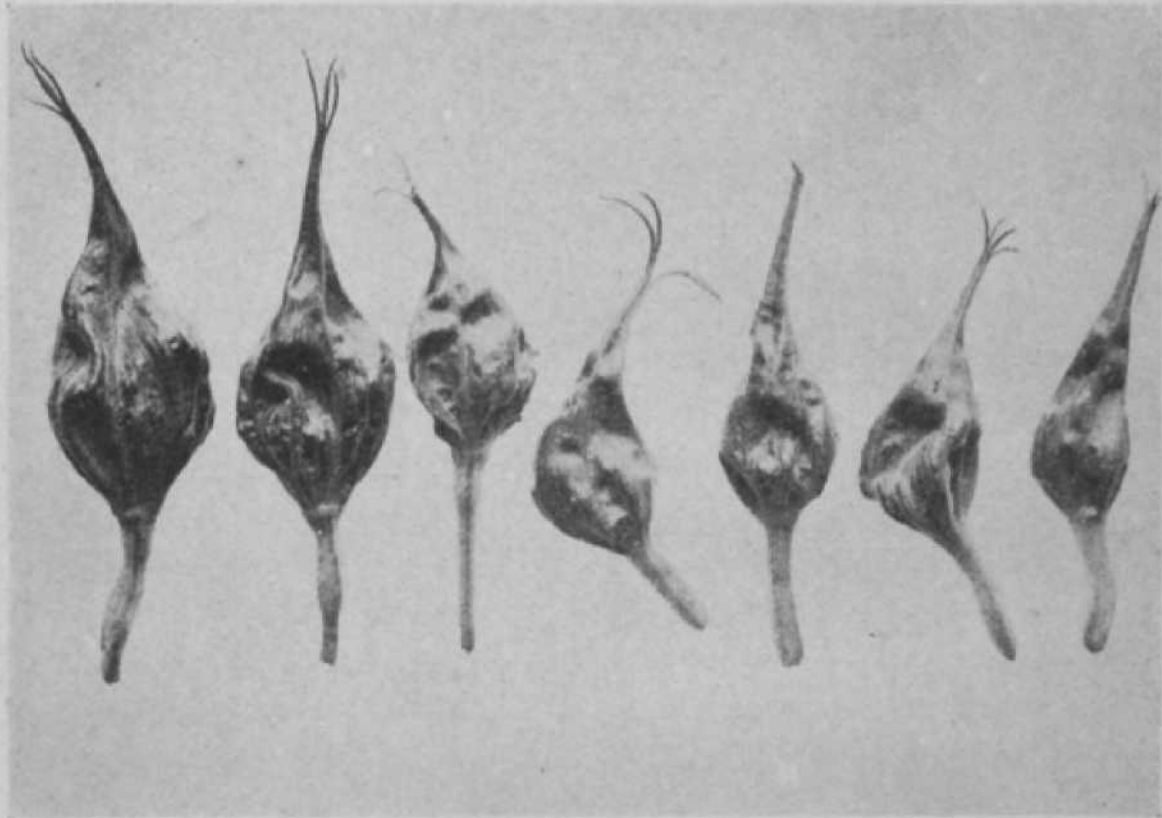


Fin. H4.—**Vireso&nt buds, showing baggy** *oelyi* **utd ftbsenee** of lt\\|kiuitln.....

Home of the cells in an unknown **manner.** **In 1912,** a **periclinal** chimera, partly devoid of chloroplasts. developed to maturity from **the** *Lom&rckiafta* **race** from Lancashire. "Anotlier interesting variation **occurred** (133) in a race from Lancashire which we **have** called *Oe. molt [flora.* Among 376 offspring of *one* individual, forming a **nearly** constant race, J5, 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 ease in a race called *Oc. Ckilemis),* 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
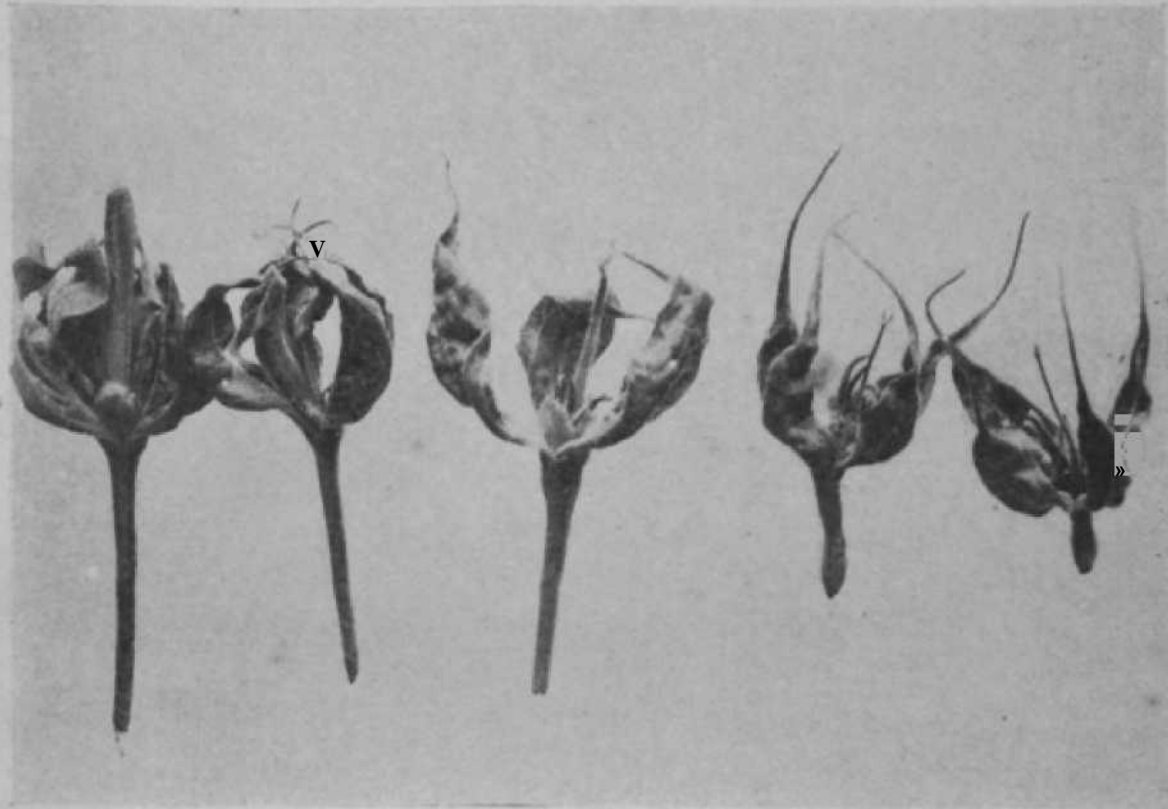


Flo, 85.- **Vireacunt flowtea, nho wing various abnormalities.**

peculiarities of the virescent buds arc shown in **Fig.** 64, **and** of the opened flowers in Fig, 05. The aepals a*e green and baggy, the hypanthiutn completely fails to develop, though a woody stalk frequently develops below bhe **ovary,** the petals are rudimentary$_f$ and the style slender arid 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 **ars** formed.

# CHAPTER VI

## THE OYTOLOGICAL BASIS OF THE MUTATION PHENOMENA

TT 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 *lota* 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 *hta,* 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 fin Oe. *LamarcJdana]* 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 botween the thicker and the more delicate threads is becoming more apparent.
*d.* First appearance of chromosomes, as long and coiled bodies.
c, /. 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.
?. 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.
*I.* 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 began 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.*
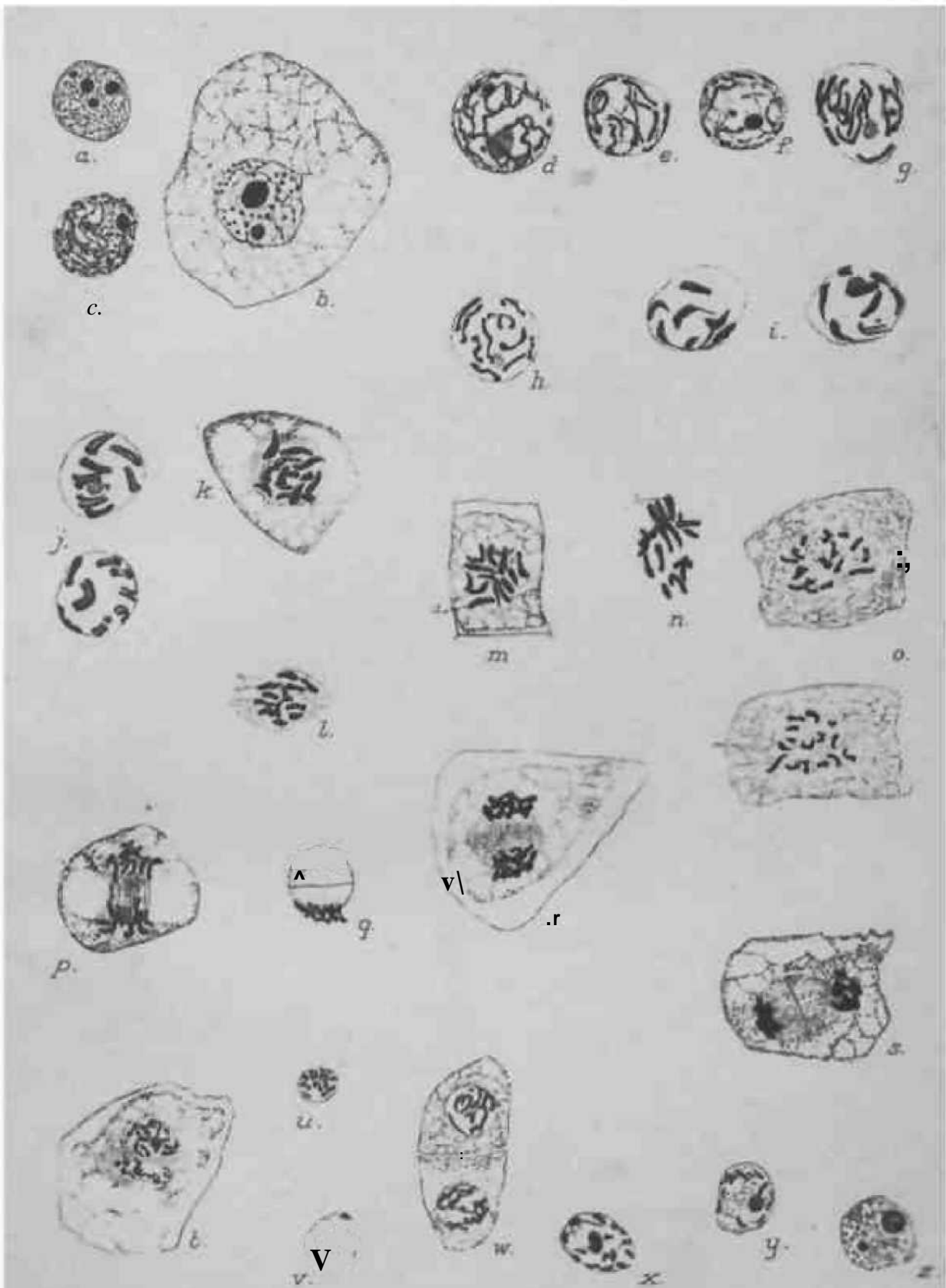
**Fig.66.**

**Uttudi** in the iiin:e]lu$ of tV. *fata*
From the *Amtah of Botany.*

lum in which the threads are more or less moniliform, like chains of delicate beads.    The spaces between these threads arc 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 (&, *c*).    Precisely how this takes place is not entirely clear.    The threads may be thought of as interstices or spaces in the nucleai; 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 fibrillae *(k),* the split in the chromosomes closes up, and the nuclear membrane disappears.    The chromosomes" now become arranged on the spindle *(I)* formed by the delicate cytoplasmic fibrillae, 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 *(ri),* 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.

Tn metaphase the chromosomes split lengthwise and in juiaphase move towards the poles of the spindle (o-r). At the poles they form a clo.se group, while indications oE 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 *(tv).* Fresh nucleoli are developed in the nucleus meantime (#), 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

**V.. :,**
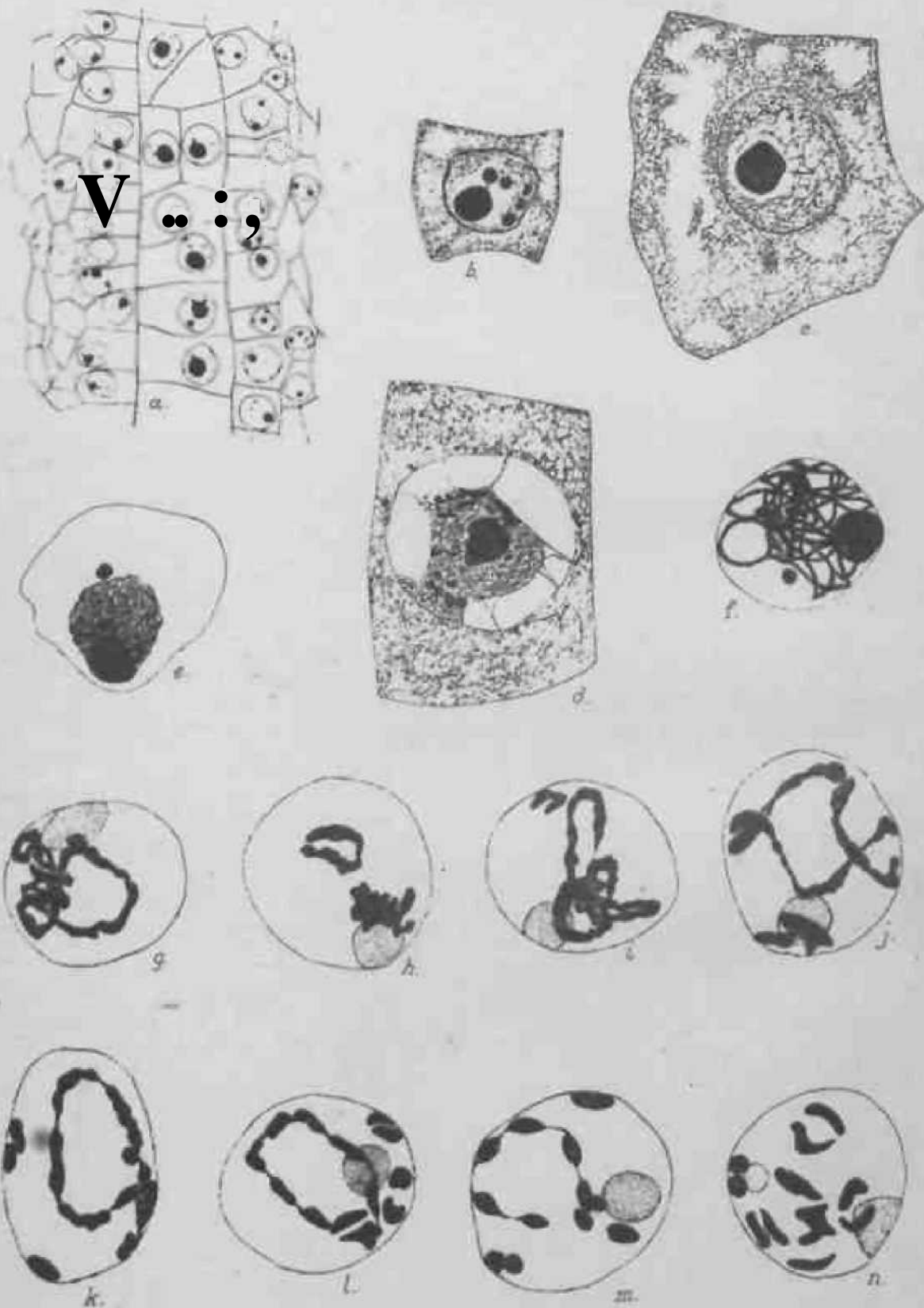
Fig. 67.

Mctosis (ctirly srages) in ihe |K>lkn mother edit of CV. *rubrinervis.* from tlic *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 undilferentiated from the other cells of the anther, and all are quite small (Fig. 67, &), 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

*Via.* 07.—STAGES OK MKTOSTS TN *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.
*/.* After synapsia 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.
*1.* Spireme uncoiling from second contraction.
*j.* Spireme segmented in three places, each segment showing constrictions which will form the chromosomes.
*h.* Constriction of spireme farther advanced ; chromosomes elongated, connected by bands of linin.
*/.* 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.* Tho 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. (57 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. 68,6).

The existence of these openings from one mother cell to another makes possible a curious phenomenon of
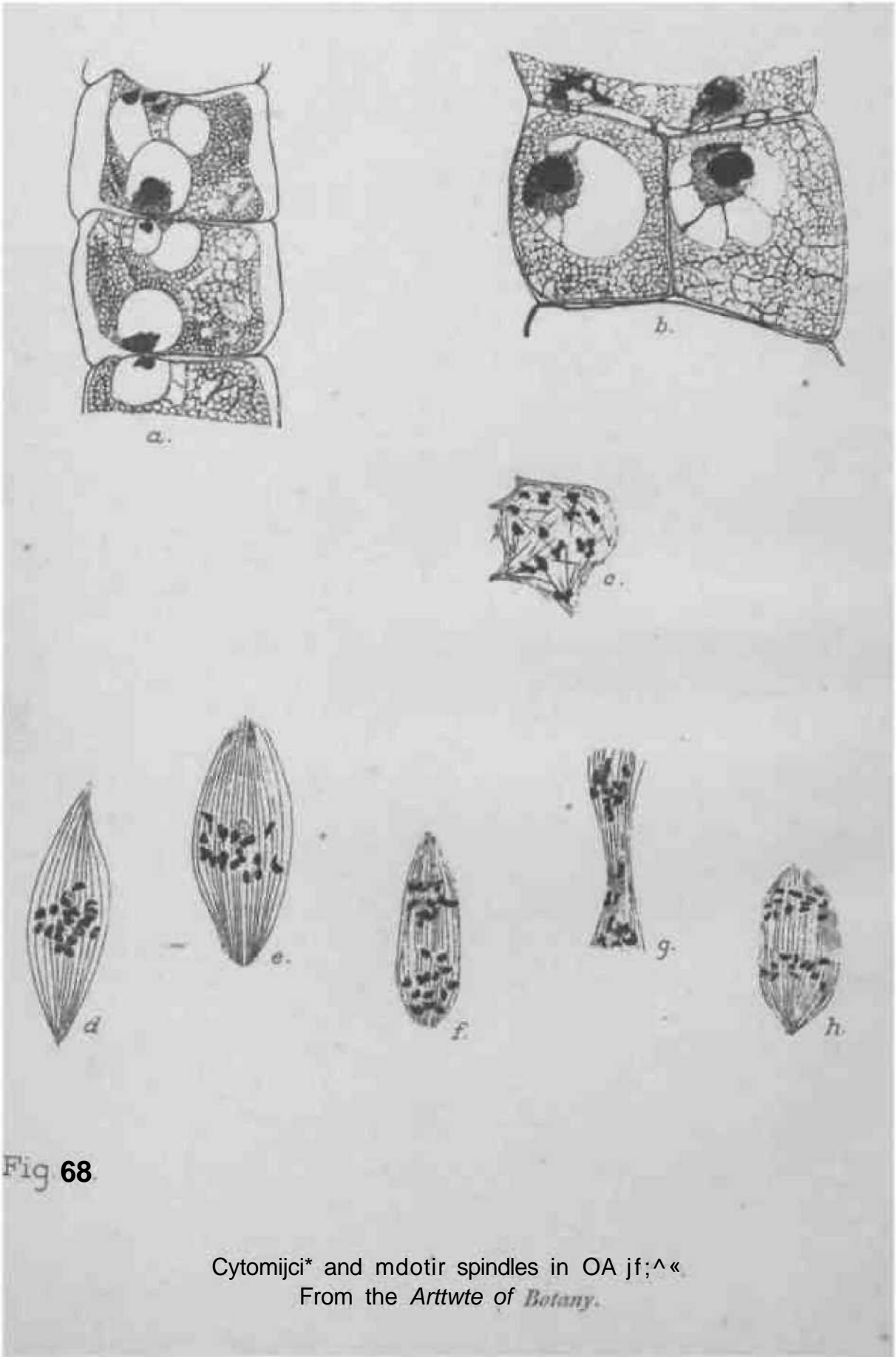
Fig **68**

Cytomijci* and mdotir spindles in OA jf;^«
From the *Arttwte 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 mothex-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, 6). 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.

6. A case in which this extrusion of chromatic material has taken place and the nuclei have moved back to tho centre of the cell.

*c,d.* Heterotypic metaphases, showing the scattered and loosely-paired arrangement of the chromosomes.

c. Heterotypic anaphase ; the lower pole of the spindle shows the lull number of 14 chromosomes.

/. Later anaphase ; several chromosomes havo a median constriction.

*g.* Homotypic prophaso, 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 *Anruda 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, /), until, from resembling a ball of yarn, it becomes a short, heavy* tortuous thread in the nuclear cavity (Fig. //). The spireme, in the stage shown by Fig./, is often nionili-form 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 under-goes 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 I.  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 segmenta-tion of the spireme in Oenothera, continue to shorten and thicken, but delicate linin connections remain between

them for some time (Fig. 67, *I, 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 *giyas*.

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

N

from the normal have been described in various plants, chiefly hybrids, and particularly in Ocnnthera. 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 tog,* shows a few of the conditions observable
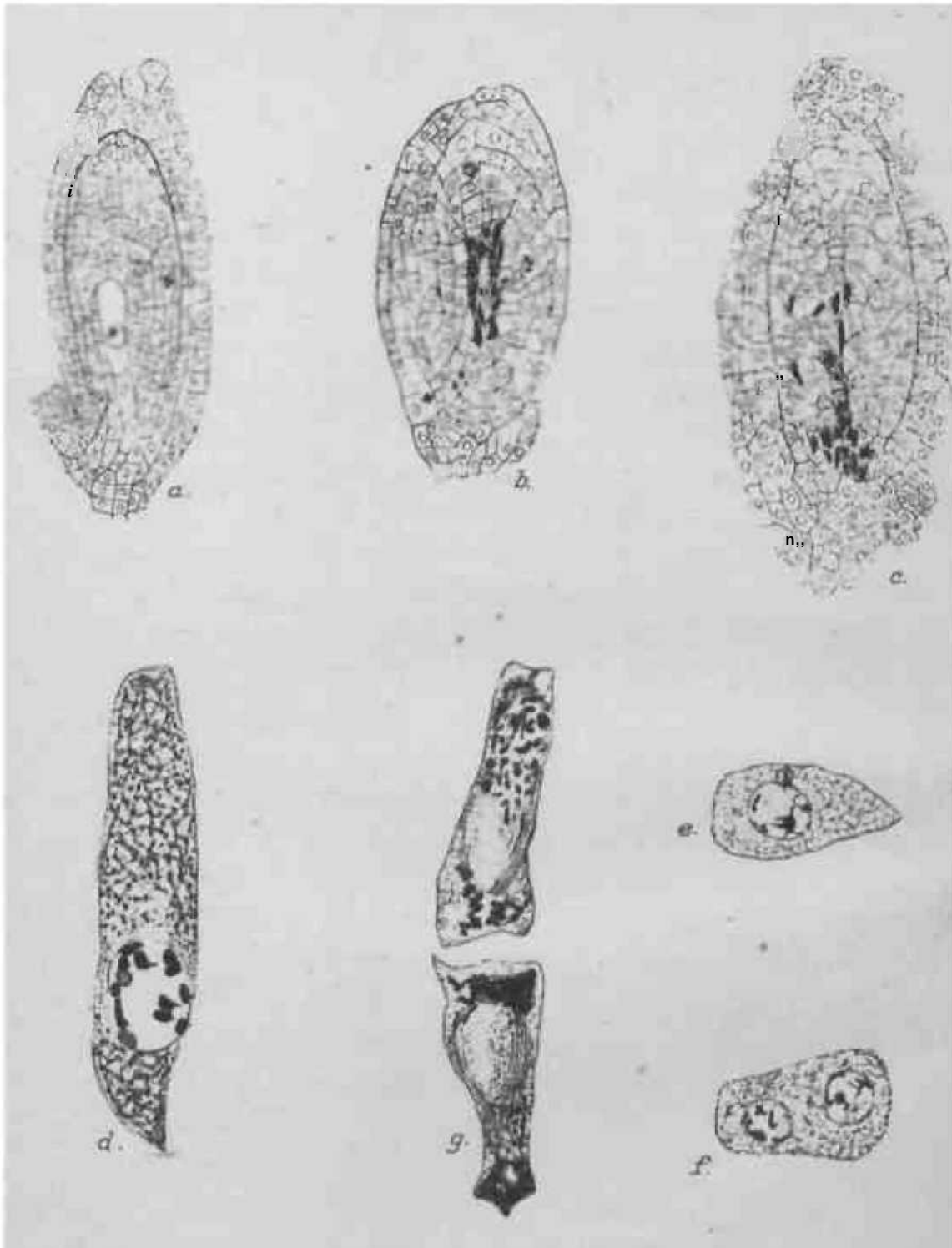
Fig.69-

Ovults ond nic^;i3jKjrc* in *Oe. lata.*

() **Ovule** showin^ mcy p s ore mathef cell in aynapiis- () **Ovule with** pre-&ynapt'C mfgasporc mother Cttl Surrounded by tlc^cncrating {d;irk) cells of Oic **nuodlJo»i** *id* Ovule with raw of megiujHircs, and many **degenerating** cells m the tuicdkis. *(if)* .Mcgasporc mother cciJ In d i k i » i s . *(\*-/)* Mqfautpore itifttlier cells whictt i r e nltnuriTtally smalt ^ same ihiigniticaiiuti UK ^ (f) Kovr of **nu^upott\*** de^t;ncranjig in tlu> humuiypic te ohhase.

in the ovules and megaspores of *lain.*   Fig. (>9, *a* is 21
longitudinal section of an ovule, showing the megaspore
mother cell in synapsis.   Frequently, in the nucellus of
*lota,* various cells surrounding the megaspores are found
to be breaking down.   This is seen in Fig. 69, &, 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 magni-
fied in Fig. 69, rf, 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. 69,6, /, which are on the same scale of magnification as
Fig. 69, *d.*   Some factor, which we may call " lack of nutri-
tion/' 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 mega-
spores.

   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 distri-
bution of the chromosomes in the heterotypic mitosis
of the pollen mother-cell, in *rubrinervis.*   We afterwards

                                        **N  2**

TAIILK   XIT.
Chromosome Xumbers in Oonothurn.

| Type. | Author. | Chromosome number. |
|---|---|---|
| *Oe. longiflora* | Beer, 1906 | 14 |
| Oe. *Lamarckiana,* Ser. | Geerts, 1907; Gates, 1907; Lutz, 1907; Davis, 1911 | 14 |
| *Oe. (jrandiflora,* ttnhmdor. | Davis, 1909 | 14 |
| Oe. *biennis,* L | Gates, 1909; Davis, 1910 | 14 |
| Oe. *tnuricata,* L | Stomps, 1912 | 14 |
| Oe. *cruciata,* Xutt | Stomps, 1912 | 14 |
| Oe. *Millers'\*,* do Vriox | Stomps, 1912 | 14 |
| Oe. mut. *rubrinervis,* do Vricss | (Jates, 1908 | 14 |
| Oe. mut. *rubricalyjc,* (Jates | (Jates and Thomas, 1914 | 14 |
| Oe. mut. *nanella,* de Vries i | (Jates, 1908; Lutz, 1908 | 14 |
| Oe. mut. *gigas,* de Vries | Lutz, 1907; Gates, 1908, 1911,1913; Davis, 1911 | 28 |
| Oe. mut. *gigas,* from Sweden | Gates and Thomas | 28 |
| Oe. mut. */afrc* x mut. *gigas (i)* | Gates, 1909 | 20 |
| Oe. mut. *semi gigas,* Stomps | Stomps, 1912; Lutz, 1912 | 21 |
| Oe. *laevifolia,* de Vries | Gates, 1909 | 14 |
| Oe. *brevistylis,* de Vries | Gates | 14 |
| Oe. mut. *lata,* de Vries (see Fig. 37, p. 107) | Lutz, 1912[1]; Gates, 1912; (Jates and Thomas, 1914 | 15 |
| *Oe.* mut. *semilata,* Gates (see Figs. 38 40, pp. 108 113) | Gates and Thomas, 1914[s] | 15 |
| Oe. mut. *incurvala,* dates (♀J) (see Figs. 50, 57, pp. 148-9) | N. Thomas, 1914 | 15 |
| Oe. *biennis* mut. *lata,* Gates (see Fig. 60, p. 155) | Gates and Thomas, 1914 | 15 |
| Oe. *lata rubricalyx* | Gates and Thomas, 1914 | 15 |
| *Oe. biennis setnigigas,* Stomps | Stomps, 1912 | 21 |
| Smaller-flowered offspring of *gigas* ("1*J 1.4) | Gates and Thomas (one plant) | 27 |
| Narrow-leaved offspring of *gigas* (^.P) (see Fig. 53, p. 129) " | Gates (one plant) | 27 or 28 |
| Mutant from *lata* selfed | Lutz, 1912 | 22 |
| Oe. mut. *gigas* x *lata rubricalyx* (^) (see Figs. 74-75, p. 191) | Gates and Thomas (one plant) | 22 |
| Oe. **mut.** *rubricalyx* x *gigas* (}J) (see Figs. 76-77, p. 193) | Gates and Thomas (one plant) | 21 |
| Offspring of *lata* x *gigas* | 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 *hia* x *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* x *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, wnile in plants a Zofo-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 jfef.

*yranulosus* 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
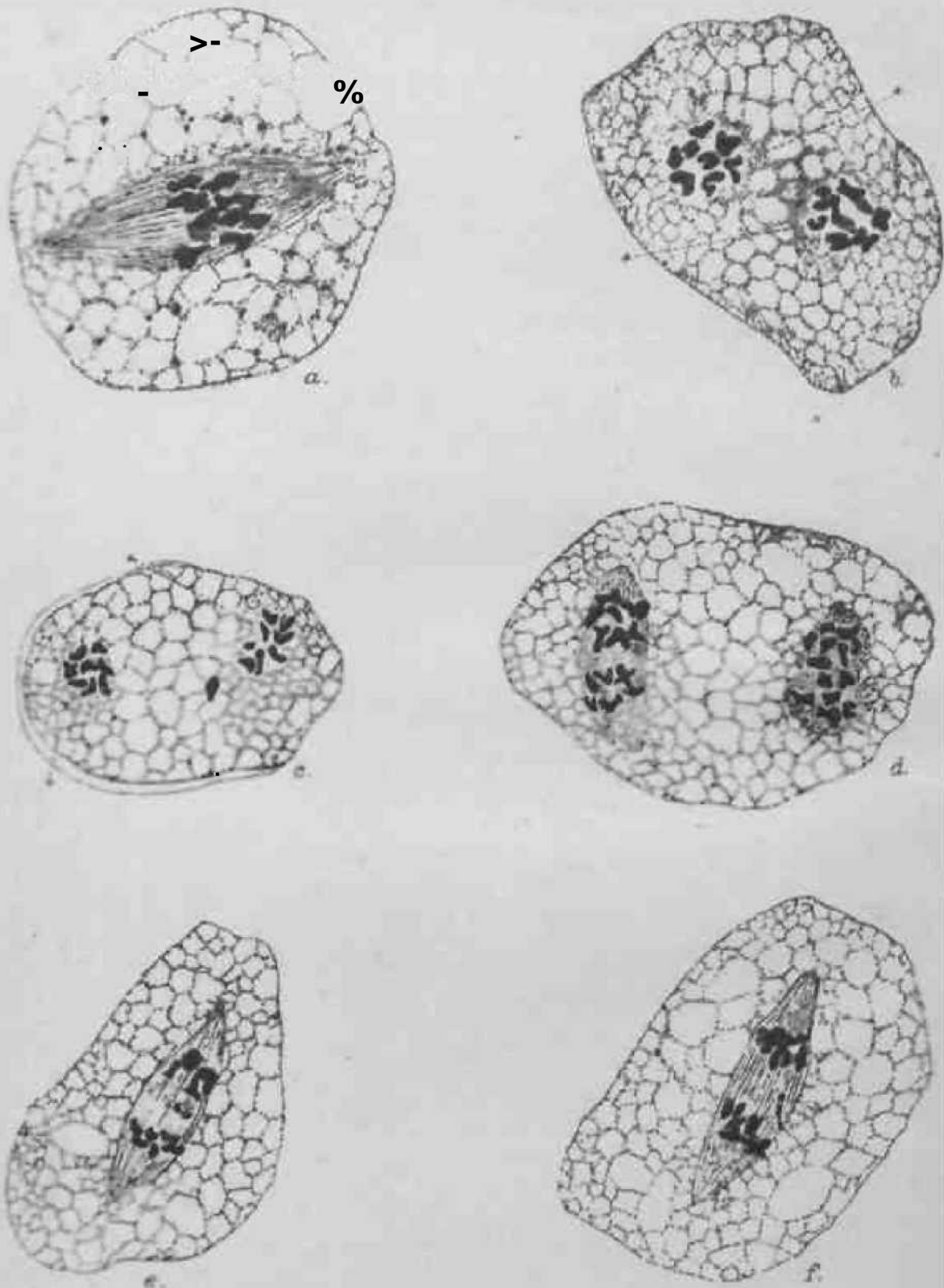
**Fig 70**

Meiotic divisions in the pollen mother cells uf *[a) Qt> rubrirafyx sinii* (*b–f*) *Oe. lata rttbriatfyx* from the *Qtturt, Jcunt. Aticr. Set.*

(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, 6, 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, 6, c, 71, a,'d₉ 72, 6, 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, / ) ; (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, 6, *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 \ chromosome *(s),* showing that the extra chromosome split in the first meiotic division.

The same, showing 7£ chromosomes in the left-hand group, and in the right-hand group 6 whole chromosomes, a \ chromosome («) and a small fragment. The 15th chromosome is in the cytoplasm between the two nuclei.

«• 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.

*c-h* 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 Hpindle 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. ScL,* after Miss N. Thomas, x 1930.

chromosomes are not infrequently left behind to degenerate on the heterotypic and homotypic spindles (Figs. 70, *c, e, /,* 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. hi such cases the individuality of certain chromosomes is probably not strictly maintained, and this may be a source of variation in the *hta-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.   *Triflovly*

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

FIG. **71.-** *Oe. bienni/t Uita₉* I'OLI<KN MOTHKIJ CKLLN.

a. **Uutorotypic spindle, .allowing 14 chroi nonunion. The 15th is on the next section. Several of the chromosomes axe 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 \ chromosome ; the upper group contains 6 whole and a \ chromosome. Hence in the heterotypic mitosis one chromosome split and another was distributed to the wrong nucleus.—From *Quart. Journ. Mlcr. Sel.,* after Miss N. Thomas,   x 1930.**
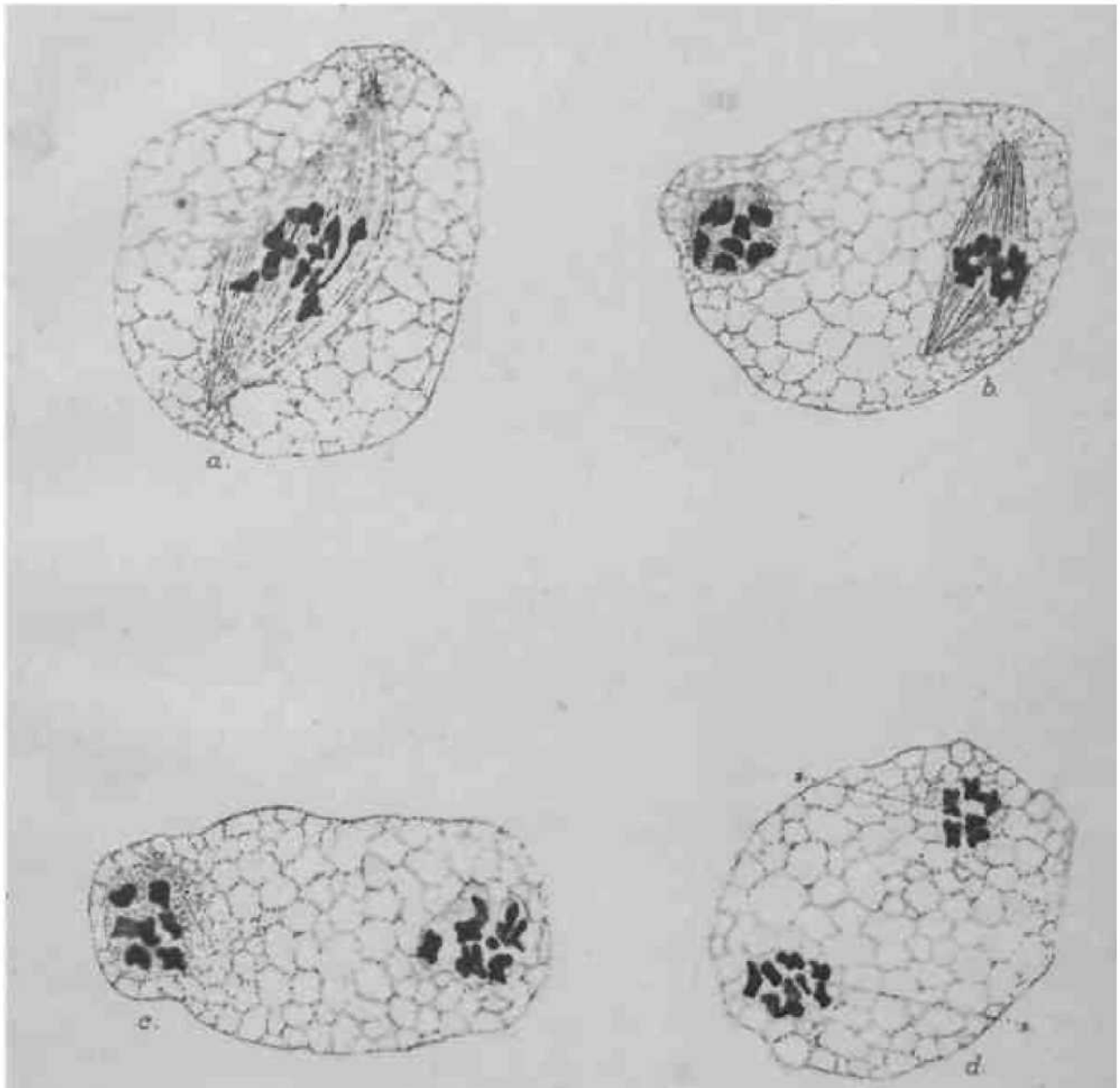
Fig. 71.

Meiotic divisions in Itie pollen mother cells o{ (V. Ar>«*tf *tufa*. from Ihc (J«^/, *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 3» 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* $_9$ 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* x
*gigas*.  It is possible that such plants come from the
iipogamous 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. **7 2L—MUTANTS KEKEMBLINC;** *Oe. lata,* **POLLEN MOTHEII CELLS.**

*a.* Normal heterotypic spindle, showing 15 chromosomes in their
usual scattered arrangement.
*b.* Heterotypic anaphase showing 9 cliromosomes moving to one pole
and 5 to the other:   The fifteenth chromosome has been pulled
into two parts, leaving a trail of cliromatin between them.
*c.* This spindle has been cut, but it shows two chromosomes pulling
apart and losing some of their chromatic substance.   The chromo-
somes are much smaller than normal.
*d.* Homotypic metaphase showing in the upper group 7J chromosomes,
in the lower group 6J, and between the groups several fragments
which together constitute the 15th chromosome, which was left
behind on the heterotypic spindle. - -From *Quart. Journ. Micr. ScL,*
after Miss N. Thomas,   x 1930.
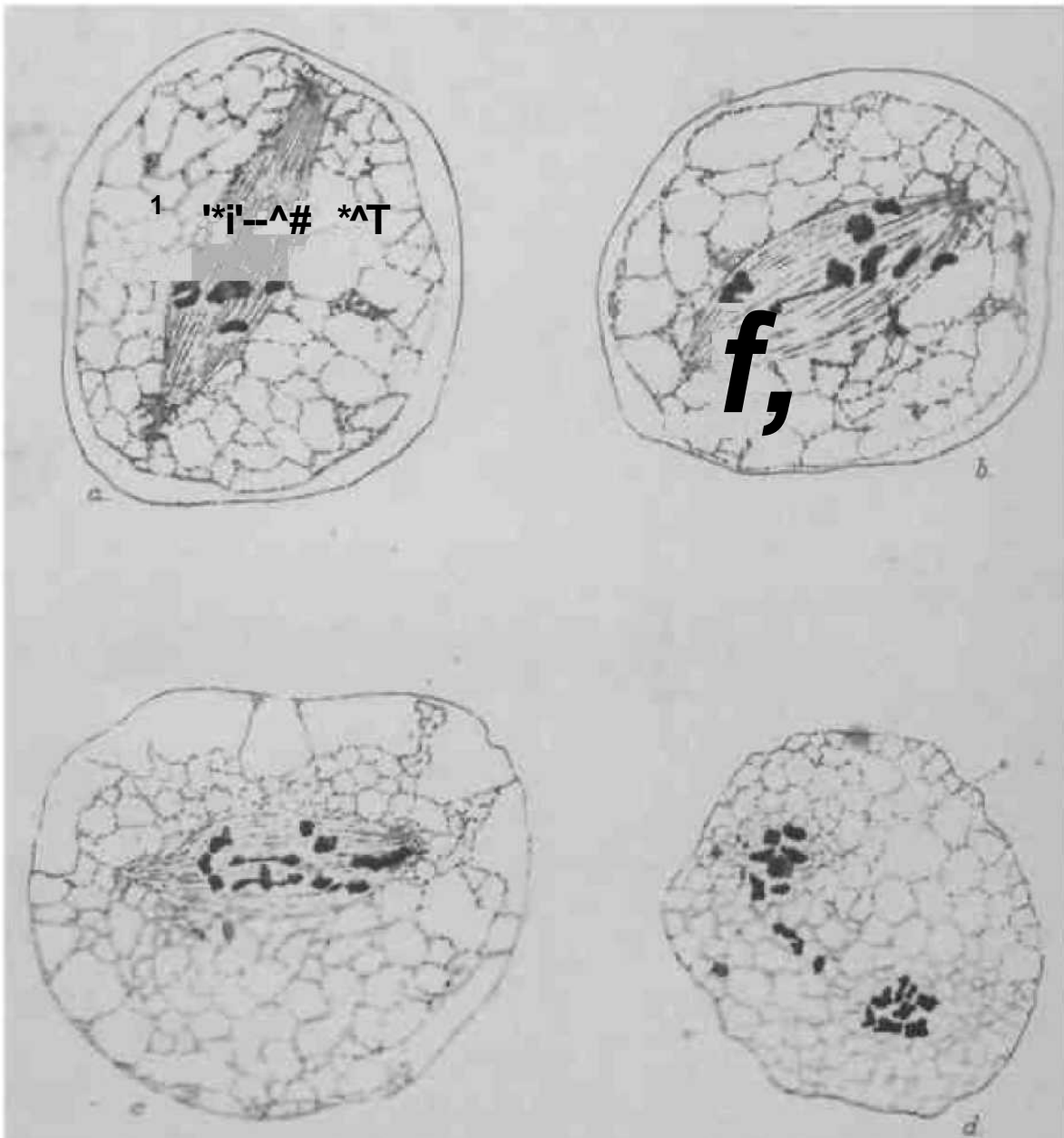
Fig. 72.

Meiotk tJimiont in A*/U-)iku mutants from Sweden, ... ui the *Qtitwi. Ji-ttrn, fffpr, ;i...*

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, (6) from 8 4- 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 seema fairly strong evidence, although it is at present indirect, that diploid eggs occur both in *lata* and *Lainarckiana,* and that they can be fertilised.

The plant having 20 chromosomes, in the $F_x$ of *lata*  x *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*  x *lata rubricalyx* (see p. 191), doubtless came from 14? + 8£ 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, 6) 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* x *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* x *gigas*.

*a.* A homotypic spindle showing 11 bivalent chromosomes.
*b.* Homotypic metaphase, showing 10 + 11 chromosomes.
*c.* Homotypic telophaso; two of the nuclei contain 10 chromosomes each, and one chromosome is left behind on the spindle.
*d.* Homotypic metaphase in *gigas* x *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.
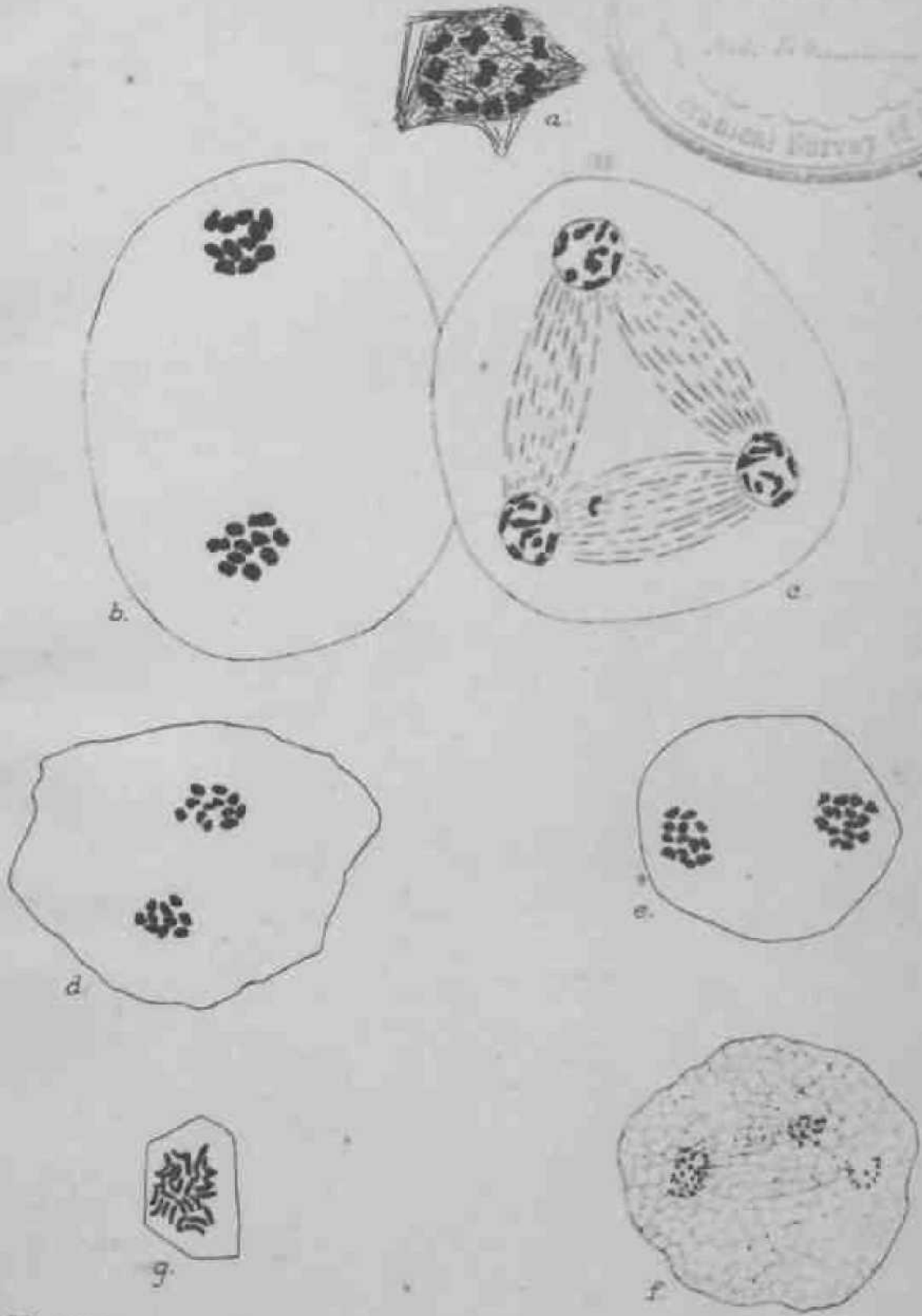
Meiotic divisions *(a-f)* in *Ot. fata* XJJ^WJ. *(tJ)* in *gigas x lata rubricalyx*,
and *(e-g)* in certain ·j^f«J raos* The figures are unequally magnified.
*Figs. a-c AT\** from the *Botanical Gasette.*

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 *lota* x *giqas* 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, !t 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 Pygsera 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* x *lota 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 IOtshrom6»0itHs&&nd 12 groupft having i_ tdtrofjiri-ttdmee each. The greater numlier nf uVs *may* have been produced by chromosomes being Jt^ft nut of the hetero-typic telophaw. In only a aingle c&Sfi was a Hoar count of tt group uf 11 chromosomes made, although PIX doubtful cases iiwc observed- In one clear Mwt* 13 chromosanws were found in the daughter nttcloua, ami in another (not in the santfl cell) tone, tha oorresporwiing groups not being cou.nt«l>)«. N«>t tsfz*quBnt£y otaa i«r twa chromosomes were left hehirul *nn tht-* heteitrtypic nr homotypio spindles, :tml in th** latter cswe tiifv frequently appeared to be degenerating.

\ M-ries of uther bt€^alarities were observed, similar to those aln-^ilv meniicmet) (p. ifiS). Thin one daughfc nuHeiH in mtericinesiB DQntahted only fii chromosomes, anrl one hunuotypfc mctatphftfio pdascHaed JA chromosomes, allowing thai oertaan cihixzraasamcs satEwtames ciplit an the beterotypic spiudle just si in /'*/'' farms, Chiomoeomie* are mofe fi>'i|u<'ntlv k>ft behind nn the tuanofrypic titan the hetep-typi( Kpiodle, HIKI several rasra wure eonntod in which imly nine chromoiomes bud entered the homotypi telopha^*. Henri[1] ire conclude that *a* CODSderubk tiuml«»r of the pollen jrniins will contain only nine chromoflomes ahhougli tho niajurity will probably conttftn 10, 11, or 12.

*te* already pointed out, the *2*2* chromosomes of tihia nn]ivuliLJil were prohubly derived, eiglii of them From *fata* *,MK\* 14 *fnmi gigaA,* uml there id no abviww rt'uson why T!he heterotypit' sejyfrvgiUii>n slunihl )w u^tiullv 10 + 12. Comparit>on <>f thw behaviour with that *if other 22-chTOino* ome pUnto will \*e nei-CANirv before it will Iw (Hwsilite to interpret this rfMiiIt further, but in miy case it nrould aeem thai the [iluMiii cootek in a geoenJ way the distribution which take plait*, anil there is BO evkitnoe at all that tlic iliiution bears any definite relation *to* the source of the clirouiosonit^- /.*.. whether from *fata* or *pupm.* Of course this result might be anticipated, since the extra

rhromoHorrm of *faht* is merely .» duplicate "f ›»n‹[4] ••! tl others, probably wit html any rlmiig*[1] in ttu properties, ami similarly the //wo* chromosomes **appeal** to **be** it erely a double set of the *Ijmnarckiam* bodies. The relation between the chromosome number and the morphology of the pollen grainy in this plant will \w con£dexed on p, 2\A
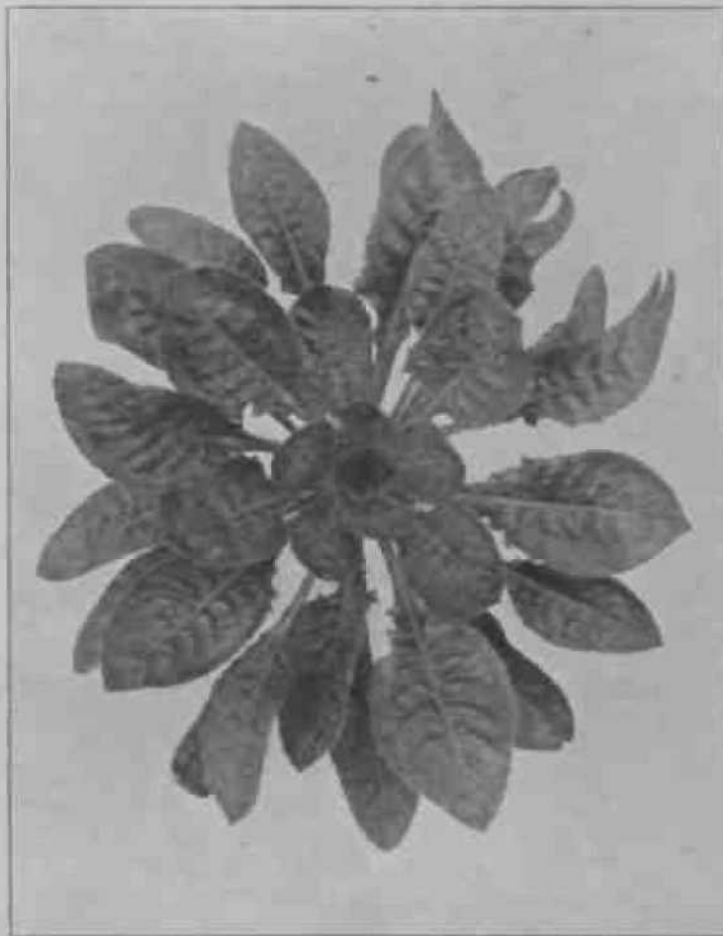


*Fu.. ~4.—* Rosette of *gigas × lata rubricalyx* (22 chromo^HUCft).

The plant of which the chnimugoiue **behaviour** i^ described in ih*» last two parugrapha, was the ouly one which developed from inir «-rosa ,71l70$ x ia/a *rubncalyr,** The rosette & shown in Fig. 74, and the u|Jj>er part of th? flowering plant in Fig, 75. They show a striking тсsv m**blaaoe** *to gitjan {cf.* Figa. 43—15, pp. Ufl-123), though **there** are conspicuous differences, particularly in the full-grown

|il,mi. Tbuo nisH.lv resembled ilu- Bwedish giant mom than tiled* Vrieai&n feypd, hiving busd jugs *w* the leaves. Since the *Inta nthriwhjx* parent contained *grandiflora* as one of ita ancestors, WP an* inclined to believe that the Sweiiisl» nice of *iMttmrrkitiutt* liiis been derivpd through crossing <*f tin- original *ijamarcMam* with *grandiflora.*

\u. ?>. — Ov. gigas × lata ...telkialye.
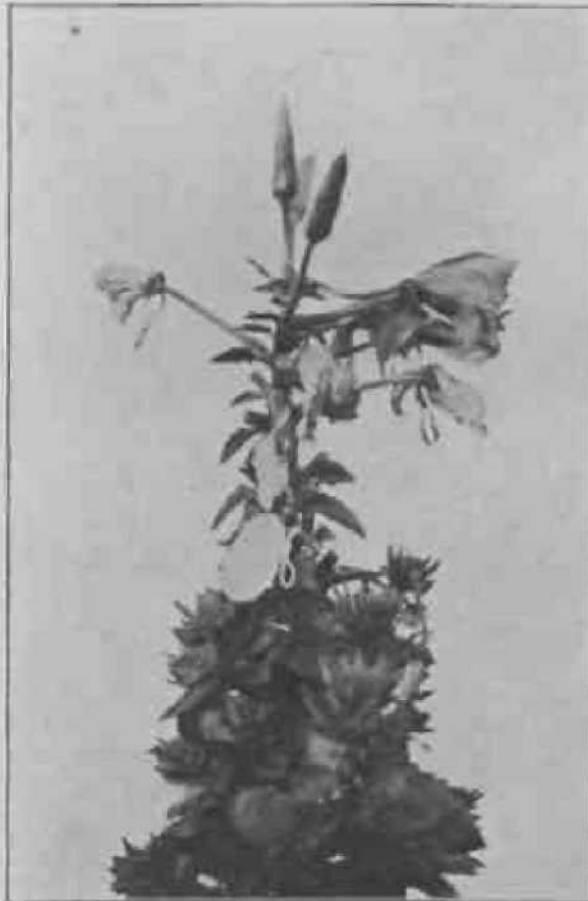
especially as other lacti^ point to the stime conclusion, The stem of the above plant WOK clenfwly olothetl with leaves; the buds large, having &*[>»1A with red OOloui pattern 7 AnrJ red blotches on tlio hypuiithium ; the leiives with pink midrilu and sermted margins. The flower dimensions were us follows : petals, 4il Dim. long x 71 mm. broad, ikrk yellow ; f»v«.ry, 14-19 mm. fong ; livpanthium, 52-57 mm. $\m\g_t$ 4r4*5 mm. in liimneter; hurl cone,

45 jura, long, 12-13 mm. in diameter at base ; scpnl tips, 4-5 mm. long. The capsules **were remarkably square,** and not contracted at the top. The plant thus resembled *ijiifits* more than *rubrimlyx* in all features except pigmentation which was intermediate- For the pollen grains, seo p. 513.

In Figs* 76 imcl 77 ai"c shown photographs of a plant
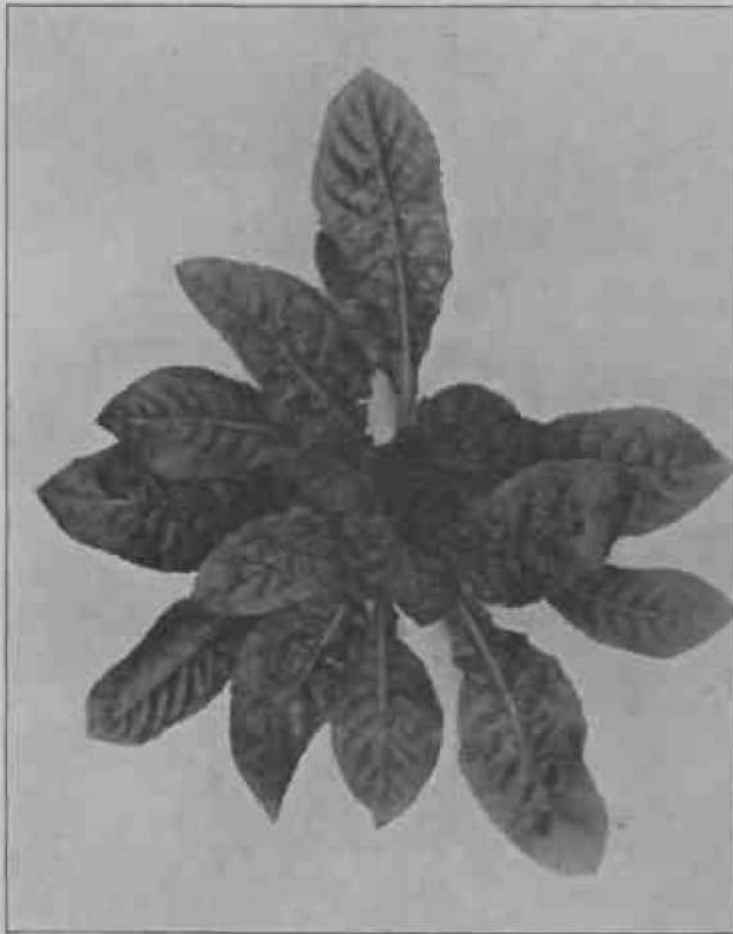


Fig. 76-—**RW«tt».ol** *rubrivalyx* ∴ *gigas*
(21 chromosomes).

from *ruhrivalyx* X jrujraj, **having** 21 chromosomes. The rosette and the liowtij ing shoot resembled *tfu/ns [cf*\* Figs, 74 and 75) ; the buds were red as in *rtibritalyx,* but pale. This plant was afterwards potted **in** the greenhouse and tth'ii cut back. **Several** shoots which subsequently fieve-tojjotl resembled *m* foliage the parent plant, but oiw- **braaob**

wa-, **much** nearer *Lamartki<ma* **mul** another intermediate, In tin* Utter branches a lots of **chromowmrt** liml **probably** tak^n plat*.

It is clear that triploidy leads **bo tike prodactaon** of **many** tu_-w rhromo-iwmc-Qiimlwrs,, through the irregularities it introduces into the meiotic phenomena. All these irregu-



Fig. 77.—Oe. rubricalyx × gigas.

lnritics are germinal change *{>ar* fvro&nce, but only a jM>rtiun of tht'iii is capable uf giving riite **to** vinhk ii.-rm **cells.** It is at present unknown **whetlw** the UUJHIKT alone determines Uif vialiilitv. *tT* **wfaetbei** jMrtinilar **chcomo-** some i njiihitiMtiou^ will, owing t« inri>ittpHtil>ility. f«il to produce an embryo After fortillation. It ia **conceivabfe** tluit the fonnation <f **boampfttibte** I-^TII hi nations **withoal** change ol tiumfwr in **tiw 14-chrotDOMiirw** Oenotheras

(allowed by the loose pairing in nieiosis), 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 Gregory[1] (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 ta.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. |
|---|---|---|---|---|
| | | *x* | *2x* | |
| SEED PLANTS. | | | | |
| *Potentilla rupestris* | — | 8 | 16 | Forenbacher.1914[1] |
| *P. sylvestris* ... | — | 16 | 32 | Forenbacher,1914 |
| *P. anserina* ... | — | 16 | 32 | Forenbacher,1914 |
| *P. reptans.* .... | — | 16 | 32 | Forenbacher,1914 |
| *Alchemilla atoensis* | Fertilised ... | 16 | 32 | Murbeck, 1901 |
| *A. grossidens* ... | Fertilised ... | 16 | 32 | Strasburger, 1904 |
| *A. gelida* ...... | Fertilised ... | 16 | 32 | Strasburger, 1904 |
| *A. pentaphylla* ... | Fertilised ... | 32 | 64 | Strasburger, 1904 |
| *Eualchemilla—* | | | | |
| *A. acutangula* ... | — | 32 | 64 | Murbeck, 1901 |
| *A. apedosa* ... | Apogamous ... | 32 | 64 | Strasburger, 1904 |
| *A. splendens* ... | — | 32 | 64 | Strasburger, 1904 |
| *A.fallax* ...... | Apogamous ... | 32 | 64 | Strasburger, 1904 |
| *A. micans.* ...... | Apogamous ... | 32 | 64 | Strasburger, 1904 |
| *Antennaria dioica* | Fertilised ... | 12—14 | 24—28 | Juel, 1900 |
| *A. alpina* ...... | Apogamous ... | — | 45—50 | Juel, 1900 |
| *Hieracium venomm* | Fertilised ... | 7 | 14 | Rosenberg, 1907 |
| *H. auricula* ... | Fertilised ... | 9 | 18 | Rosenberg, 1907 |
| *H. umbellatum* ... | Fertilised ... | 9 | 18 | Juel, 1905 |
| *H. excellens...* { | Partly apogamous and aposporous | 17 | 34 | Rosenberg, 1907 |
| *H.flageUarc* ... | Apogamous ... | 21 | about 42 | Rosenberg, 1907 |
| *Taraxacum confertum* ... ... | — | 8 | 16 | Rosenberg, 1909 |
| *T. officinale...* ... | — | 12—13 | 26—30 | Juel, 1905 |
| *Droaera rotundifolia* ... ... | Fertilised ... | 10 | 20 | Rosenberg, 1903 |
| *D. longifolia* ... | Fertilised ... | 20 | 40 (smaller) | Rosenberg, 1903 |
| *Crepi8 virens* ... | Fertilised ... | 3 | 6 | Rosenberg, 1909, Dieby, 1914 |
| *C. tectorum* ... | — | 4 | 8 | Juel, 1905 |
| *C. taraxacifolia* ... | — | 4 | 8 | Digby, 1914 |
| *O. lanceolata* var. *platyphyllum* ... | — | 5 | 10 | Tabara and Ishikawa, 1912 |
| *C.japonica* ... | — | 8 | 16 | Tahara, 1910 |
| *Saxifraga sponhemica* ...... | — | 15 | 30 | Pace, 1912 |
| *8, granulata* ... | — | 30 | 60 | Juel, 1907 |
| *Dahlia coronata* ... | — | — | 32 | Ishikawa, 1911 |

**For the references see generai bibliography.**

"FABLE **XIII.**—*contd.*

| Name. | Reproduction. | Chromosomes. | | Author. |
| | | x | 2x | |
| --- | --- | --- | --- | --- |
| SEED PLANTS. | | | | |
| *D. variabilis* (nine varieties) | — | — | 64 | fshikawa, 1911 |
| *Thalictrum minus* | Fertilised ... | 12 | 24 | Overtoil, 1909 |
| *T. purpurascens* | Apogamous ... | 24 | 48 | Overton, 1909 |
| *Rosa livida*[1] ... | Fertilised ... | 8 | 16 | Strasburger, 1904 |
| *R. cinnamomea* ... | Fertilised ... | 8 | 16 | Strasburger, 1904 |
| *R. canina* (many forms) | Fertilised ... | 8 | 16 | /Strasburger, 1904 V Rosenberg, 1909 |
| *R. canina pertsaticifolia* | Apogamous ... | 16—17 | 33—34 | Rosenberg, 1909 |
| *R. glauca* (one form) | Apogamous ... | 16–17 | 33–34 | Rosenberg, 1909 |
| *Rumex Acetom* ... | Apogamous ... | 8 | 16 | Roth, 1906 |
| *R. hispanicus* ... | Apogamous ... | 8 | 16 | Rcfth, 1906 |
| *R. arifoliuu* ... | Apogamous ... | 8 | 16 | Roth, 1906 |
| *R. nivalis* ... | Apogamous ... | 8 | 16 | Roth, 1906 |
| *R. scutatus*[2] ... | — | (12) | 24 | Roth, 1906 |
| *R. Acetosella* ... | Apogamous ... | (16) | 32 | Roth, 1906 |
| *R. cordifolinv*[4] ... | — | (40) | 80 | Roth, 1906 |
| *Wikstroemia canescens* ... | Fertilised ... | 9 | 18 | Strasburger, 1910 |
| *r. indica* ... | Apogamous ... | 26 | 26—28'" gemini. | (Winkler, 1906; I Strasburger, 1910 |
| *Houttuynia cordabt* 'l'arthenogcnctic | — | | 52—56 | /Shibata and \Miyake, 1908 |
| *Daphne alpina* ... | Fertilised ... | 9 | 18 | Osawa, 1913 |
| *t). mezereum* ... | Fertilised ... | 9 | 18 | Strasburger, 1909 |
| *t). pseudo-me?ereum*[1] | Fertilised ... | 0 | IS | Osawa, 1913 |
| *I), kiusiana* ... \ | Fertilised ... | 9 | 18 | Osawa, 1913 |
| *D. odora.* .... | Sterile ... ... | 14 | 28 | Osawa, 1913 |

[1] Stratiburger points out that the genus Rub us 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.

[1] 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.

* 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 *Houttouynia cordata.* another member of the *Balanophoraceae,* is tetraploid in comparison with If. *indica.*

**TABLE XIII.**—*contd.*

| Name. | Reproduction. | Chromosomes. | | Author. |
|---|---|---|---|---|
| | | $x$ | $2x$ | |
| SEED PLANTS. | | | | |
| *Morus indica* ... | — | 14 | 28 | **Tahara, 1910** |
| *M. alba* var. *Roso* | — | 14 | 28 | **Tahara, 1910** |
| *M. alba* var. *Shiro-WO8G* . . . . . . | — | 17 | 40—50 | **Tahara, 1910** |
| *Funkia ovata* ... | Fertilised ... | 24 | 48[1] | Sykes, **1908** |
| *F. Sieboldiana* ... | Fertilised ... | 242 | 48 | Strasburger,1899 Sykes, **1908;** Miyake, **1905** |
| *Gyro8tachy8 gracilis* | — | 15 | 30 | Pace, **1914** |
| *0. cernua* . . . . . . | — | 30 | 60 | Pace, **1914** |
| *Oenothera Lamarck-iana*. . . . . . . . | Fertilised ... | **7** | 14 | (Geerts, **1907** ; I Gates, **1907** |
| *Oe. gigas* . . . . . . | Fertilised ... | 14 | 28 | /Lutz, **1907;** I Gates, **1908** |
| *Hordeum distichum* | Self-pollinating | 7 | 14 | Nakao, **1911** |
| *Secale cereale* ... | Self-pollinating | 8 | 16 | Nakao, **1911** |
| *Triticwn vulgar e*... | Self-ppllinating | 8 | 16 | E. Overton, **1893;** Koernicke, **1896;** Nakao, **1911** |
| *T. dicoccoides* ... | Self-pollinating | 8 | 16 | **Bally, 1912** |
| *Aegilops ovata* ... | Self-pollinating | 16 | 32 | **Bally, 1912** |
| *Primula floribunda* | Fertilised ... | 9 | 18 | **Digby, 1912** |
| *P. verticillata* ... | Fertilised ... | 9 | 18 | **Digby, 1912** |
| *P. verticillata* X *P. floribunda* ... (=*P. verticillata* | Fertilised ... | 9 | 18 | **Digby, 1912** |
| -*P. Kewensis* (type) (=*p.floribunda verticillata*) | Self-sterile (no pin-flowers) | **9** | 18 | **Digby, 1912** |
| P. *Kewensis* (seed-ling) (from a pin-flower) [6] | Fertile ... | 18 | 36 | **Digby, 1912** |
| **P. Kewenai8 jari-**nosa (by selec-tion) | Fertile ... ... | 18 | 36 | **Digby, 1912** |
| **P. Keivensis fari-**no8a (from P. verticillata x P. floribunda isa-bellina) | Fertile ... ... | 18 | 36 | **Digby, 1912** |

[1] **This number is tetraploid as compared with many other Liliaceai, 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 account* for the failure of the original P. *Kewensis* to set seed***

TABLE XIII.—contd.

| Name. | Reproduction. | Chrome•somes. | | Author. |
|---|---|---|---|---|
| | | X | 2x | |
| **SEED PLANTS.** | | | | |
| P. *floribunda isa-bellina* X P. *Kewensis* (type) (=P. *floribunda isabellina* F₁) | Fertile ...... | 9 | 18 | Digby, 1912 |
| P. *Kewensis* (type) X P. *floribunda isabellina* | Sterile ...... | — | — | Digby, 1912 |
| P. *floribunda isa-bellina* x P. *Kewensis* (seed-ling) ( = P. *floribunda isa-bellina,* F,) | Fertile ...... | 9 | 18 | Digby, 1912 |
| PrimwZa *sincnsw* | Fertile ...... | 12 | 24 | Gregory, 1914 |
| PnmieZa *sinensis* giant race. | Fertile ...... | 24 | 48 | Gregory, 1914 |
| *Musa sapientum* var. "Dole" | Sterile ...... | 8 | 16 | Tischler, 1910 |
| M, *sapientum wax.* " *RodjahSiam*" | Sterile ... | 16 | 32 | Tischler, 1910 |
| M. *sapientum* var. "Kladi" ... | Sterile ...... | 24 | 48 | Tischler, 1910 |
| *Viola glabella,* Nutt | — | 6 | 12 | Miyaji, 1913 |
| F. *phalacrocarpa,* Makino ...... | — | | | Miyaji, 1913 |
| F. *grypoceras,* A. Gray ...... | — | 10 | 20 | Miyaji, 1913 |
| F- *verecunda A.Gray* | — | io | 20 | Miyaji, 1913 |
| F. *nipponica,* Maxim | — | 10 | 20 | Miyaji, 1313 |
| F. *Okuboi,* Makino | — | 12 | 24 | Miyaji, 1913 |
| F. *Okuboi,* var. *glabra* Makino... | — | 12[1] | 24 | Miyaji, 1913 |
| V. *japonica,* Langsd | — | 24[2] | 48 | Miyaji, 1913 |
| F. *patrini,* D.C.... | — | 36(?) | 72(?) | Miyaji, 1913 |
| **BRYOPHYTE3.** | | | | |
| *Mnium fiornum* ... | Normal ... | 6 | 12 | M. Wilson, 1911 |
| ikf. *homurti bivalens* | Aposporous ... | 12 | — | Él. and Ém. , Marchal, 1911 |
| *Bryum capillare* ... | Normal. . . . . | 10 | 20 | Él. and Ém. , Marchal, 1911 |
| 5. *capillare bivalens* | Aposporous ... | 20 | — | Él. and Ém. Marchal, 1911 |
| *Amblystegium ser-pens* ...... | 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. |
|---|---|---|---|---|
| | | *x* | *2x* | |

<table>
<tr><td colspan="5" align="center">BRYOPHYTES.</td></tr>
<tr><td><i>A. serpens bivalens</i></td><td>Aposporous ...</td><td>24</td><td>48[1]</td><td>Él. and Ém. Marchal, 1911</td></tr>
<tr><td><i>A. irriguum</i> ...</td><td>Normal . . . .</td><td>.12</td><td>24</td><td>Ém. Marchal, 1912</td></tr>
<tr><td><i>A. riparium</i> ...</td><td>Normal ... ...</td><td>24</td><td>—</td><td>Ém. Marchal, 1912</td></tr>
<tr><td colspan="5" align="center">PTEBIDOPHYTES.</td></tr>
<tr><td><i>Scolopendrium vulgare.</i> . . . . . . . .</td><td>—</td><td>32</td><td>64</td><td><b>Stevens, 1898</b></td></tr>
<tr><td><i>Cystopteris fragilis</i></td><td>—</td><td>32</td><td>64</td><td><b>Stevens, 1898</b></td></tr>
<tr><td><i>Pteris aquilina</i> ...</td><td>—</td><td>32</td><td>64</td><td><b>Stevens, 1898</b></td></tr>
<tr><td><i>Alsophila excelsa</i></td><td>—</td><td>about 60</td><td>—</td><td><b>R. P. Gregory, 1904</b></td></tr>
<tr><td><i>Nephrodium molle</i></td><td>Fertilised ...</td><td><b>64 or 66</b></td><td>128or132</td><td><b>Yamanouchi, 1908</b></td></tr>
<tr><td><i>Nephrodium molle</i></td><td>Induced apogamy</td><td>64 or 66</td><td>64 or 66</td><td><b>Yamanouchi, 1908</b></td></tr>
<tr><td><i>Athryium Filix-foemina.</i> . . . . .</td><td>Fertilised ...</td><td>38—40</td><td>76—80</td><td>Farmer <b>and Digby, 1907</b></td></tr>
<tr><td><i>A. F.</i> var. <i>clarissima,</i> Bolton ...</td><td>Aposporous and apogamous</td><td>84</td><td>84</td><td><b>Farmer and Digby, 1907</b></td></tr>
<tr><td><i>A. F.</i> var. <i>clarissima,</i> Jones ...</td><td>Aposporous and apogamous</td><td>90</td><td>90</td><td><b>Farmer and . Digby, 1907</b></td></tr>
<tr><td><i>A. F.</i> var. <i>unconglomeratum,</i> Stansfield</td><td>Aposporous and apogamous</td><td>100</td><td>100</td><td><b>Farmer and Digby, 1CX7</b></td></tr>
<tr><td><i>Lastrea pseudo-mas</i></td><td>Fertilised ...</td><td>72</td><td><b>144</b></td><td><b>Farmer and Digby, 1907</b></td></tr>
<tr><td><i>L.p.</i> var. <i>polydactyla,</i> Wills ...</td><td>Apogamous and aposporous</td><td>64—66</td><td><b>132</b></td><td><b>Farmer and Digby, 1907</b></td></tr>
<tr><td><i>L.p.</i> var. <i>polydactyla,</i> Dadds ...</td><td>Apogamous ...</td><td>90(?)</td><td><b>130(?)</b></td><td><b>Farmer and Digby, 1907</b></td></tr>
<tr><td><i>L.p.</i> var. <i>cristata apospora,</i> Druery</td><td>Apogamous and aposporous</td><td>60</td><td><b>66(?)</b></td><td><b>Farmer and Digby, 1907</b></td></tr>
<tr><td><i>MarsiUa vestita</i> ...</td><td>Fertilised ...</td><td>16</td><td><b>32</b></td><td>Strasburger, 1907</td></tr>
<tr><td><i>M. quadrifolia</i> ...</td><td>Fertilised ...</td><td>16</td><td><b>32</b></td><td>Strasburger, 1907</td></tr>
<tr><td><i>M. data</i> ... ...</td><td>Fertilised ...</td><td>16</td><td><b>32</b></td><td>Strasburger, 1907</td></tr>
<tr><td><i>M. hirsute,...</i> ...</td><td>Fertilised ...</td><td>16</td><td><b>32</b></td><td>Strasburger, 1907</td></tr>
<tr><td><i>M. Drummondii</i> ...</td><td>Apogamous ...</td><td>32</td><td><b>32</b></td><td>Strasburger, 1907</td></tr>
<tr><td colspan="5" align="center">ANIMALS.</td></tr>
<tr><td><i>Ascaris megalocephala univalens</i> i</td><td>Sexual ... ...</td><td><b>1</b></td><td><b>2</b></td><td><b>Boveri, 1887</b></td></tr>
<tr><td><i>A.m. bivalens</i> ...</td><td>Sexual ... ...</td><td><b>2</b></td><td><b>4</b></td><td><b>Boveri, 1887</b></td></tr>
</table>

[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 | 2x | |
| | | ANIMALS. | | |
| A. lumbricoides univalens...... | Sexual ... ... | 12 | 24 | Boveri, 1887 |
| A.I. bivalens ... | Sexual ... ... | 24 | 48 | Boveri, 1887 |
| Styelopsis ...... | — | — | 8 or 4 | Julin(361) |
| Planaria ....... | — | — | 6 or 3 | Stevens(361) |
| Helix pomatia ... | — | — | 48 or 24 | — |
| Echinus microtuher-culatus ...... | — | 9 | 18 | Boveri, 1888 |
| K. microtubcrctila-} tUfi. ....... j | — | 18 | 36 [ | Boveri, 1902 and Stevens, 1902 |
| Asterias vulgar is | — | 9(♂) | 18 | Tennant, 1907 |
| A. Forbesii\t) ... | - - | 18 | 36 | Tennant, 1907 |
| Artemia salina, fromCagliari ... | Sexual ...... | — | 42 | Artom, 1911 |
| A. salina, from Capodistria ... | Parthenogenetie | — | 84 | Artom, 1911 |
| Cyclops strenuus | COPEPOUA ... | 11 | 22 | Braun, 1909 |
| G. insignia...... | ,, | 11 | 22 | Braun, 1909 |
| C. bicuspidotus ... | ,, | 9 | 18 | Braun, 1909 ; Chambers, 1912 |
| C. bicuspidtUus var. odessana...... | ,, | 9 | 18 | Braun, 1909 |
| C. Dybowskii ... | ,, | 9 | 18 | Braun, 1909 |
| C. fuscus..... I | ,, | 7 | 14 | Braun, 1909; Chambers, 1912 |
| C. alhidus ... | ,, | 7 | 14 | Braun, 1909; Chambers, 1912 |
| (. LeuckarU ... | ,, | 7 | 14 | Braun, 1909 |
| C. serrukttius ... , | ,, | 6 }-2m. i | 12 + 2m. | Braun, 1909 |
| C. phaleratus ... | ,, | 6 + lh. | 12+lh. | Braun, 1909; Chambers, 1912 |
| C. viridis ...... | ,, | 6 | 12 | |
| C. viridis var. parcus Herrick | ,, | 3 | 6 | Chambers, 1912 |
| C, viridis var. a/nericanus, Marsh | ,, | 5 | 10 | Chambers, 1912 |
| C. viridis war. brevi-spinosus ... | ,, | 2 | 4 | Chambers, 1912 |
| C. modestus...... | ,, | 4 | 8 | Chambers, 1912 |
| C. diaphanus ... | ,, | 6 | 12 | Braun, 1909 |
| C. prasinus ... | ,, | 5+lm. | 10+lm. | Braun, 1909 |
| C. di8tinctus ... | ,, | 5+lh. | 10+lh. | Braun, 1909 |
| C. vernalis...... | ,, | 5 | 10 | Braun, 1909 |
| C. gracilis ...... | ,, | 3 | 6 | Braun,1909 |
| Harmostes reflexulus | HEMJPTERA ... | 7 | 14(9) | Montgomery, 1901 |
| Protenor belfragei | ,, | 7 | 14(9) | Montgomery, 1901 |

[1] m stands for microchromoaome == 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. |
|---|---|---|---|---|
| | | x | 2x | |
| **ANIMALS.** | | | | |
| *Leptocoris trivittatus* | HEMirTEKA ... | 7 | 14(♀) | Wilson, 1909 |
| *Chariesterus antennctior* | „ | 13 | 26(9) | Wilson, 1909 |
| *Gorynocoris distinctus* | „ | 13 | 26(?) | Wilson, 1909 |
| *Homo sapiens—* | | | | |
| Negro | — | — | 22(♂) 24(?)(♀) | Guyer, 1910,1914 Montgomery, 1912 |
| White | — | — | 47(♂) 48 m | von Winiwarter, 1912 Farmer, Moore and Walker, 1906 |
| | | | 32 | Wieman, 1913 |
| | | | 33—38[1] | |

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 Rosaceae 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 arè 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 F. *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. phahcrocarpa* the number is 24, while in the closely related and somewhat

stouter F. *japonica* the number is 48—hence tetraploid **in comparison with F. *phalacrocarpa. · V. Patrini,* which** has about 72 chromosomes, is again much larger than F. *japonica.* Compared with F. *ghbelh,* however, F. *japonica* is octoploid *(8x)* and F. *Patrini* dodecaploid (12#). The figures of Miyaji show, moreover, that the chromosomes in F. *japonica* are twice as large as in **F. *Okuboi* var. *glabra,* while in F. *grypoceras (2x = 20)*** they are more than twice as large as in F. *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 arc 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 interest'ng 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 monoecious species these diploid gametophytes produced sex organs and a tetraploid sporophyte, which produced diploid spores and so fixed the race. Tn 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 cusjridatum,* 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* x 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* x P.*floribund«>isabellina,* also gave P.**

*Kewensis farinosa* having 36 chromosomes. It appears, therefore, that the doubling is not a chance occurrence. Both *P. floribunda* x 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 Liliacese and Amaryllidaceae among plants (Miiller, 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

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[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 *parcus, 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   3·827 |
| **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 l'5O : 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 *yigas*.**

| 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 | 48-6 |
| Pollen mother cells during reduction | 10-9 | 10-3 |
| Pollen mother cells in synapsis | 18-6 | 10-8 |

layers, greater in one d'mension 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 *f/igas* 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 cmpidatum* (see p. 206) by wounding.

Measurements of *gigas* show that the organs are, in general, stouter in all their parts than in *IjamarcMana.* 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 *Lamarchiana,* 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 grains examined. | % of "good" grains. | "Good" grains. | | | Remarks. |
|---|---|---|---|---|---|---|
| | | | % 3-lobed. | % 4-lobed. | % 5 or more lobed. | |
| *Oe. gigas,* **Palermo** (W·) | | | | | | |
| (a) No. I. 6 (normal plant) . . . . . . . . . | 1050 | 27-6 | 6-2 | 86-6 | 7-2 | |
| (6) 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 | |
| *Oe, gigas,* **Sweden** (·rV) | | | | | | |
| (a) No. II. 1 ... ... | 948 | 36-8 | 9-5 | 87-7 | 2·9 | |
| (6) H I. 1 offspring of(o) . . . . . . . . . | 188 | 39*9 | 1·1 | 95·2 | 3-7 | |
| *Oe, Lamarckiana (a)* ... | 910 | 67·6 | 100 | 0 | 0 | |
| (6) from *semilata* (jf£) | 269 | 48.3 | 100 | 0[1] | 0 | Two "bad" 4-lobed . grains were found.[1] |
| (c) from *lata-like* type (H) . . . . . . . . . | 217 | 24-9 | 100 | 0 | 0 | |
| *Lota rubricalyx* X *rubri-* calyx (r⁴n). 14-chromosome offspring... | 330 | 78-5 | 99-6 | 0-39 * | 0 | One " good and two " bad " 4-lobed grains were observed.[2] |

TABLE *XVI.—*ontd.*

| Plant. | Total number examined. | % of "good" | " Good " grains. | | | Remarks |
|---|---|---|---|---|---|---|
| | | | % co lobed. | % 4-lobed. | % or more bo ol. | |
| *lata* x *lata rubricalyx* (fj) | 334 | 76-9 | 99-6 | 0-39[8] | 0 | One "good" and three "b a d" 4-lobed grains were observed.[8] |
| (o) 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) ••• *rubricalyx* X *Lamarckiana*(\%) . . . . . . | 469 | 81-9 | 98-96 | 1-04[b] | 0 | Four "good" and one "b a d" 4-lobed grain were found." |
| *lata rubricalyx* selfed(?$) (14 chromosomes)* • | 302 | 67-2 | 86-2 | 13-8« | 0 | Twenty-eight "g o o d" and ten " bad " 4-lobed grains were found." |
| *semilata*, Sweden (?£) (15 chromosomes) | 211 | 22-8 | 93-7 | 6-3[7] | 0 | Three " good "4-lobed grains.[7] |
| Sweden, another culture (ff). No. I. 3 (15 chromosomes).. | 217 | 23-5 | 100 | 0 | 0 | |
| *lata-like,* Sweden (15 chromosomes) (îJ) • | 201 | 24-3 | 96 | 4[8] | 0 | Two "good[1]* and five " bad " 4-lobed grains, and one with five lobes.[8] |
| *rubricalyx* x *gigas* (H) (21 chromosomes) … | 106 | 18-9 | 35 | 65 | 0 | |
| *gigaa* x *lota rubricalyx* (f$) (22 chromosomes) | 281 | 11-4 | 0[9] | 87-5 | 12-5 | There were ten triangular grains, all bad.[9] |

In Table XVI are givAi 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 chromosomés, as shown by the fact that their offspring produce about 25 per cent, *semilaia* 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* x *lota 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* x *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. Tjamarckiana* 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,/, 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 x 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 prophases 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 *-fe* 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 chromo omes 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 Artbiidung)* 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, arid (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 $F_x$ 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., rvbrinerws, lota,* and *nandla,*** splitting  occurs  in  the  E\.   Both parent types appear, and both breed true in subsequent generations.   Thus in 1907 he obtained from *Lamarckiana* x *nanella* in four crosses a total $F_x$ 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* x ***brevistyUs* and *nanella* x *lamfolia* also produced both**

parent types in F,.  In the same way, *Ijamarciciana* x *rubrinervis* and its reciprocal both gave *Jjamarckiana* and *rubrinervis* in F,.  The total number of *Fi offspring in the first case was 6,430, of which 59 per cent, were *rubrinervis*,[#1] **and in the reciprocal (*rubrinervis* x *Lamarckiana*),** in a total $F_x$ of 3,639 there were 50 per cent, *rubrinervis.*[1]

We have obtained the same results.  Thus in 1906 the cross *rulwinervis* x *Lamarckiana* was made twice, producing in the first case an F, of 38 plants, of which 32 were *rubrinervis,* five *Lamarckiana,* and one undetermined.  In the second case the F! 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 *Ijamarckiana* similarly gave an $F_2$ of 19 *Tjamarckiana.* This is shown in the accompanying diagram :---

*rnhriMrmï*  x  *Lamnrrkimm*

Fj    *rnbrimnHH*  (49)        *Jxnnarrkiana*  (16)        *latu*  (1)

F₂    *rubriucrris*  (82)        *Lamarrkiana*  (19).
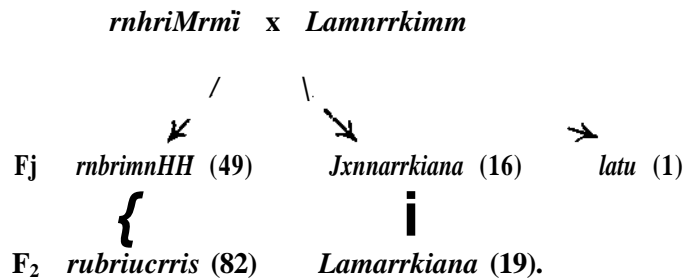
In Table XVII (page 223) are several similar results, though the numbers are small.

In Mendelian hybrids, when there is splitting in the F, 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, 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 Fj differ from the *ntbrinervis* mutant chiefly in being less brittle, and he has called them *subrobusta.***

*rubrinervis.* **Both came from the union of a *Lamarck-iana*** 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 $F_x$ 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 | *Lamarckiana* x *rubrinervis,* | 68 | *Lamarckiana* 22 $+$ *rubrin.* 45 $+$ 1 mutant. |
| 1910 I | *Lamk.* X *rubricalyx,* F, ... | 11 | *Lamk.* 2 + *rubrin.* & *rubri- > calyx* 8 + 1 mutant. |
| 1910 | *rubricalyx* x *Lamk.* F, ... | 4 | *Lamk.* 1 + *rubricalyr* 3. |
| 1907 | *rubrinervie* X *nanella,* F, ... | 42 | *Lamk.* 20 + *rubrin.* 20 + *lata* 1. |
| 1907 | *rubrinervis* X *nanella,* F, ... | 3 | *Lamk.* 1 + *rubrinervis* 2. |
| 1910 | *rubrinervia* X *nanella,* F, ... | 79 | *Lamk.* 25 (?) + *rubrin.* 52 (?) + 2 aberrant. |
| 1910 | *rubricalyx* X *nanella,* F, ... | 42 | *Lamk.* 7 + *rubricalyx* 35 |
| 1907 | *lata* x *rubrinenris,* F, ... | 4 | *Lamk.* 3 + *lata* 1. The *Lamk.* remained true in F₄ and F₆. |

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 x nanella,* for in this cross the $F_x$ 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* x *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 x labile pangen = split in P,,
inactive pangen x active pangen = split in $F_2$.

In the origin of *nanella* as a mutation, the aZto-pangen for height has passed into an inactive condition, from the labile condition which it occupies in *Lamarckiana.* Hence *Lamarckiana* x *nanella* or the reciprocal will split in the $P_{1s}$ On the other hand, *rubrinervis* x *nanella,* as is well known, produces an F! 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 :—



*ruhrinervin* x *nanella*

*Lamarckiana*  *rubrinervia*  *rubrinervis*

*Lamarckiana*  *rubrinervis  nanella*  *rubrinervis.*
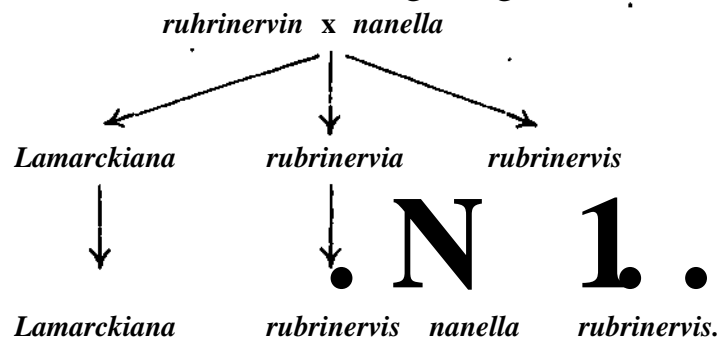
This cross is in itself another proof that the mutants are not due merely to the loss of different " factors " from *Lamarckiana*;  for if that were the case the above cross should give *Lamarckiana* only (just as two white races of sweet pea produced the Sicilian sweet pea again), but *rubrinervis* always appears as well in the $F_t$.  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* x *nanella* only splits off dwarfs in $F_2$ and not in F,; are both explained by the single assumption that in *rubrinervis* the afca-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 x inactive in *rubrinervis* x *nanella* (corresponding to presence x absence in the Mendelian terminology) shows dominance and $F_2$ splitting.  In *Oe. muricaia* x *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 x nanella gives dwarfs in F,, while** *rubrinervis* x *nanella* first produces dwarfs in P..

### 2.—*Mendelian  Characters*

We have already seen that some crosses between mutants, such as *rubrinervis* x *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 x brevistylis the peculiarities of bremstylis** behave as a Mendelian recessive, reappearing in the $F_2$, but the ratios often depart widely from Mendelian expectation (see p. 93). Again, *ruhricalyx* appeared as a new Mendelian dominant character from *ruhrinervis.* The original mutant was heterozygous and its offspring produced 25 per cent, *ruhrinervis* (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 *ruhrinervis.* The query is as to whether some of the offspring (rosettes) were *ruhrinervis,* since the *ruhricalyx* parent was probably heterozygous. Very likely pure *ruhricalyx* x *ruhrinervis* would give F, all *rubricalyx* and $F_2$ 3 : 1 , though this point has not yet been finally determined.

<div align="center">

**TABLE XVJ11.**

*Oe.* **mut.** *rubricalyx* **crosses.**

</div>

| Date. | Cross. | No. of offspring. | Result. |
|---|---|---|---|
| 1910 | *rubricalyx* x *Lamh...* | 81 | F,. *rubricalyx* 54(?) + *Lamk.* 2 6 + 1 mutant. |
| 1910 | *Lamk.* x *rubricalyx...* | 45 | F₁. *rubricalyx* 32(?) + *Lamk.* E) + 4 aberrant. |
| 1910 | *rubricalyx* x *nanella* | 42 | F₁. *rubricalyx* 35(?) + *Lamk.* 7 (?) |
| 1910 | *rubricalyx* x *rubrinervis.* | 47 | |
| 1910 | *bienni8* x *rubricalyx* | 34 | F₁. *veiulina* + *laeta* (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-

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[1] **These plants remained rosettes and it was uncertain whether they were all *rubricalyx* or whether some *rubrinervis* appeared in the $F_v$**

development, *in V* there is sharp splitting, though in different ratios.   For *a.* summary of the results, see *grandijlara* x *ruhricatyx,* p. 255.

*0e. to VtMyUs* and *tnhnmhjx* are tbfi f^nly mutants which how sin i pi'- Monde I i; m bcMviout when c/oesed with their jare»t. on© of them lifMfi^t rt^^yivc, the other dominant, tliougli the evidanco in the rase of *hmn&tyUs* is nat inclusive.

### 3.—*Dwarf Crime**

The mie:-pected apjwjiraacse of large numbers *oi* dwarfs in intorspficilir ciroeaea has been a feature «f our F_a hybrids of (*ftuntlijlora* x *rttbrietdtfx* (1&4) and its reciprocal ;  and Davis (60) baa obtained similar results in (*jrandiflora* x *hiennis.   Whih* their appearance m the cuituwa was i Hurpriae, it wat» fomid on looking up the records that they imght have been expecte*.! to appear. In 1D09 the rvoas *rubrioafyx x namlfa WAS* made, tiw mother plant bring hoterozygoiis for rod. The Fi ofTs]niii*r eonsisted of *Lamarckiana, rubrinervis*_t a J I d *rubricalyx,* and one of the latter



Flu.  Tft—Dwarf rosette from '*. *ffrnnttijtam* × (*hi. nibricaifft.*

Wtti used tx> make tlie. <jt×« *yrandifttm y. nthrimhjx** The (*frandjjhra* parent was shown k> give uniforni offspring *whoa* aelfed.   The above otos yielded !-IT ]>lanta, wlvch were uniform except with regard to the hetorozygous *rutricalyx* eharna^or  A|.|<h'xiimit<.*]y lialf the plants po»- sessed and I14I/ kcked tlii> character.   Five R XumiHe? were raised, and two of tlieae contained dwarfs.   TIIIH pciiigr«43 is ftbown in Table XIX.   The numbers wens tto tiill : 22 dwarf, and *23* toll so d^arf.   Tliiit is, a ratio of practical! v three tnlk to one dwarf in one family, and one

hill to two fJwwrfa iii another.   A young roKctte of one itf fchoso dwadb w wen in Fig. 78, and a full-grown phint in Pip, 7W.   1⁺V- HO shows one ⊲f the** dwarf* in bloom. 11 is very much larger tliiiti *itanHfu.* urn I *yvt* it luu* Hhort internodes, characteristic **branching, «nd** very brittle leaves and stems.

Pmirfe of thft same typo appeared in the reciprocal



Fɪɢ.  *grandiflora* × '*. *tutu* rt'ni: **firnl** reciprocal

crosj, hut in this raw tiny **were** inherited from tlic ***grati&i-Jtorn*** parent.  The pedigree is **shown** in Titble XX.  l» will be seen that the *ipdtu)ijtara* jwirrut was rapaMi[1] nf pro^-during dwarfs whi«-h lirtui tame, in the proportion of about one dwnrf to 7'« tulb-   The F̄, **OOntairrtd only** tiills. liut two of the nin? F̧ families **coatwuod dwarfa.**  Tin- latter **appeared** iti the rutio I ; ti"4, showing that the tendency

to produce dwarfs in the ratio of about one dwarf to seven tails was inherited from the *grandiflora* grandparent.

TABLE   XIX.

*ruhricalyx* x *naue/la* **1909**

/ \

/ \

*Lamarckiana* (7)     *rnbrkalyx* and *rubrinervi** (35)

↓

No. IV. 2.

(iKAKDIKLOKA   X   (RUBRICALYX)   1910

↓

55 (uniform)

↓

480 (uniform)

147 uniform rosettes      F,   1911

*red buds*          *yreen hutls*
34 (in flower)       23 (in flower)

1

No. XL 9.      %      No. 1. 1.

1          II          1

*tall      dwarf    tall      dwarf*
1912.  F.₂   60        22      23         50

TABLE   XX.

*rubricalyx*                    *qramlifiora*

*rnhrinercù* (11)   *rubricalyx* (33)   *tall* (38)   *dwarf*   {&)   1909

UUBRICALYX       X  UKANDIFLORA           y

23 *dwarj*   1910

67 uniform rosettes

1911  *red buds*                     *yrteit budu*
30 (in          flower)             28 (in flower)

No. X. 3                        No. VII. 5

1                              1

*tall      dioarf*               *tall      dwarf*
1912   51        9                  70        10

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

tie **carrytog** the **capacity** for **producing** dwarfs, and that these clwurfo must be regarded an mutants, although their frflqtrcnt'v **is amah higher khan has** b«Mi **previously reodrded.** Row thi^ high **tsapacity' has** }»een product*! ts **a (jueatian** which rant not be **answers!** at the present

Fio. 80.—Dwarf type of Fig. 79 in bloom.

tim~j, but that it is inherit**! Ennn **generation bo generation** is shown by thcae experiment*. That t!i.« **problem** is $u$ different **one** from that in rh<? **reedjnfocwl** *warn* (**Table** XIX) where nanism wiis intiwlncod h}⁣ • niaaing unth $A$ dwarf, is **flhown by** the very HHIL-II **larger** and oiitirL*ty **difierent** ratios (3 : I and I : 2) **produced** la the latter case, although the type af **dwarf** was the saine.

The $F_3$ cultures from *grandiflora* x *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* x *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.

<div align="center">TABLE XXI.</div>

**Dwarfs in $F_3$ families of *grandiflora* x *rubricalyx* and reciprocal.**

| $F_3$ Culture. | Offspring. Tail. | Dwarf | Ratio. | Parent $F_2$ Culture." Tall: Dwarf. | Parent $F_2$ plant. |
|---|---|---|---|---|---|
| | 107 | 2 | 53-5:1 | 60:22 | No. II. 3, tall |
| | 222 | 48 | 4-6:1 | 60:22 | No. 11.11. tall |
| W | 34 | 249 | 1: 7-3 | 23:50 | No. 1.13, dwarf |
| W | 18 | 2 | 9: 1 | 23:50 | No. 11.19, tall |
| | 275 | 3 | 91-7: 1 | 115:0 | I « III. 5, tall |
| | 220 | 12 | 18-3:1 | 119:0 | if II. 4, tall |
| W | 56 | 1 | 56: 1 | 51:9 | Jg III. 1, tall |
| | 38 | 1 | 38: 1 | 51:9 | jS III. 2, tall |

Hence we see that in the $F_2$ family which contained 3 tails : 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 (JJ) 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 tails produced 9 tails to 1 dwarf, a correspondingly large decrease. These facts furnish the best evidence that the proportion of tails and dwarfs 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 tails 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 $i$ The wide fluctuations in the percentage of types in many Oenothera crosses must be explained in a similar manner.

Of the reciprocal cross, *mbricalyx* x *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 tails, while two of the $F_L$, families produced dwarfs in the ratio of about 1 : $6^\#4$. In the $F_{:i}$, 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 $F_a$ 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 XXL 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* x *rubricalyx)* **x** *(rubricalyx* **x** *grandiflora),* **which yielded 45 tails :** 8 dwarfs (5*6 : 1). One of the tall offspring was selfed and produced 141 tails : 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* x *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 $F_2$ (10*30 Lb) produced 992 offspring, of which 147 or 1 : 57 (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.

TABUS XXU.

{//•a *ndiflora*   x   *bitn n*i>

| | | | | | |
|---|---|---|---|---|---|
| 1910. | 10-30 La. | | | 1030 Hi. F, | |
| | I | | | I | |
| 1911. | tall | dwarf | 11 ·42 f. | tall | dwarf F$_2$ |
| | 1310 | 141 | | 845 | 147 |
| 1912. | tall | dwarf | 48 dwarfs. | tall dwarf | tall dwarf | 65 |
| | 241 | 18 | | 54 8 | 357 .20 | dwarfs. F$_3$ |
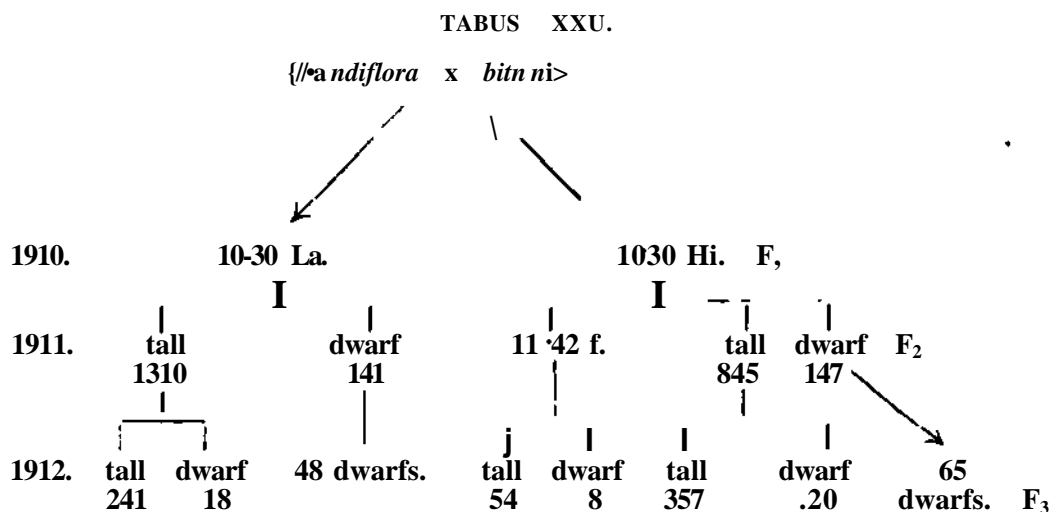
The size of flower also varied greatly. This type bred true in $F_3$, and one of the tall F., plants produced the same type of dwarf in $F_3$ to the number of 18 in 259 (= 1 : 13*4 or 7 per cent.). Thus the frequency of dwarfs in the $F_8$ (7 per cent.) was not a wide departure from that (9*7 per cent.) of the $F_2$.

The other type of dwarfs, which also bred true, appeared in $F_2$ with a frequency of 1 : 5'7 or 14*8 per cent., but in $F_3$ 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 $F_3$ than in $F_2$. 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* x *Oe. biennis* produces in P\ 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 $F_x$ composed of tall plants, the same as *Lamarckiana* x *biennis.* Only occasionally, in larger cultures, did dwarfs appear in F,. Thus in de Vries's crosses the $F_t$ offspring were mostly dwarfs, while in our crosses using other races they were mostly tails. From the fact that tails and dwarfs both appear in the F, of this cross, de Vries concludes, as previously explained (p. 224), that in the pollen of *biennis,* the ato-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 *lota* 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* x *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 $F_t$ 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* x *gigas* the flowers of the Fj though intermediate in size were all cruciate; *gigas* x *cruciata* produced 105 plants; of which 14 flowered, 13 of them having cruciate and one broad-linear petals. •

It is noteworthy that *biennis* x *gigas* and *gigas* x *biennis* both give a single type which is intermediate between the parents, for this contrasts with *biennis* x **Lamarckiana in which the twin types** *(laeta* **and** *vdutina)* appear (see p. 245). From the fact that *gigas* produces only one F, type in all these crosses, de Vries concludes that in it the Zaeta-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 *(heta-* and *velutina-Tpio&ucmg)* 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 aij. independent change.

*Gigas* x *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* x *gigas,* as well as by *gigas* x *brevistylis, gigas* x *rubrinervis* (17 plants) and *rubrinervis* x *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* x *Lamarckiana* which were identical with the F, 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* x *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 *làta* x *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* x *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* x *gigas,* as did also the F, of *rubrinervis* x *gigas* (236 plants). The F₂ of the latter cross contained 16 plants, of which 10 were *rubrinervis,* the remainder like the F,." 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* x *Lamarckiana)* x *gigas* and its reciprocal have yielded de Vries (425) a hybrid race (120 plants) which is again intermediate between *gigas* x *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* x *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 re-semble *(jigas* x *Lamarckiana.*

*Oe. (gigas* x *Lamarckiana)* x *Lamarckiana* and its reciprocal also produced 120 plants of which 30 bloomed. They were somewhat earlier and taller than the hybrids de-scribed in the last paragraph, with long inflorescences and buds somewhat thicker than in *Lamarckiana.* They ap-peared 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 *gigas₉* the *lata-semilata* series of forms gives hybrids which split in $F_x$. 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 Zato-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* x *Lamarciciana* 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 $F_x$ family consisting of five *lota* and **eight *Lamarckiana.*  Again, *lata* x *rubrinervis* produced** 534 plants, of which 13 per cent, were *lata.*

*Nanella,* on the other hand, produces three types in $F_{1s}$ *lata, Lamarckiana,* **and *nanella,* about a third of each.** That is, *lata* x *nanella* splits in $¥_x$ both as regards the *lata* characters and height, from which it is concluded that the a#a-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* x *biennis* gives a single intermediate type, but *lata* x *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* x *biennis* gave, in au $F_L$ of 258 plants, 53 per cent, having *lata* characters.

***Lamarckiana* x *Hookeri* gives the twin types *laeta* and** *velutipa* in $F_:$ (see p. 242);  and as might now be expected, **lota x *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 *latd-*** *velutina* also have 15 chromosomes.  These two forms will both doubtless split in their offspring into the ordinary and the Zata-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 naneUa,* 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 Zafo-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** *Icevifolia),* when crossed with *Lamarckiana,* split in F, and afterwards breed true; (2) *lata* and *semilata* under the same conditions split in ¥, 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* **x** *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.* Thuff *Hookeri* x *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* x *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 :—

*Hookeri* x *ttirit/om* = ($x$ nucleus + $x$ cytoplasm) + $y$ nucleus
*Strigosa* x *]lookeri* = (//    „    + //    „    ) + $x$    „

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* x *Lamarckiana, Cockerelli* x *Lamarckiana, strigosa* x *Lamarckiana,*** and their reciprocals. The same result is obtained when ***Lamarckiana* is replaced by *nanella, brevistylif,* and other** derivatives. Thus *Hookeri* x *Lamarckiana* gave de Vries the following result:—

*Hookeri  x  Lamarckiana*

*laeta* **(17)**          *velutina* **(59)**

*faefa* **(11)**    *velutina* **(103)**    *velutina* **(54)**

*laeta* **(48)**    *velutina* **(71).**
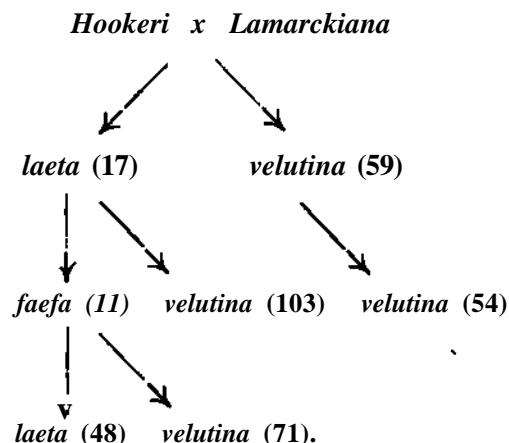
If now we examine the heterogamous species we find that their reciprocal crosses are quite unlike, showing clearly that their pollen grains and egg cells are carrying different qualities. The species shown to be in this condition are **Oe. biennis, Oe. muricata, Oe. cruciata, Oe. Millersi, and** *Oe. 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 mayjbe 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* x *biennis,* however, it is found that in the $F_x$ 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* x *biennis* splits in $F_2$, splitting off a form resembling *Hookeri.*  The following diagram shows what happens :—

<div align="center">

*Oe. Hookeri* x *biennU*

*ruhiennis*

*ruhiennis*          " *Hookeri*"

*rubiennis*    " *Hookeri"*    *"Hookeri."*

</div>
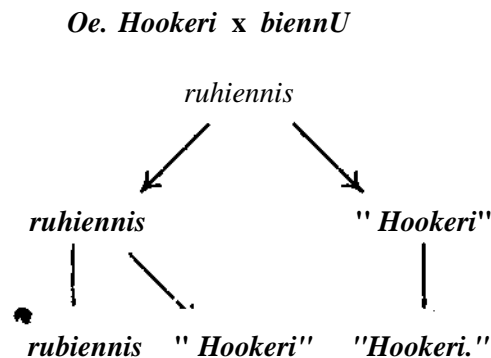
An understanding of the constitution of heterogamous species is obtained by crossing them reciprocally with

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* x *Uennis* gave an F! 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, *Uennis* x *Cockeretli,* gave a uniform green and constant type called *conica,* which resembled most strongly the pollen parent.  Similarly, *biennis* x *biennis* Chicago and *biennis* x *Hookeri* produce a *conica* type.  On the other hand, *biennis* x *cruciata, biennis* x *muricata,* and *Lamarckiana* x *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! 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 $F_x$ 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,.  Thus in *biennis* x *nanella,* we obtained in 1910 an Fj of 43 plants, of which 28 were *velutina,* seven *laeta,* six dwarfs and two aberrant.

The rosettes of *laeta* and *velutina* from *biennis* x *Iamarckiana* 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 *velvtina*.  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 :—

<div align="center">

*biennia*  x  *Lamarckiava*

/          \

*laeta* **15**          *celntiua* **24**

↓                ↓

*laeta* **21**          *refutina* **51**.

</div>
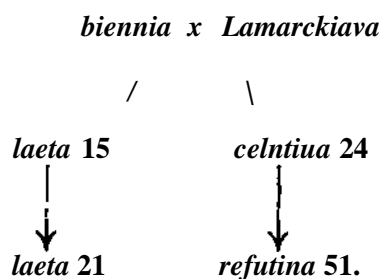
Similar results w#e derived from *biennis* x *Icevifolia,* *biennis* **x** *rubricahx* **and** *biennis* **x** *nanella*.  **There is** therefore no doubt that this is a characteristic type of behaviour.

Although both twin types bleed true, their male and

IPw, HI.- RwQtia of famfa fcjme in FV of *(k bkunh* ×
ig. 82).



Fig. 82.—Rosette of *velutina* type from
*Oe. biennis* × *Lamarckiana.*

female germ cells are unlike, as is shown by crossing th*em* rec'4>roca11y.  *Ixirta* x *vduiifta* then givt*> both parent types, while *whitina x foela* gives 100 per cent, *faeta,* AJeo *(wrtmi-n* x iw^« produces only *//rrfa* mid *hwmis x rrffttitto* only *trbfihw.*   By bgeniouy rejwoniii^ from these and other results, <^ Vries ooncludea fchat in ?HfAi the



Fiu. 83.—*Laeta* twin type from
Oe. *biemis* × *Lamarckiana*
(cf. Fig. 84).

Fiu. HI.—*Velutina* twin type from
Oe. *biemis* × *Lamarckiana.*

*laeto*-p&ngeus cf the'polltii are in the active and the egg cellB in t!i'- labile condition, while 'm *wbttina* they ate in the inactive condition in both eggs and ptiHeti.

When *kiemm* rhicagn and *crrrciata* utt? pollinated by *hnnamkimia ox* its derivatives, another pair of twin tyi<> den HI and tarn, ut^ ]iroduc«<l_t and &nw remains coniatant while *laxa* splits off a third type called aim.

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 racfc of *Oe. mvricata* from Venedig, he found that *muricata* x *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* x *Lamarckiana* the embryos degenerated still earlier.

On the contrary, in *biennis* x *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* x *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 :  109 bad).  Evidently, then, one of the twin types, corresponding to *laęta,* 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* x *muricata* and *muricata* x *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 *heta-vehttina* factor, the two types of homozygous embryos degenerating.  Selective elimination of embrvos 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.—*Doable 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* x *biennis* in many crosses gave always a uniform $¥_x$ (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* x *muricata* produced a uniform $¥_x$ 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 x M) x (M x B) and (M x B) x (B x M).  The former was found to produce a hybrid almost identical with *biennis*[9] 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* x *biennis)* x *muricata* [ = (M)B x M] gave *muricata,* and *(biennis* x *muricata)* x *biennis* [ = (B)M x B] gave *biennis.* Tn the same way (M)B x B produced (M)B and B x (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_y* and Davis (77, 79, 80) has studied *grandiflora* x *biennis.* First let us consider *grandiflora* x *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 $F_Y$ and $F_3$ are given in my paper (154), to which reference should be made.**

TABLE XXIII.

Comparison of the Main Characters of the Parents.

| *Oe. grandiflora,* Solander. | *Oe,* mut. *rubricalyx,* Gates. |
|---|---|
| 1. Leaves of rosettes thin, nearly or quite smooth, with *pale red blotches* on the surface; petioles and midribs always wholly *green* on ventral surface and usually also on *dorsal surface.* • | 1. Leaves of rosettes thicker, more pubescent, considerably crinkled, without red blotches on the blade; petioles and midribs more or less bright red on the *ventral* 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 *rubrinervis* until the buds appear.) |
| 2. Rosette stage more or less *evanescent* and often entirely omitted, the plants being physiologically <sup>iC</sup> early" in their development. | 2. *Rosette stage well developed,* the plants being physiologically *later* in their development. |
| 3. Later rosette leaves characteristic in shape, long and rather broad - pointed, with long, irregularly margined petiole.<sup>1</sup> (See Figs. 85, 86, and 1, p. 13). | 3. Leaves of mature rosette rather narrow-pointed. |
| 4. btem leaves thin, *smooth, pointed at both ends ;* petioles green. (See Fig. 89, p. 261) | 4. Stem leaves thicker, *crinkled, broad and sessile or aurate at base,* except the lower ones ; petioles red ventrally and sometimes less so on the dorsal surface. |
| 5. Buds *green* throughout or with a small amount of red on the sepals (see Fig. 87). | 5. Hypanthium and sepals, especially their median ridges, *deep red* (see Fig. 36, p. 105). |
| 6. -Duds *slender* and *rounded,* sepals *thin,* sepal tips long and setaceous (Fig. 87). | 6. Buds *stouter, quadrangular,* sepals *thick,* sepal tips shorter and stouter (Fig. 36). |
| 7. Buds wholly *glabrous,* or covered only with a soft, inconspicuous pubescence of *short hairs.* | 7. Buds covered with soft pubescence, and in addition a conspicuous *long, pointed type of hair* arising from *red papillae.* |
| 8. Flowers usually somewhat smaller than in *rubricalyx* and others of the *Lamarckiana* series (petals 30-40 mm. in length). | 8. Petals about 40 mm. in length. |

. <sup>J</sup> The most cliaracteristic type of leaf, with prominent basal lobes, is always omitted under the usual conditions of culture, so it need not be considered here.

**TtfK PABfcNT TVH;s**

The tAvu types **dftfes** from each other in every **feature throughout** till stages of their **development**

**The F, and F rosulta** tmve **already been** published. b»it
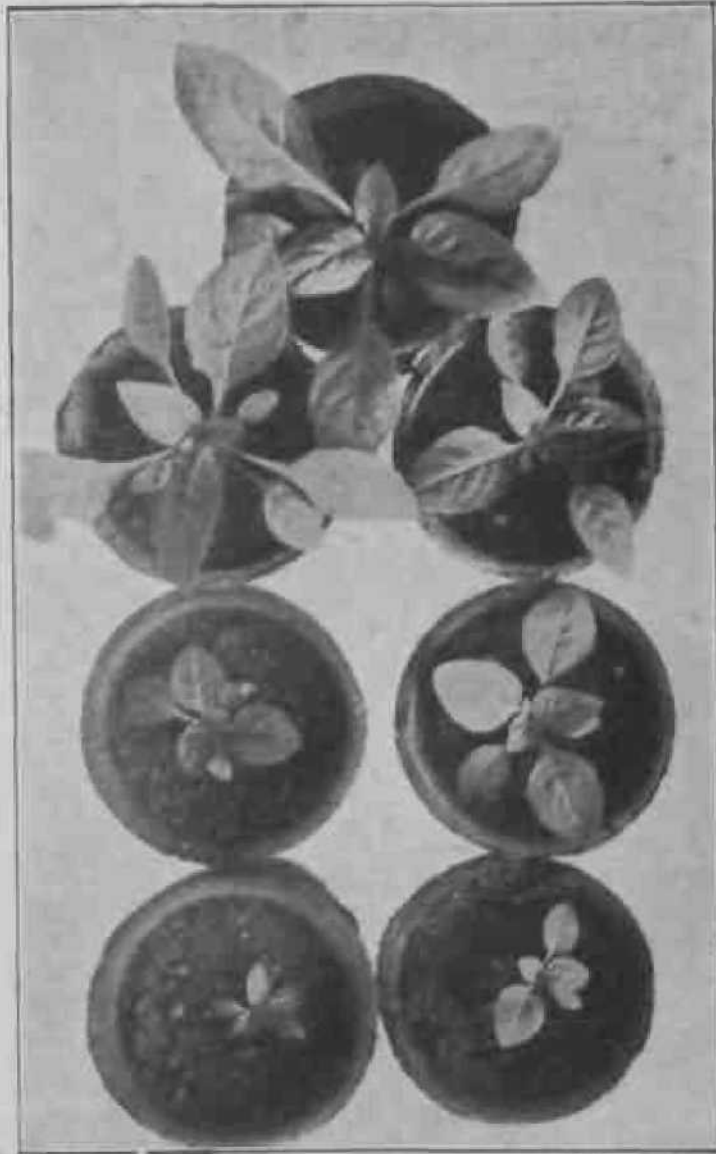


Fɪɢ 85. — Seedlings of *Oe. grandiflora.*

the $h\backslash_t$ *grown* in **101** $H_t$ **will** *he* **included hers** *m* well. We have Already **described** t!ii> **inheritance of** ftwarfism in tliesv • ifwifics [see $p_t$ ^127), Wo **may** roasidor next the inhori- tanoc o( tlie red **pigtaeartfttion** (R) which **difltingidflbei** rubrivaly i: Imru *mbrinjervit* ami all the other forma.
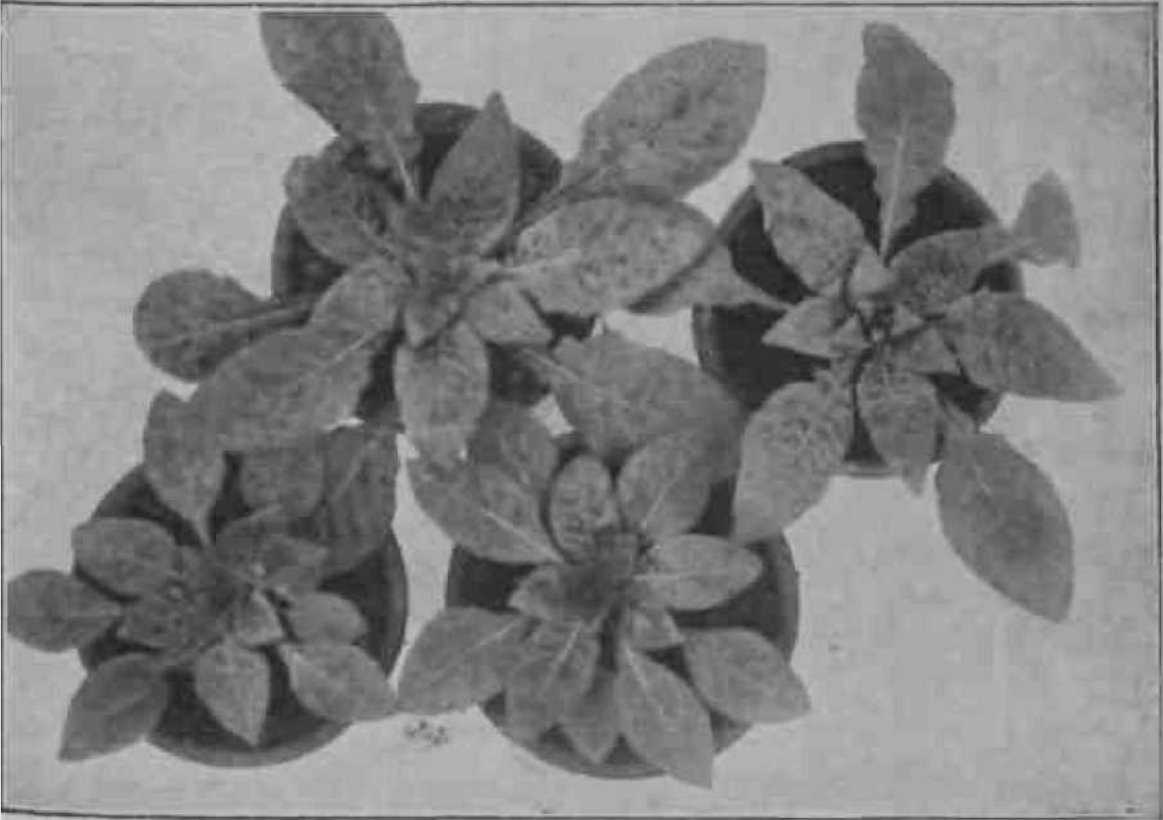
I i ,   ee( -V,,nni! f*wil«ti of *th. ttrmutfjhtrti* ftcm Alabama
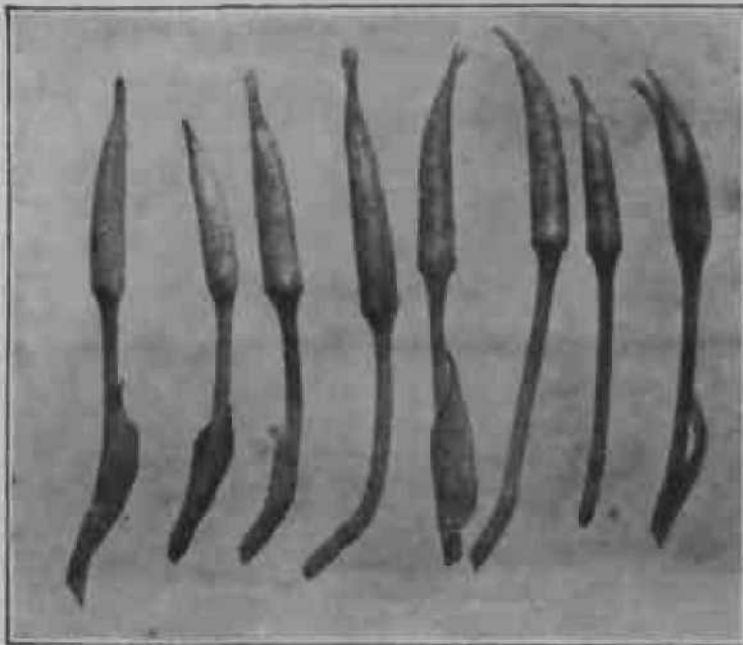


FIG. 87.—Buds of *Oe. grandiflora* (cf. F[1]*^ :w, ì. I[05]).

### § A.—*Inheritance of* R

The origin of R through a mutation is explained else-where (see p. 102). In the first cross with *grandiflora* it behaves as a sharp dominant Mendelian unit. In both *grandiflora* x *nibricalyx* 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 $F_3$ 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. |
|---|---|---|
| *grandiflora* x *rubricalyx,* $F_a$ . . . . . . . . | 5 | 504 |
| *rubricalyx* x *grandiflora, b\* . . . . . . . . | 12 | 1039 |
| (*grandiflora* x *rubricalyx*) x *grandiflora* . . | 3 | 373 |
| (*rubricalyx* x *grandiflora*) x *grandiflora* . . | 4 | 579 |
| (*rubricalyx* x *grandiflora*) x *rubricalyx* . . | 1 | |
| (*rubricalyx* x *grandiflora*) x (*grandiflora* x *rubricalyx*) . . . . . . . . . | 1 | 44 |
| (*grandiflora* x *rubricalyx*) x (*rubricalyx* x **grandiflora**). . . . . . . . . . . . | 3 | 62 |
| | | 193 |
| | 29 | 2794 |

The proportions of red-budded and green-budded plants in the various $F_a$ 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, plant (No. VII. 2), and all show approximately the same 5 : 1 ratio. Hence it must be concluded that different $¥_x$ plants, though externally alike, have the capacity of producing the dominant and recessive characters in different pro-portions.

TABLE XXV.

Distribution of the Dominant Character, R, in $F_a$.

| No. of 1912 culture. | No. of F, parent plant. | Character of buds in parent F, plant. | Offspring, | | Ratio. |
|---|---|---|---|---|---|
| | | | R. | r. | |
| I. *grandiflora* x *rubricalyx*, $F_2$ | | | | | |
| Cult. 48 (a) | IX. 4 | red buds | 68 | 16 | 4·25 : 1 |
| Cult. 49 (6) | 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. A. *rubricalyx* x *grandiflora*. $F_2$ | | | | | |
| Cult. 55 (a) | VII. 2 | red buds | 66 | 13 | 5·0 : 1 |
| Cult. 59 (5) | IV. 4 | red buds | 45 | 14 | 3-2 : 1 |
| Cult. 60 (c) | X. 3 | red buds | 47 | 3[1] | 15·7 : 1 |
| Cult. 61(6) | 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, parent plant. | Character of buds in $F_2$ parent plant. | Offspring. | | Ratio. |
|---|---|---|---|---|---|
| | | | B. | r. | |
| I. *grandiflora* x *rubricalyx*, $F_3$. | | | | | |
| 93 | 42. II. 18 | red buds (B) | 280 | 0 | |
| 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 | 4·125:1 |
| 98 | 50. III. 2 | red buds .. | 237 | 56 | 4-23 :1 |
| 99 | 50. IV. 8 | red buds .. | 4 | 0 | |

' 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 F₂ parent plant. | Character of buds in *b* parent plant. | Offspring. R. r | | Ratio. |
|---|---|---|---|---|---|

**1. *grandiflora x rubricalyx*, F₃.**

| | | | | | |
|---|---|---|---|---|---|
| 100 • | 50. V. 2 | red buds .. | 275 | 0 | |
| 101 | 50. VI. 5 | red buds .. | 97 | 0 | |
| 102 | 53. — 15 | *rubrinervis* (ru) | 0 | 5 | |
| 103 | 53. TT. 3 | green buds (r) | 0 | 109 | |
| 104 | 53. TT. 11 | green buds (r) | 0 | 270 | |
| 105 . | 54. 1. 13 | intermediate in pigmentation. | 283 | | |
| 106 | 54. TT. 19 | intermediate in pigmentation. | 20 | | |

**IT. *rubricalyx x grandiflora*, F₃**

| | | | | | |
|---|---|---|---|---|---|
| 108 | 55. T. 3 | red buds (R) | 57 | 31 | 1-84: I |
| 109 | 55. I. 4 | red buds (R) | 155 | 0 | |
| 110 | 55. 1. 5 | red buds (R) | 6 | 0 | |
| 111 | 55. ]. 6 | red buds (R) | 22 | 6 | 3-7 : I |
| 112 | 55. TI. 1 | red buds (R) | 2 | 3 | |
| 113 | 55. TT. 4 | green buds (r) | 0 | 181 | |
| 114 | 55. TTT. 1 | red buds (R) | 112 | 69 | 1-6 : 1 |
| 115 | 55. IV. 1 | red buds (R) | 13 | 0 | |
| 117 | 56. IT. 1 | red buds (R) | 12 | 2 | |
| 118 | 56. II. 7 | green buds (r) | 0 | 53 | |
| 120 | 56. TTI. 5 | red buds (R) | ≳78ru. | | |
| 121 | 56. TV. 1 | green buds (r) | 0 | 22 fir. | |
| 123 | 58. F. 2 | *rubrinervis* buds ru. | 21 ni. | 17 gr. | |
| 124 | 58. 11. 2 | green buds (r) | 0 | 5gr. | |
| 125 | 58. TT. 4 | green x red buds (R). | 182 | 29 | 6-3 : 1 |
| 126 | 58. IV. I | green x red buds R. | 4 | .2 | |
| 127 | 58. IV. 2 | green x red buds gr. | 0 | 18 gr. | |
| 133 | 60. ITT. 1 | red buds (R) | 55 | 2 | 27-5: 1 |
| 134 | 60. TTT. 2 | red buds (R) | 37 | 2 | 18-5: 1 |
| 138 | 62. T. 2 | red buds (R) | 14 | 0 | |
| 141 | 62. IT. 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. | |
| 14? | 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. TI. 1 | green buds (r) | 0 | 185 | |
| 148 | 64. TV. 1 | red buds (R) | 80 | 34 | 2·4 : 1 |
| 149 | 65. III. 12 | intermediate buds. | 186 | | |
| 150 | 65. III. 5 | green buds (*gr*) | 0 | 88gr. | |
| 156 | 66. IV. I | green buds (ru) | 28 ru. | | |
| 157 | 66. IV. 9 | green buds (ru) | 165ru. | | |

From this table several interesting facts appear. Among the 13 $F_3$ families from *grandifiora x 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* x *gran&ijlwa,* 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 ¥.> 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 $R_s$ and $F_8$. 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* x *rubrinervis* and many Mendelian crosses, sharp alternation results, with development or non-development of the dominant character. But if, as in *rubricalyx* x *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* x *grandiflora)* x *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 meta-
bolisms, differ from either parent in lU'iirly all their
features.  They give blends, and when crossed back with
one of **the** parents these blends may be blended again.

### **fin.**  -*Inheritance  of  Foliage-characters*

Blended  conditions  in  these  hybrids  are  shown  as
regards the pubescence, shape of buds, rate of development,



Fl*:.  **Hy.**—*OP*. *grandiflora* jfr<f>wii  Jit  S r.  L m i i s.  M...

time  of  flowering,  and  foliage.  In  all  these  cases, **there**
is iutt'nnediacy in the F,, **with** a variable condition running

FIG. 89.—*Oe. grandiflora* as grown in England.



FIG. 90.—*Oe. grandiflora* × *rubricalyx*, F₁ rosette.

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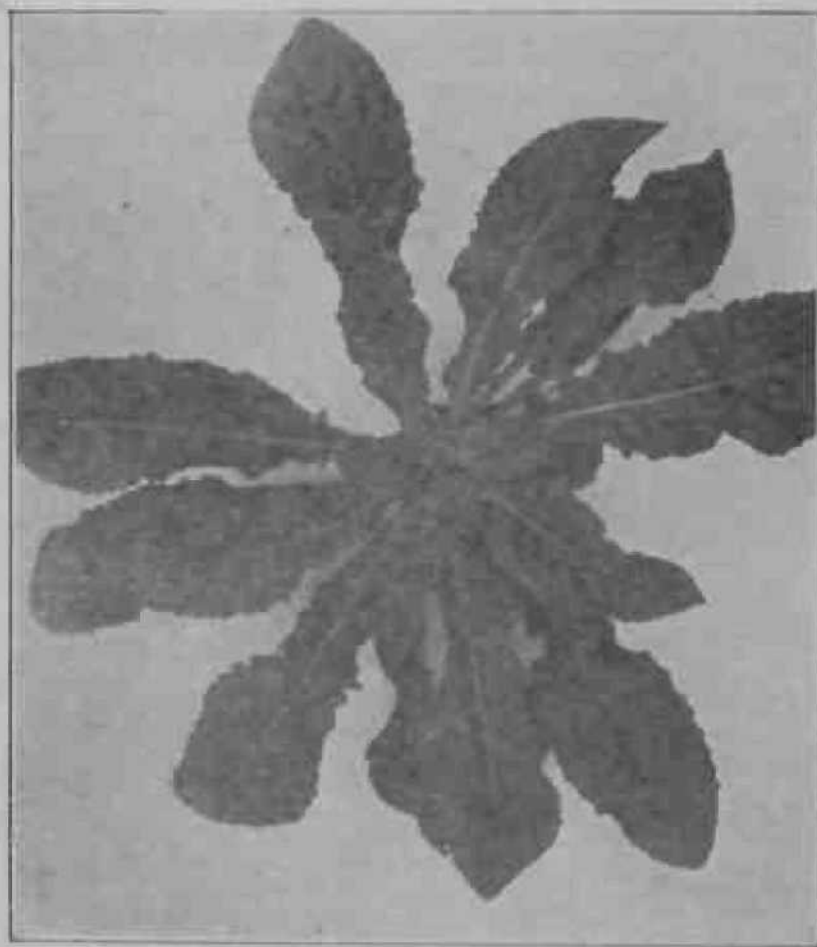
**towards** Imtli **p^nmti in** K. East* in particular, has cn(tauvoiijr<l **very** pf*rsnitisivclv **to show** invc£tif$ntorB thiit then* is stune **adyvttsga** in ^upposin^ *awh* a **condition** tu arise* through the **chance** diatribatJon **ol** luimlK'w o| rigiJ **multiple** *fjict4>ni' fnr *v^vh* **dhatactet. Bat** tt is rkuly impossible to apply this **conception** with any



K i *, „ i'l. Ge, 11. ct. rubricalyx × grantiiflora, y, rosette.

**advantage** fi • ihi> **foliage chtttaotets** in these Oenothera

Amoug l>b[nliujf clianirti'rs. on which we have made *a* large **amount ^ if detailed olwarvatkai,** we can consider Lore only th≪ mttin faote n^ardiny **the** foliage iti crosses' between *ijmmhjhm* **and** *rubricaUfp,* Fi^a. **1 (p. 13)**

and 34 (p- KW) show **rosettes of tlit- parerri** :-p*-ies, **md** Figs. ft8, till **and** 33 (p. 1U4) tin- full-grown **plants,** "I he F, rosette* **of** tJi *m* **proe** oaaee axe **unifottu,** inter **mediate between the xmawfe, and somcwbat** unlike oi»cl( other {m> ]'igs. 9i i  Di), .Tin- *AUU* is trtn[1] **oi the fully** developed I' i*Luit^ *(cf.* rY ts wi *'i Ftg&* so **and** 5).



Fig. \*Z — "• .", *it.ttly* × *grandiflora,* F,

In **the** h[1], **of** which we gi w five fanriBea from *(fi'tt,<f;(hu* , × *rubrtcalyx* urul 1^ bunilk froa *rubrkm* × *tjran&iflvta,* **aambmag in** all 1T943 plaints, a **complet** series of iuiermediut. **forma** i^ fouml, **and** these arc, La general, the same for **both reciprocal otosa** s. A **few oj** them urc illustrated in Figs. **'93** to *HI.* li ach fainily, f<ir

FIG. 93.—*Oe. grandiflora × rubricalyx*, $F_r$ Fulia^ ½ – L ½.



FIG. 94.—*Oe. grandiflora × rubricalyx*, $F_2$. Foliage p – b. s.

the must part, gave **the** whole writs of $F_2$ for $ma_t$ **though** **there** were certain **differences between** famili-s. Tli-re were, **however,** apparently **00 complete** reversions to the foliage of **either parent.**

The 45 JV, familws; **which wt*w dfiriyed** fnim different



FIG. 95.— Oe. grandiflora × rubrie:....
1 = 1 foliage p...

K. mdividotila, «*uv ia moj iaai \*-ry uniform, ftile titatiitjg **around** tfw* OLmdition o4 1 h*- K jmn'm. In *name* **Curuiuw tin:** fhieiititttUm wax CMIV.....K tuwrww, n.u«l ti number of **kuch** unifi-rni and *ch&nu* teris tic rwea **wcuc** produced. **Other** fmniliee were nv re viwuibfe m **(Certain features^** and a few ahowttJ ;t considerable ran, e of variation.

**The** grmt bulk **of the plants came neatest either** parent, but **;i Dun^ber** of irow **branded** *vtuxa* ateu occurred. These nro mil h!i-ri<k **and** i HT **meld** y com hmationa **of** faet*irs$_t$ fo: tliey l>rt't-il **true** *ami* **like foliage** lunis. **and** pigmentation aU s how **nial** fication i<j* *ii(* the originiil **characters. Th**e



**Km. flB. ^.** *rubriculyc* × *grandiflora*, F$_2$
**Fli**age p.s.

**conception** <f "purity o£ the **gametes'** il<^s not apply here ; there M Mending imrtofld.

Ad a nionnfl of classify ing rnnghly *tho* main fttliuge **characteia** we have usctl th<* f<illowing **symbols:** ;> = leaf pointed *At* baa<j$_t$ 6 = broad at **base** : *c* = crinkled, *s* • smooth or free from crinkling. Intermediate conditions were represented by fractions. A large nuiulber

of the F, plants were **carefully** classiliwl w> far *as* this system would permit, but it **Ittttst** ht* understood that the variation is n-allv **eontmaoas** HM **I cannot** be represented umirutdy by **any** d assific **ation.** In this system *p.s.*, ft>t **example,** iotlitates « piaut h«™g Wves **Dearly**



Fio. ft?.—tJ W X ubrirouls grandiflore<, F₂
ge p.s.

**smooth nud pointed »1** base, **hen<»** resembling *grandiflora,* j ru^aiiii **h^vicg leavw averaging about Iwlf «a** broad **at base oe** *ntbricdyt,* with u **qiuotei flw? amoont** of crinkling. Similarly « = the amount of **long** h airs oo flu- **buds of** *rttbricahfx,* **and fractions<rf** thi^ tin* number present in tim **hybrid^.**

With tlww* bok, i W n-presffiit* one of ih* pl miH (No. 11} in an K, family numbering 312 individuals, **whose foliage ia** indicated **by** the formula 5 . **Tiiis family was** derived from *m $F_t$ plant ({II . I. 2, sec Table XXVI), having the sunie foli&ga-formula. The whole culture fluctuated about this mean. The buds *itso varied somewhat iti **putafK&Md,** having V ^ ° 'ᵒⁿff hair»ₜ and the **eepftte** wt*re all very uniformly dark rod



Fig. 98.— Ge. grandiflora × rubricalyx, F₂.

(Rd) **in colour.** V\a, **99** ehowa another K plant (**No. JJ £11.4**), decived feam an K pbwit (No. ^* _ 1J1. -j) **having the** formula **Lj.., ?»*»,** whose leavea were *as* **broad at** base as iu *fibrwaltfi-* hut **only** lutlf us nuu-h (rinkled. This **F, culture contained 299** i>ia: a ad oxhibit^d the whole mnpr of variation **between the** two original **paien** The **individual** in **Fig,** i)» stinwl **rather dose to** *rubrktttyx**

Fig, UHi irimwiitK one **plant (No.** 'flf. V. **I)** in a rfrnurkubly uniform b\ faoiily of ioi> indtvidiiuLs derived from

FIG. 99.—Oe. _____
fouls nil, stout.



FIG. 100.—Oe. _grandiflora_ × _rubricalyx_.
F₃ family.

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No. ½½. **Jl. 3.** **Thk rpce** *tf*n{ rniirh hearer *grandiflora* thitn *rtthriati'/i.* **trot** Wl [.Kvidiiwly **narrow,** rlutiely rcpand- ikhtiouljitr **foliagp.** TIL^ **buds resembled those of** *tfrmuli*- flora,* **lifting Blender but somewh&i nnalkr, They were** sliglitlv fiqiiiiri^h, rovored **with** *Win** pubesccuw, witfi only **raw** long lmirs, the wpal.s yellowish-green. **In another** *h\* fainily (Xo. **105) derived** fnun a dwarf (No. ½½



FIG. **101** .—*Oe. grandiflora × rubricalyx*, F₃, in offspring of dwarf F₂ type. Cf. Figs. 78 to 80 (p. 227 ff.).

I. 13) the 3-J talJ offspring were uU of on<* typi[1]. JIS **aiiown** in Fig. i<<i. The **teaveo were** *. J drooping, tiw bttutoEea spreading; tin? **liiirln** glfthrods, slender to trtouter and squarish, und the pigmontation of **the buda WM** dearly intermediate Jind nearly **Qniform,** bt'ing jiale red on the sepnls und very pale *m tho hypiuithium. Suih *a* race shows peculiarities in every feature, und if found wild

might well iie described hy " splitters *' us u species. Many uthex equally distinct F, r&<es were obt&uietL

These ure unlv a few samples EOCO tin* Fu races whivh p?e« drriviMl from *gtafulijtofQ* × *ruhrimtfrr.* Wfl )t»vo obtftinod immbeis u: equ.Uy nnexpected races from spells of thp i¹ntercrossiu_' rU.»iiol hc-u• iit Birkenhead.



Fm. itftf — *'tr. rubricalge* × buds green, slender. From saute p̂, faiioly RN Tivi, I".

Atnoug K_h f:imilif!S frimi *ruUrUvilyx* y *gfatndiflora,* Fig?. 109 in⊲ 103 are from culture Ni», 113, showing tin* range oi wuiiitiQii i» to ɪ>ɪɪM.·ɪv unifoaD *grand{flora* race. The buds varied frutii nmiult-ij. slender, greenish iiiiti smooth *m hi grundiflora* (Ftg. *J*7) to stouter, squarish, and with ' lo»g hftirs (Fig. 30). These plauts also differed

J'I-., *LtKi-Of. ruin,'•• • • x grandflora*, F₂, **bads gttttt, i n t W** stout (ef. Fig. 102).



Fin. I»K. if*-, *mbriratgur,* x jmntrfutorrt, K,, buds red.

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**considerably** in foliage, **though they** all **had smooth** leaves resembling *yrauxhfiotn.* Tins steins JHUI **the** midribs of tli*» leaves were reel. Another h\ family (No. 115)—tt very hamlaome typc^—in reprr^riU'ii hv Fig. **104. The** buds w«re light **red, Bfltaewhat** squnrish_T soft-pubescent



Fio. 105i — n._ *rubricalyx × grandiflora,* ½
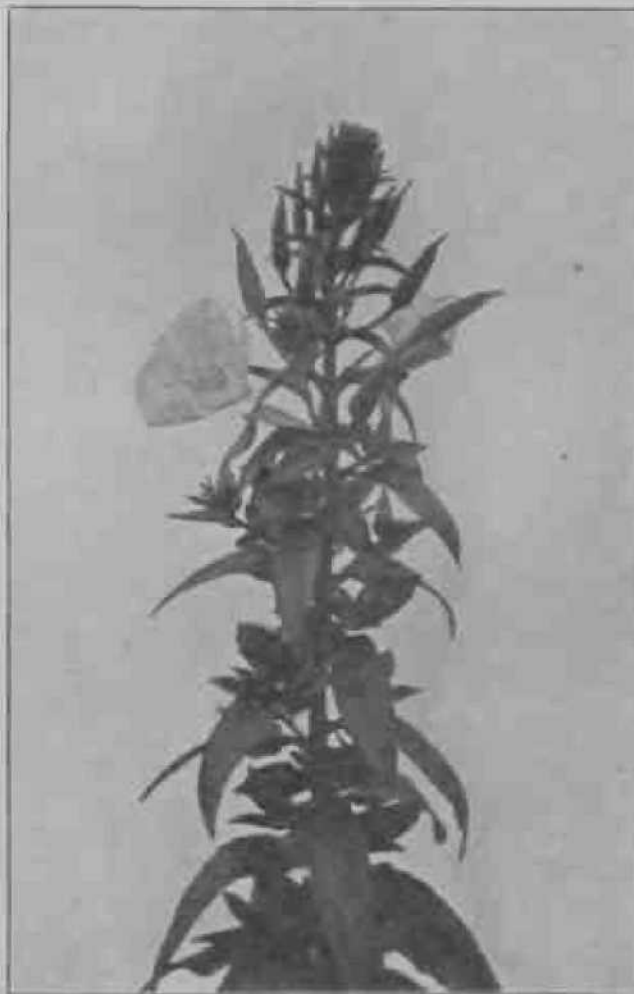
without **kmg** hairs; the leaves A' . s, rwarjy smooth, mill-rilia white. Finally, Fig. L06 sihowi 11 plant **front** unotlu-r $F_n$ **culture** (No. **14fi** . \"III. I'll). This family uuTnhvi-'l **186** piauttt. It was dcrivoil from an *V* **plant** (65. 111. **12J** whose f4»liHge was b. |[5]. **and** tho **pigmeiita^oD** the int-eniietliate between *rvbricalyz and* rubrinervis. offspring rimu' tnu\ *not* on!y to the iritoimediate

pigmentation but **in foliage as well,** the leaved Iwing recorded *m b,* «. **wtrli white midribs and little** variation.

The **erasa (ru&rtoaJui;** • *iji<nnlijlortt}* x rufericw^ai **yielded an oflsppng of U plants whieb** wore ngn-in nn the **average** JUT. .....diate between .their .**parents in Colktge,**



Fii.. 106. (On. rubricalsir × grandiflora) × rub Foliage ¹.¼.

although tluM- **ahowod conajdeimble variation. One oi** thent **it¹ illafitlutBd in Pig, 106,** Ttir **tradi in nil wet\*** <lurk rwl. **PSgB, 107, k»« and i"!»** are taken *kam* \*!'» niTspring of **thres** diiTorpnt **itiilividtmtn in** tin\* **abova qt0a&** **The cnltores were grown in 1919 and numbered respectively 157,** IT. and 98 plants. The **tracts were** < lark **rwl** in oil. **To**

the lii^st cult tin- Hit- fotiugi? varied fromttruooth to consider-
ably crinkled.    The second culture, whiott wa« derived *horn*
a plant (N*J. `\'.i` II. 2) which wus almost identical with
*rubrimlij.i\* consisted of 17 LiHHvifluak$_r$ 15 of which were
indistinguishable from *tuhricalg-r* [rf$_t$ Figs, his ami S5),
one was *fata* and one pnilmlilv *at&Hifja,* Hen re ill        this



Fig. 107.—(Oe. rubricalyx × grandiflora)
× rubricalyx, F₂ (cf. Fig. i".?).

family, there A\;I^ complete *egrega tinn to one parent.
The third culture cautf from *a* plant wlior- foliage-formula
WHS recoidccl aa J . ^,   Thfl oame typte tti leaf ie fotuid in
the ofFHjirittg. as shown bj¹ Fig. IOD-

    If m>w we examine fcke resttha rf *{rubric*alyx × *gmndi-
flortt)* x *grandifiora* :i cross whicl was made ("u timefl
ttith u total of 30(t pknte—we Bgain obtain hyhri-l-
                                          T  .J

Fig. 108.—(*O; nitii'i* ti(y,r × g;*i\diflora*) × 4 *b tt,icalyc*. F~2~ (cf. Fig 35, *4* KH).



Fig*. UK).—(*Or. rubri*Ml\ff* X *grandiflora*) × *rubricalyc*, I~2~ >•/. Fi^K 107, 108).

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intermediate between the patents, although with 5Ol1l0 variation. One of these (from Cult. No, ^4) is shown in Fig, **110.** Fig*. I11 **and IIS** are different offspring ef **bbe** same cross (Unit. No. j A), the tatter having narrow foliage. They (iit* nil uhviolish* nearer *yntnrfiflttm* tluiii *rttbrimlyx*'* 'h ey constitute n now Ijlemlml though variable type



F ıo. **Hit,** — {/>(-, i<v *brimlyx* × ^ *andiflora)* × *grandiflora.* *Foliage p.s. (cf. Fig. 89. p, **SrtJ)**

which **ie** abou **:** **1** *grandiflora* a III 1 *rtihnvalyx.* En m two plantsol tJu» \a\v>T cross [i nh. Mo, •.•.), Eamilieq w-ere grown in HM3. Tln$^i$v contarned rcapectavaly 15 mid 10 plitnt«$_H$ One of **tie latter** i* -h(*vm iti Fig. **113.** "I he burls ure *spotted* with red. rh<* colour pattern being£ brokoji ttp, a« not injteq uently bsppeoa it* tlii.- bftck-crosa with *tjnmdijlora.* The foliiLge is :ilf'» chftmctraisttJ, resembling that of *(jrandijl&rfi* **but** with some crinkling.

These **few** selected *c&sta* will *ho* **aufikaeni** bo show the ondlca* **variety** of forms occurrinu in **tbese** crosses, and the hopeless **impossibility** of trying ⇐ **apply to** them **a** conception of Jix*ˡ*] **segregating** imito, TIMH is all the im>re



FIG. MI.—(*Œ. rubricalyx × grandiflora*) *grandiflora*. Foliage I¹*

impossible because frequently **theft** is a <•onsiderable range *'ti* **variation m** tta foliage **oi** *A* **single individual***

Mn the other IULIKI, there iw n distinct **tendency foj** characters to v;irv indr[}('nilfiltly. In BOmd P₂ tainih'== certain l>iul **obawctera** urr **variable wrhile** tlu< foliage ts relatively jmifnnit. and in **other** fatnili* s tie CCvejtsa *may* be the cuae. Again, thei'O apj^urs to l>e a teudenry for

tlit? population (•» return towards the «irigiaul **parent types,** though this **w** very **difficult t«» estimate when** surli H host of rhEtnH'ter^liffererw'tyi is **concerned-** Tin- **objection to** the application of tht; concgptiOTL of Mentieünn **Erti** ts tM tlifc*o rhumct^rs is rh^refore **that,** adhongli they vai^



Fıo. 112.—(Oc. rubriec. x grandiflora) x grandiflora. liage p.s. narrow.

more or K-> **uwdepeadently, they dd** not **conie on!** " pure.' **but modified and** lil^n-(ed. TJu* kteii **tWt** the i-ham<Tfi> of orgfttiisiii- **are mutually Lndcpendent** ><t T»HC!I ntluvr JIHH **therefore been OTewanphasuffld,** f<r **they** ore n'ally **dependent** upon *mch* other **in various ways foi the mannai and** degree «»i tjn'ir **Kfprcsfiioo** tit tlie oriiatu^m tuul **UihentuudO** in later gtMiertitii>n>.

We have already **pointed out thafc in** various doubic-**reciproca] hybrids of Oenothera** tiiyre is segregation in «uch a way **that** one or **other** of the giandpureutuL types reappear. This is not true, however, of the double **reciprocal** crosses Iwstween *grutulijtom m%<\ ntlyrMijj-*. Thus *{rubrimhff* x *tjmndijtwa)* x *{yfamlijhrtt × ruhrhihfx)* ought in **this-**



!'ᵐ **L13,** *(Oe. rubricalyx × grandiflora)* × *grandiflora,* F₂. Buds red-spotted.

way **to produce pqiB** *ruhrknUjx*. But Hi **gjVCp** instaul aeri*'> **of** *forms* like the other *tfmwUJhira* hybrids. One of the plants from this ***atom*** *m* F_d i» shown in Fig, **114.** It clearly resembles *grmulijfom* mther more than *rubricalyx.* A number of other second generation **families** ***horn*** these double-reciprocal crosses gave similar ro-nlts.

**In** closing this account of crosses between *rubriettlyx*

and *grawliflom,* we may conclude that although the character R, which originates through **a mutation,** is dominant **in** its morphological aspect, *Le,y* as regards the extent **and distribution** of the pigmentation, yet the amount of pigment produced or the capacity of the cells for antho-

F«J. 114.—(*Oe. rubricalyx* x *>tntmlijl(trti)* × (*grandiflora* x *ntbtKnttj.s*), *V..*

cyaiiin-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 hflicvii . . .he. diii[1] W tin- **fad that** \\\v character-ciifference, R, rwides in **one** •')ii-omoaoiiie. See Chapter IX,

R : r in different F.j families is also incompatible with the shuffling of fixed Mendelian units. All that can be said is that *grandiflora* exerts an inhibiting effect on antho-cyanin-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 per-centage 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 $F_:$, 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 *grandi-flora,* carrying the hybrids to the $F_3$ generation. These crosses give a strikingly different kind of beliaviour, which is more in harmony with the results obtained by de Vries in crosses between *Lamarckiana* and other species. Thus the $F_2$ 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 ancl

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 $F_L$ 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 ol)«cure 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.   Tt 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. Tjamarckiana* 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 Onagraceae, 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 geifn 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 süch 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 quitg healthy in appearance. An exactly parallel mutant has been obtained by de Vries (425, Fig. 109, p. 303) in *Oe. muricata* x *(biennis* x *muricata)* which gives a race of pure *muricata.*

<div align="center">

TABLK **XXVII.**

**Mutants in F$_2$ hybrid\*\* of *grandiflora* and *rubricalyx*.**

</div>

| Cult. | No. of plant. | Mutation. |
|-------|---------------|-----------|
| 49 | I VIII. 10 | Mutant. (?) teratological. |
| 50 | I. 8 | Same as last, but small and poorty developed. |
| 50 | II. 3 | *Lata-Mke,* leaves crinkled, many somewhat sickle-shaped ; plant small. |
| 50 | III. 13 | Leaves sickle-shaped ; pathological ? |
| 50 | VI. ✤ | Plant small, with very narrow, imperfectly developed leaves. |
| 53 | II. 7 | Near *semilata grandiflora* (see Fig. 41, p. 114). |
| GO | I. 20 | *Lota rubricalyx.* |
| 60 | 1. 13 | Same as last; died in July. |
| 62 | I. 7 | *Semilata grandiflora.* |
| 67 | II. 6 | Leaves very narrow and linear. Pathological ? (See Fig.\* 61, p. 160). |

Two othec 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* x *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).  Tt 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 *rubricaJyx* 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 F₂ 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 i'urthei- 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* x *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).  Xow 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. graivdijlora* 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 $F_.$ generation contained a plant (II 42 /) 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 $F^*$ mutant in these crosses (11. 42 *j)* resembled *ellipica,* having very narrow leaves and sterile anthers. This plant was poll nated from one of the *grandiflora-like* $F_.$ hybrids, and its offspring included 5 like *eUiptica* 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 *It. polyantliemus* 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 *It affinis,* Wh. and X.; (4) a type having leaves white tomentose beneath, like some Fi hybrids of *It. tomeniosa* x *R. polyanthenws,* **and (5) a wholly distinct** form with deep green foliage, pyramidal leafy inflorescence and deep red flowers. Giants also occurred in the offspring **of *Jt. insularis, It. radula,* and *I\. 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 *partialtyinheTited* 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

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[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, Johannsen'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 transi^on 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 besn 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 *lota* x *Iximarckiana,* 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. iMmarclciana* 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. Lamdrckiana.* 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 *lota* 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. Tn *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. Zato, 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

**miner 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. K. Miiller (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

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[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 meiotie 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 mole-cule 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-

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[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 chromo-some-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 chromo-some 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 **lota.**

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 expres-sion 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 part'cular 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 mjitations 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, (6) in shape and size of the chromosomes, or in the arrangement of their substance; (2) chemical or functional changes in *(a)* whole chromosomes or (6)

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 ground-work 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-sub- stance 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 specula- tive part of the subject appears to be sufficiently served by the pangen theory of de Vries. Its obvious advan- tages, 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 *lota* 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 *rdfo* 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.

Experimentally induced

⎧ Leptinotarsa, Tower (376).
⎪ *PhaHCum cuspitlafum, ft* and E. Marchal (258).
⎨ *AspergUln* niger,* Schiemann (331).
⎪ *Trypanosoma Brunei,* Werbitzki (90).
⎪ *BacilhiH prodigiovus,* Wolf (454).
⎩ ^*Bacillus anthracis,* Mine. Henri (179).

Mutations.-^Produced by wounding—*Zta may* Pennaylranica* var. *vraecox,* Blaringhem (27).
var. *pseudo-androgyiia,* Blaringhem (28).

" K,pontaneoiis.'-Producing a series of new forms f ^nothera, de Vries (41»)
i.Drosoplnla, Morgan (270, 273).

| *in* asexual micro-organisms : | In sexual higher organisms : Oenothera. | | | | |
|---|---|---|---|---|---|
| **I** *Bacillus roll,* Barber (9). *Bacterium rofi mutabife,* Massini (90). | Completely inherited ; *0*. rubrinerris.* | Originating as a heterozygous dominant character : *Oe. t'uhricalyx.* | Completely inherited recessive character: *Oe. nanefla.* *Oe. brrcixfylis.* | Inherited usually in a small percentage : *Oe. lata.* *Ot. snnilatn.* *Oe. itti urratn.* | Partly reverting ami otherwise inconstant. *Oe. scintillans.* |
| Originating through a physical or morphological change: *Of. (jigas,* de Vries. *(h. temigigatt,* Stomps (351) *Oe. la/a,* de Vries *Oe. Htmilatu,* de Vries. *Trypa-noHoma JSvatm,* etc., Laveran and Roudsky (90). | Originating through «i chemical or physiological change : *Oe. 1'nh'h'alyx,* Crates (KM). *Bacillus coft-fypho*Hs,* Twort (JMt). *Trypnvo*oma Lewi*i.'* (iowler (90). | Originating through loss or latency of a character : *MeJaxoma #cripta,* Me-Cracken (243). "Cretin" sweet pea, Bateson and Punnett (17). *Peromyxcus leucopux nor.'horacentti* mut. *albir///tf,* Castle (49). | Originating through modification of a character: *Capselfa 1rur*a 2^^oris* mut. *Jfeer/eri,* Solnis-Laubach (344). Probably many others. | Originating through a quantitative change : Mutants in hooded rats, Castle (52). | Originating through reversion : *Zea may* tunicata,* East. |

**Originating.**

**In the wild.**
*Pcromyxcus leiicopui noveboracensi** mut. *afbidus,* Castle (40).
*Potentilla verjia* mut. *monophylla,* Domin (92)
*Helianthus tenticidnris* mut. *coronatus,* Cockerell (37).
*Amphidavys bctidarin* var. *doubledayaria,* Bateson (18).
*Cwreba {Ctrthiola) sacchariwt* var. *atrala,* Bateson (18).

**In cultivation.**
*Primula officinal U* mut. *horticola,*
Domin (9-2).
*Melandrium album* with small leaves, Baur *(21).*

**Originating.**

**In meio.sis :**
*Oe. lota.*
*Oe. rubricalyx.*
*Oe. biennvt .semiyiyas.*
*//. fentieularift* **mut.**
*roronatua,* Cockerell.

**In fertilisation or subse-**
**quently :**
*Oe. gigax'i*
Periclinal and sectorial
chimeras? Baur (19).

**As vegetative mutation.**

**In pure races :**
*PJiaseolu* rulyuri*,*
Johannsen (2(Ni).

**Through segregation in**
somatic cells of hetero-
zygous races :
*Solanum tuherosuni,* East
(96).
*Veronica longifolia* x V. 1.
*alba,* de Vries (398).

Through change in somatic cells from
hoiiiozygous to heterozygous condition.
*Mirahili* Jcilapa rarityata,* Correns (67).

**Originating.**

**In pure races:**
*Hordeum diatithum,* Kiessling (212).

**In crosses :**
Many probable cases.
*Bombyx mori*, Toyama (378).
*Antirrhinum ?najns,* Baur (20).

**New dominant characters :**
*O*:nolhera rubricalyx* (137).
*Zeamays,* alhinistic ear, Collins (61).
*Helianthus lentictdark coronatu*,* Cockerell (57).
*Primula sinensw,* giant, Keeble (210).

**New recessive characters :**
Many dwarf varieties.
Many white varieties of flowers, and albino animals.

**Historical mutations.**

11. *Chelidonium majus lacinialum,* 1590. Sprenger.
t>. *Mircnnalts anutta laciniata,* 1719. Marchant.

3. *Fragaria vesca mtmophylla* (fᵀᴹ⁸* **Lapland.**
**761.** **Versailles.**
4. Copper I>eech, 17th century.

Originating in prehistoric time : *Oyrontachys ceniua* 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 charactej-changes into dominants and recessives, he apparently considers this  distinction  so  fundamental  that  no  other class  or

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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." Tf the presence-absence hypothesis leads thus to a *ad 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 hetero-zygous mutants—facts which, as explained in the previous chapter, offer no serious difficulties on the chromosome hypothesis.   The cytological facts are, moreover, in har-mony 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 universal-ity ?   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 recessiyes 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 emboitement 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
emboitement th^pry 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 inheri-
tance 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
!s one thing and the subsequent inheritance of that
character is a very different thing.

K 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  x  *a b* all the gametes may be either A B or *a b,* while if the parents are A *b* x *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 believo, 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 6  x  *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 $F$, 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 lather 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 palaeontological 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 Noctuidas 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, *Coereba (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 tllan 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 phytogenies 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 paleontologists in a large number of fossil forms. Palaeontologists 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 palaeontological record.

Finally, it may be observed that evolutionary thought has become so manifold as to be almost co-extensive with biology itself.  Tt 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 ortho-genetic and frequently discontinuous.

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