THREE NEW MUTATIONS IN OENOTHERA LAMARCKIANA

Interesting plant forms found in a strain of evening primrose obtained from Professor De Vries. These mutants, showing new variations in leaf structure, pigmentation of stalk and buds, and color of flowers afford further material for analysis of this important group.

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ANY one engaged extensively in breeding Oenotheras discovers many new as well as old mutant types. The less striking of these are identified with difficulty and it does not seem desirable to encumber the literature with distinctive names for them. Now and again, however, a form appears which has such definiteness that it may be profitably used in breeding experiments, and references to these are facilitated by assigning to them names in harmony with the names already published for the other mutant types.

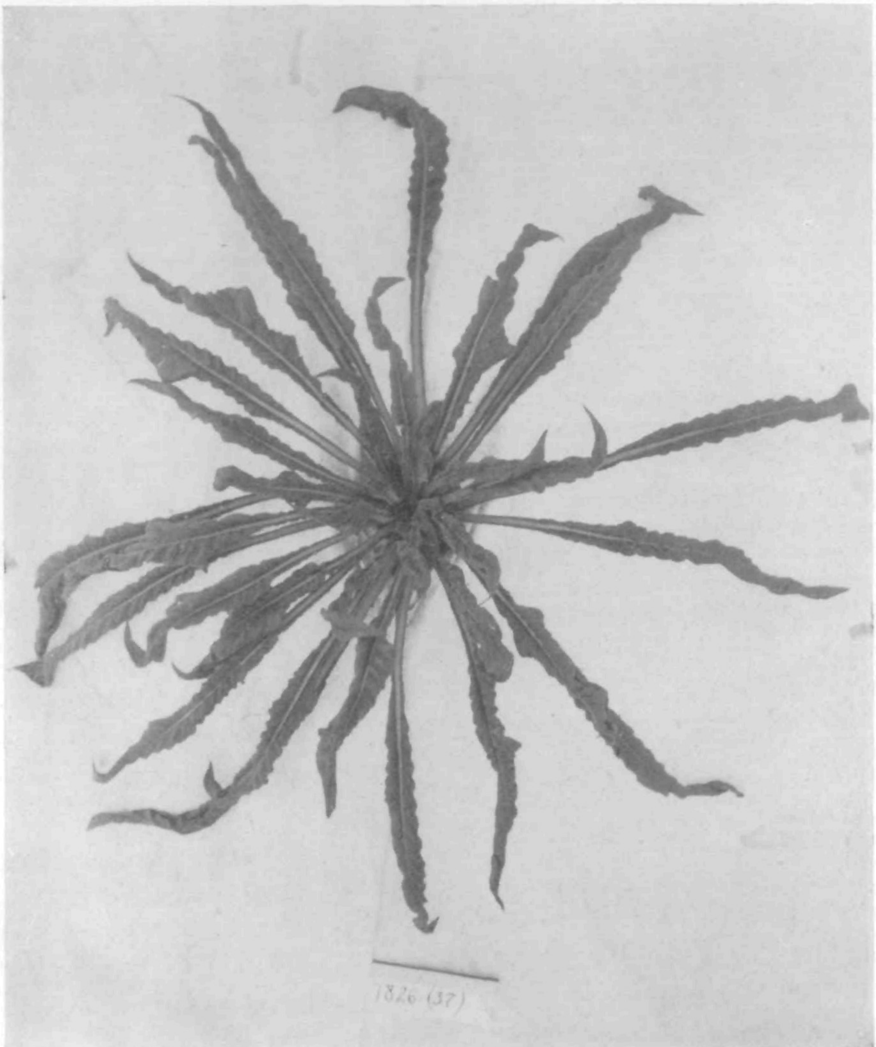
Among the mutations which have appeared in my cultures there are several which have exceptional interest and these are being used in numerous breeding experiments. Since they are destined to enter to a greater or less extent into the future literature of the group and since they have a certain amount of interest in themselves, quite independently of the experiments in which they are being employed, it seems desirable to give them a publicity which will serve to validate the names which are being used in the notes on their genetical behavior.

Since 1905 I have been keeping, in addition to many other Oenothera cultures, a strain of cross-bred *Oenothera Lamarckiana* which originated from nine original rosettes collected for me by Professor de Vries in the same field at Hilversum, Holland, from which he had secured the material for the initiation of his own Oenothera cultures about twenty years before. These cultures have been maintained, year after year, by crossings so arranged that every progeny in the strain has had four distinct grandparents. The three mutations here described have all arisen in this cross-bred strain.

Oenothera Lamarckiana mut. *funifolia* mut. nov.

DESCRIPTION OF STRUCTURE AND ORIGIN OF NEW VARIATION WITH NOTES ON ITS SIGNIFICANCE

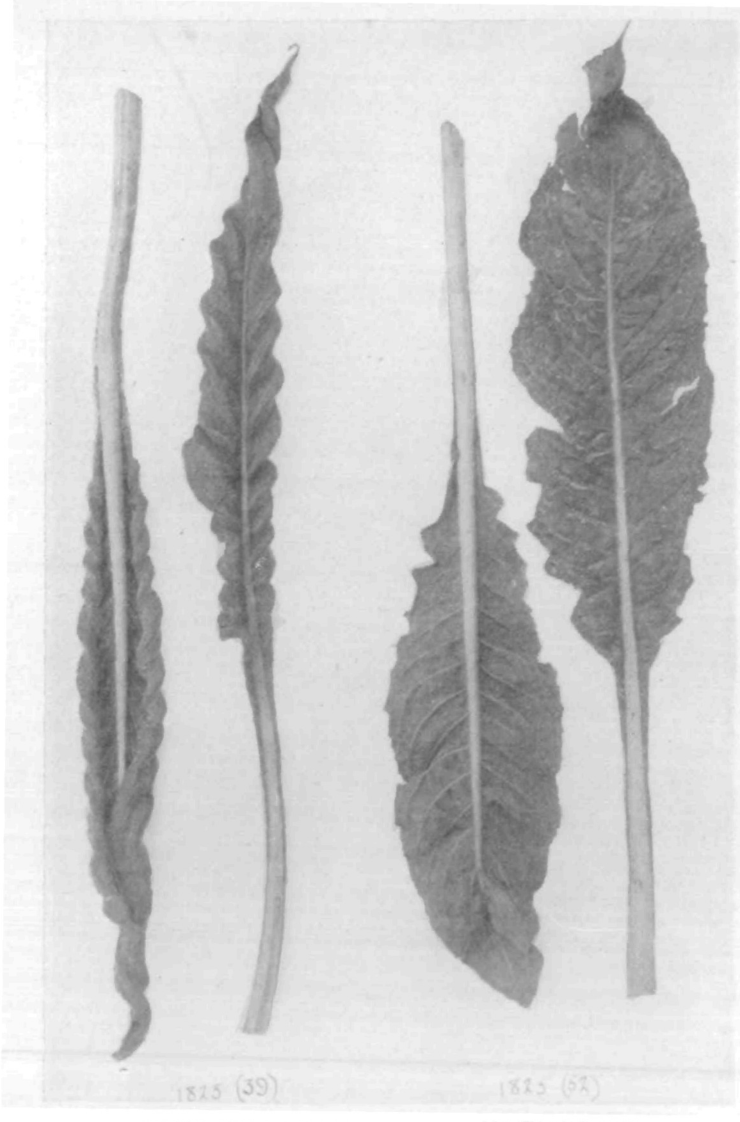
The most characteristic feature of the new mutation which I am calling *Oe. Lamarckiana* mut. *funifolia*, is the strong revoluteness or downward curl of the leaf margins, which in the best developed examples causes the leaf to have almost a cylindrical form. The leaf tissue between the lateral veins becomes more strongly contracted than the veins thus giving the leaves an appearance superficially resembling that of a braided rope, as shown in Figs. 8 and 9. Cross-sections of the leaves of *Oe. Lamarckiana* and of *Oe. Lamarckiana* mut. *funifolia* are shown in Fig. 10. Associated with this revoluteness of the leaf margins is an irregular fine rugosity of the ventral (convex) surface of the leaves which gives the plants a markedly grayish aspect (Fig. 11). In most strongly revolute specimens numerous small protuberances often occur on the ventral surface of the leaves, on either side of the midrib (Fig. 12). A section of one of these protuberances is shown in Fig. 13, where it is seen to differ in structure in no essential way from the body of the leaf from which it arises. There is also some modification of leaf outline, the leaves being usually rela-



THE FUNIFOLIA MUTANT OF OENOTHERA LAMARCKIANA

The most striking characteristic of this mutation is the curled leaf margin, which gives the appearance of braided rope, whence the name *funifolia*. It differs also from its parent, *Oe. Lamarckiana*, in having no basal branches. This is one of three new mutants which are likely to be of much use in breeding experiments, and which are described at length in the text. Photograph by James P. Kelly. (Fig. 8.)

tively narrower and, particularly in the stem-leaves, usually narrowing rather abruptly to short-acuminate apexes which are sometimes almost spinescent. Occasionally the midribs of some of the stem-leaves end in a short sub-apical spine-like spur on the under (dorsal) side of the leaf, a characteristic which is much more strikingly and consistently associated with revolute leaves in *Oenothera pratincola* mut. *formosa* Bartlett. When typically developed the *funifolia* plants can be detected readily in very early rosette stages (Fig. 14 left) but in less fully developed plants of this type the revolute character does not appear conspicuously in the earlier leaves of the rosette, and the revolute



FUNIFOLIA COMPARED WITH ITS PARENT

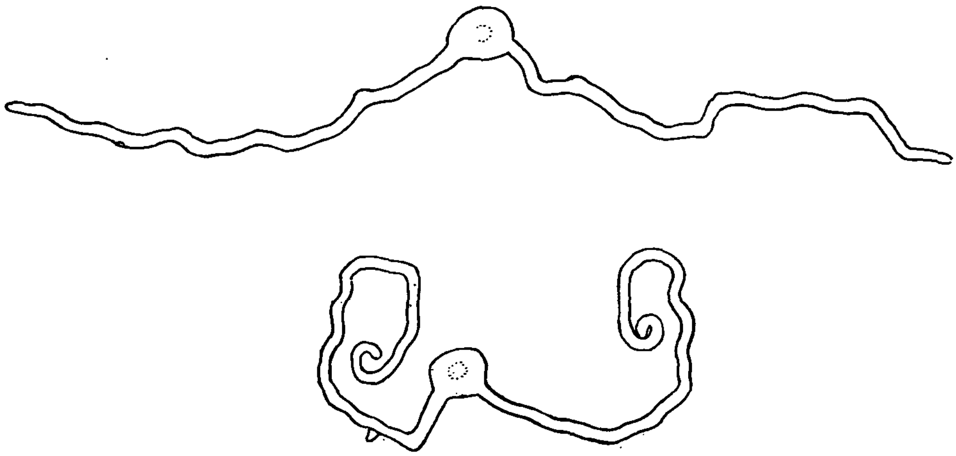
On the left are two leaves (one showing the ventral surface, the other showing the dorsal) of the *funifolia* mutant; on the right are two of the parent, *Oe. Lamarckiana*, arranged in the same manner. Here is brought out in striking manner the difference in leaf-form which has entitled the mutant to the name *funifolia*. In addition to their narrower shape, the leaves of *funifolia* are grayish on the ventral surface, a characteristic which is not found in the parent. Photograph by James P. Kelly. (Fig. 9.)

margins are limited to the basal portion of the leaf-blade. This under-development of the *funifolia* characters has been particularly noticeable in the case of *funifolia* segregates from crosses with *Oe. franciscana*. This result in the case of the *franciscana* cross is doubtless related to the fact that the latter species has thicker, stiffer leaves than *Oe. Lamarckiana*, and that the stiffness of the leaves is to a certain degree antagonistic to the revoluteness produced by the *funifolia* factor. In all cases, however, the *funifolia* character has been sufficiently well developed, that an error of classification has occurred only in one or two cases.

In the adult stage the chief difference between mut. *funifolia* and its parent, *Oe. Lamarckiana*, aside from the revolute leaves of the former, consists in the lack of basal branches in *funifolia*, such as are invariably present in *Lamarckiana*. The characteristic habits of these two forms are well shown in Figures 14 (right) and 15.

SUDDEN APPEARANCE OF SEVERAL MUTANTS OR "MASS MUTATION"

The first *funifolia* plants appeared in 1918 in pedigree family number 1720, the offspring of a self-fertilized *Lamarckiana* of the cross-bred strain mentioned above. There were five individuals of the *funifolia* type in a family consisting of 100 individuals, 90 of which were typical *Oe. Lamarckiana*. When these five plants were first observed in pot culture in the greenhouse they had the appearance shown in



LEAVES OF FUNIFOLIA AND ITS PARENT, IN CROSS SECTION

The lower diagram represents a leaf of the *funifolia* in cross section, the upper one, a leaf of *Oe. Lamarckiana*. (Fig. 10.)

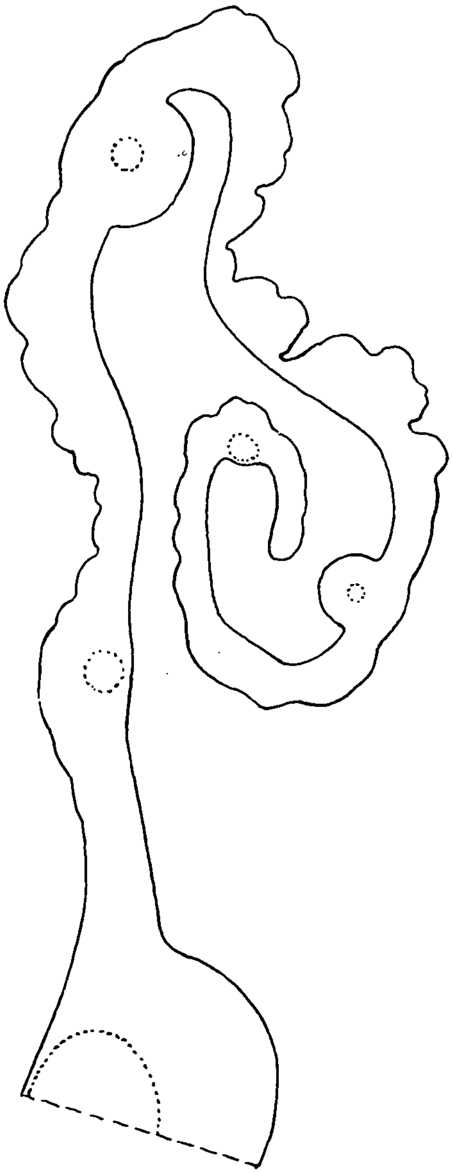
Fig. 16. At this stage the characteristic constrictions between the lateral veins are not present. The revolute leaves and grayish aspect suggested at first that these five plants were diseased, but it was demonstrated later that they were permanent normal hereditary characteristics.

This sudden quintuple appearance of a striking new type which had never before appeared in the extensive cultures of *Oe. Lamarckiana*, illustrates the phenomenon which Bartlett has called "mass-mutation," and the breeding tests which have indicated the method of origin of *funifolia*, may be used as a basis of interpretation of other cases of so-called "mass-mutation." The crosses of these five *funifolia* plants with their *Lamarckiana* sibs, and with *Lamarckiana* plants in other families, showed that the parent of family 1720 had been heterozygous for *funifolia*, but that the *funifolia* factor did not occur in any of my other *Lamarckiana* families, either in the independent strains or in the families most closely related genetically to family No. 1720. The conclusion seems justified therefore that the *funifolia* factor arose as a gene-mutation in 1916 in the production of the egg or the sperm whose mating resulted in the parent of family No. 1720.

Since *Oenothera Lamarckiana* is maintained in a heterozygous state by the presence of the two lethals, l_1 and l_2, in chromosome I, *funifolia* could become visible only through the process of crossing over. The relatively frequent crossing over of the *funifolia* factor from chromosome I*a* into chromosome I*b* or *vice versa* shows that there is an appreciable distance (possibly about 20 units) between the locus of the *funifolia* factor and the loci of the characteristic *Lamarckiana* lethals, l_1 and l_2. The only difference between "mass-mutations" and single (crossover) mutations is attributable to the fact that the loci of the former are relatively distant from the limiting lethals while the loci of the latter are very near to the lethals.

OTHER PARALLEL MUTATIONS

Perhaps the most interesting fact regarding mut. *funifolia*, is its status as a probable parallel mutation, since its characteristics are in essential agreement with those of Bartlett's *Oe. pratincola* mut. *formosa*. *Oenothera pratincola* and *Oe. Lamarckiana* are so unlike in every way that one can not logically assume a common ancestor except in a relatively remote past. If it should turn out, as I anticipate, that the *funifolia* factor in *Lamarckiana*



ENLARGED SECTIONAL VIEW OF FUNIFOLIA LEAF

One of the characteristic features of the *funifolia* mutant is the rugosity of the ventral (convex) surface. This is clearly brought out in the above drawing, which was made by J. Marion Shull from a mounted specimen. (Fig. 11.)

and the *formosa* factor in *pratincola* occupy identical loci, it will lend the strongest possible support to the view to which I have been led by other considerations, that there is a wide-spread homology of genotypic constitution in the Oenotheras. The necessary crosses have been made to test this question.

Oenothera Lamarckiana mut. *pervirens* mut. nov.

AN ALL-GREEN, RECESSIVE MUTANT FACILITATING ANALYSIS OF PIGMENTATION FACTORS

Oenothera Lamarckiana, as is well known, is characterised by pink-coned buds and greenish stems bearing numerous papillate hairs, of which the papillae are strongly reddened with anthocyanin pigment. There are, in addition, numerous characteristic details of form and size of all its parts. Breeding experiments have shown that *Oe. Lamarckiana* is a permanent heterozygote in regard to certain factors carried in one of its chromosome pairs (chromosome I), and that in one member of this pair (I*a* or "velans[1]") there is a factor for red bud-cones which is only partially dominant to the recessive factor for green or greenish bud-cones which occupies the corresponding locus in the other member, I*b* ("gaudens"[1]). It is probably the lack of complete dominance of the red-cone factor R^c, which gives *Oe. Lamarckiana* its characteristic pink cones. The presence of the recessive green-cone factor r^c is easily demonstrated by crosses between *Oe. Lamarckiana* and species characterized by green bud-cones, as this represents the back-cross of a heterozygote to the corresponding recessive and results in a 1 : 1 ratio, except as the ratio may be modified by linkage with lethal factors or by selective elimination. The presence of this receisves green-cone factor (r^c) is also evidenced by the frequency with which mutant derivatives of *Lamarckiana* have green or greenish buds. In most cases these green-budded mutants differ from *Lamarcki-*

[1] Names by which O. Renner has distinguished the two hereditary constitutions possessed by different germ-cells in *Oe. Lamarckiana*. They may be retained as names of the two members of chromosome pair No. I in this species.

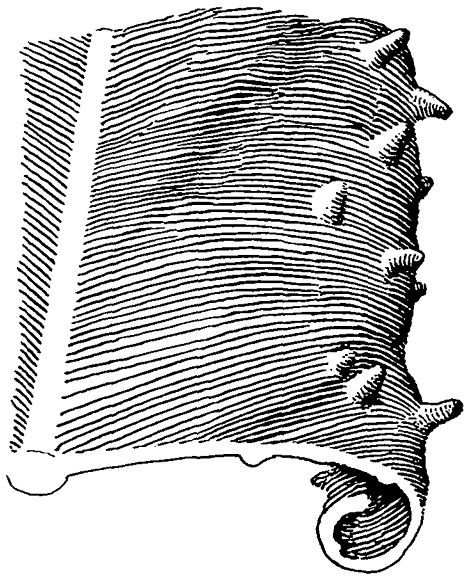
ana in many details of form, but in 1920 in family No. 193 there occurred among 78 typical *Lamarckiana* plants and 1 *bipartita*, one plant which was indistinguishable from *Lamarckiana* in nearly all details of form and size, but which had the buds entirely free from any trace of red pigment. The color of the papillae on the stems was not observed, but as all of the offspring of this plant by self-fertilization, have been wholly free from red papillae it may be assumed with assurance that this original specimen of mut. *pervirens* was characterized not only by wholly green buds, but also by wholly green stems.

SIMILARITY TO LAMARCKIANA SHOWN BY PARALLEL MUTATIONS

That mut. *pervirens* has essentially the same genotypic constitution as *Lamarckiana*, except in this complete loss of red pigmentation, is indicated by the composition of its progeny (No. 2046) for not only were there 140 *pervirens*, practically indistinguishable in form and habit from *Lamarckiana*, but there were in addition to these, two mut. *lata*, one mut. *oblonga* and one mut. *bipartita*, which differed from the parallel forms found in *Oe. Lamarckiana* only in being wholly free from red-pigmentation on buds and stems. There were also five unidentified mutants, one of which closely resembled *scintillans*, another *nanella* and a third *bipartita*.

ABSENCE OF PIGMENT AN AID TO GENETIC ANALYSIS

Since 1913 I have been tracing the genetical behavior of a factor R^s for intense reddening of the stems, but have had difficulty in many combinations because forms which do not possess this factor frequently show considerable reddening of the stems. In these the redness of the stems advances with advancing age, and is especially intensified with the onset of autumn coloration, so that classification into red-stemmed and green-stemmed series has become increasingly difficult in some crosses,with



WARTLIKE OUTGROWTHS, A CHARACTERISTIC OF THE FUNIFOLIA MUTANT

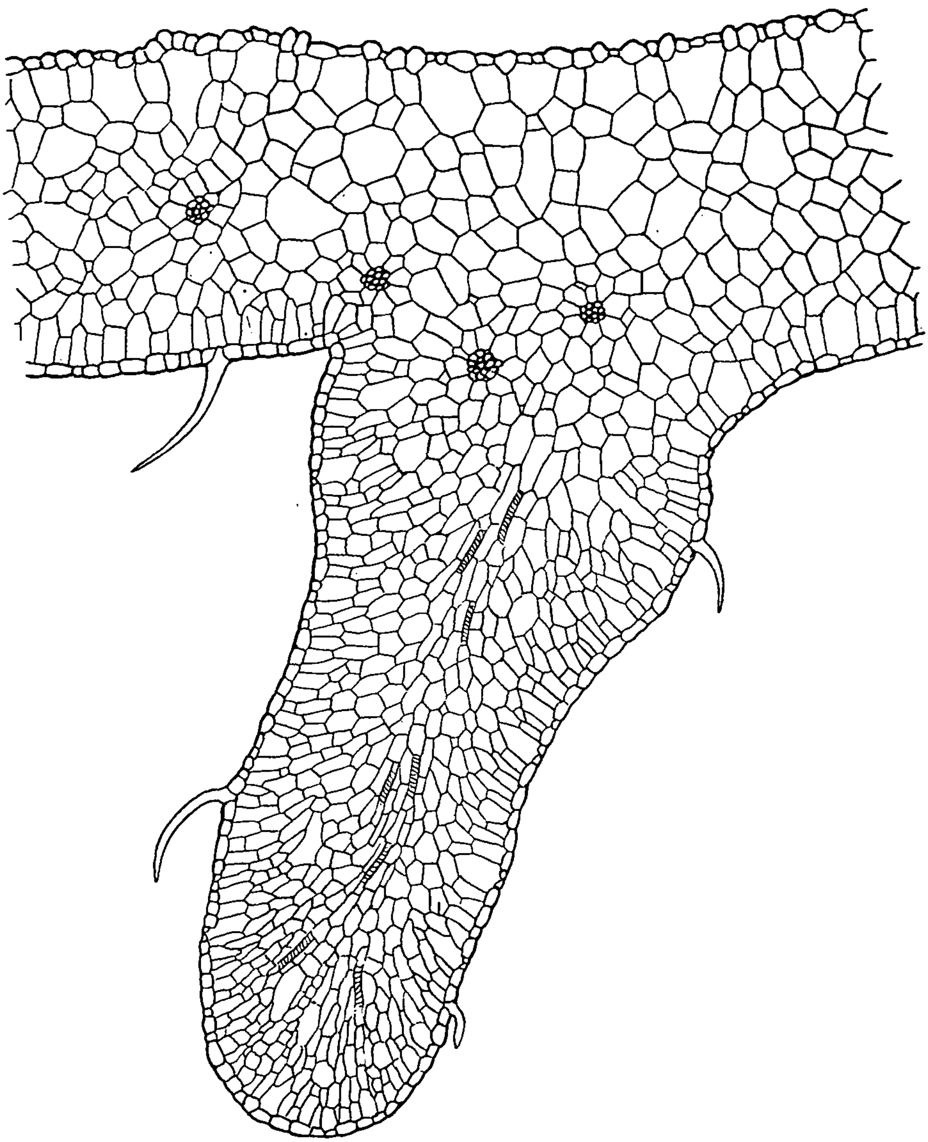
The above sketch, drawn by J. Marion Shull, shows a portion of a leaf of the funifolia mutant bearing the peculiar wartlike outgrowths which frequently occur on highly developed specimens of this type. (Fig. 12.)

the advance of the season. The great advantage to be derived from the discovery of a form wholly free from red pigmentation, and having at the same time the splendid qualities of vegetative vigor and fecundity which have made *Oenothera Lamarckiana* such a satisfactory subject for genetical studies, will be sufficiently obvious, and it may be confidently expected that with the aid of a recessive type which is free from red coloration on both buds and stems, and whose stems show no trace of autumn reddening the pigmentation factors will be capable of a much sharper analysis than has been possible heretofore.

Oenothera Lamarckiana mut. *vetaurea* mut. nov.

THE FIRST BREAK IN FLOWER COLOR IN VARIANTS OF LAMARCKIANA

Few characters are more constant throughout a large genus than is the yellow flower color of the Oenotheras.



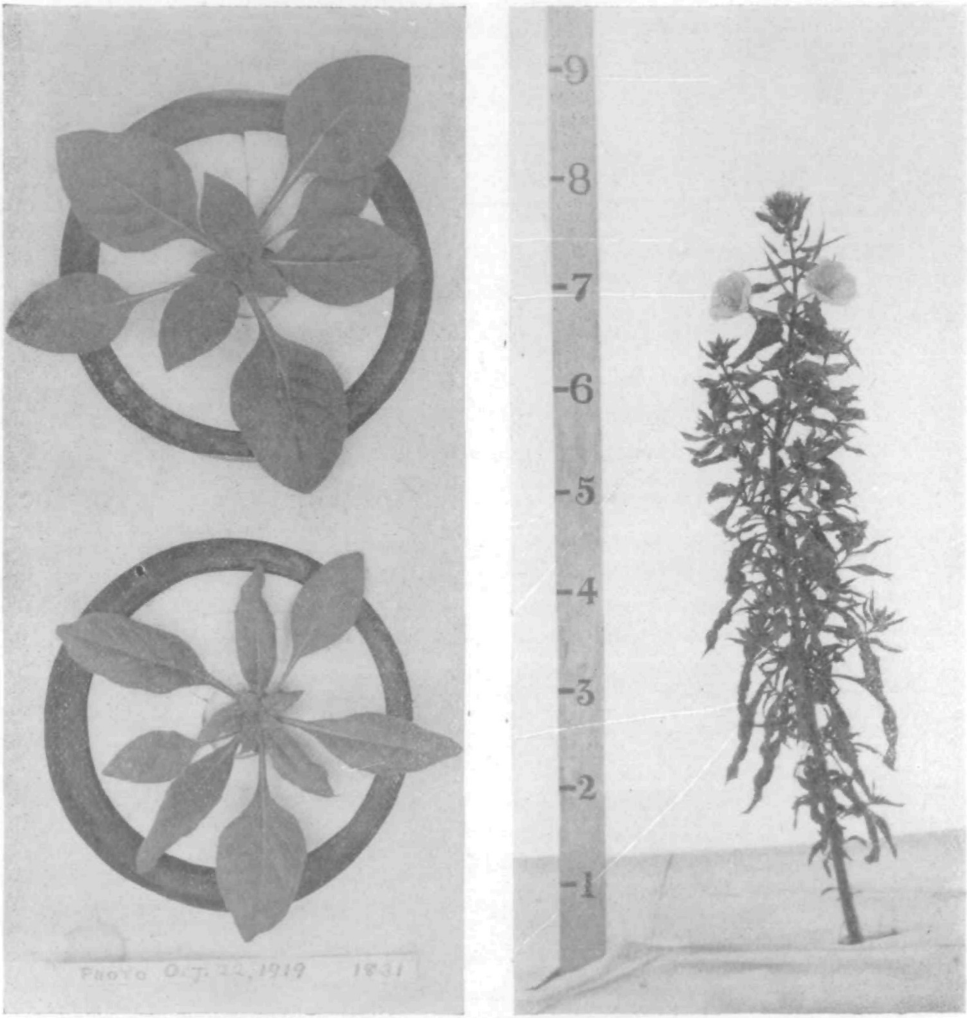
ENLARGED SECTION ON A FUNIFOLIA OUTGROWTH

In this drawing, made by J. Marion Shull, is shown in detail the structure of one of the peculiar outgrowths which characterize the *funifolia* mutant. (Fig. 13.)

For hundreds of years, however, a *sulfurea* or pale yellowish-white form of *Oe. biennis* L. has been known, widely distributed in Europe, and more recently the same variation has been observed in *Oe. suaveolens*, also, in nature. *Sulfurea*-flowered mutants have also arisen in experimental cultures of Stomps[2] and de Vries,[3] and the *sulfurea* factor has also been introduced into other species by means of hybridization, and has yielded

[2] Stomps, Theo. J. Parallele Mutationen bei *Oenothera biennis* L. Ber. Deutsch. Bot. Gesell. **32**: 179-188. 1914.

[3] de Vries, Hugo. Mutations of *Oenothera suaveolens* Desf. Genetics **3**: 1-26. 4 fig. Jan., 1918.



CHARACTERISTICS OF THE FUNIFOLIA MUTANT

The illustration on the left shows (above) a young rosette of *Oe. Lamarckiana*, and (below) one of the *funifolia* mutant. When typically developed, the mutant can be detected even in very early rosette stages.

On the right is shown an adult plant of the *funifolia* mutant. By comparison with Fig. 15, it will be seen that the mutant is distinguished from its parent by the complete lack of basal branches. (Fig. 14.)

genetic results of the utmost value in working out the genotypic constitution of the Oenotheras. So far as I know no other "break" has occurred in the flower-color of Oenothera until mut. *vetaurea* appeared in my cultures during the past summer (1921). This mutation consists in a departure from the common citron yellow color typical of all wild species of this genus, to a color which ranges from Naples yellow (Ridgway) in the more distal portions of the petals, to slightly deeper shades in the same series of colors, in the center of the flower. The filaments and the distal portion of the stigmas are approximately primulinus yellow. The warmer tone in the center gives the flowers an aspect almost as if they were aglow with a light of their own.

OENOTHERA LAMARCKIANA

Since the work of Professor Hugo De Vries with mutants of *Oe. Lamarckiana*, this plant has been extensively used by students of genetics. In the accompanying paper, Professor Shull describes three new mutants which have originated at Princeton, and which are likely to prove very useful. (Fig. 15.)

This beautiful mutation has appeared in two pedigree families (Nos. 2047 and 2052) which were progenies of two sibs in family No. 198 of my cross-bred strain of *Oe. Lamarckiana*, in 1920, and this fact makes it certain that the gene-mutation which made the realization of the *vetaurea* color possible occurred at least as early as 1919. Steps have been taken to test the extent to which the recessive *vetaurea* factor, *v*, is distributed in the cross-bred strain of *Oe. Lamarckiana* and the results of these tests should indicate whether the *vetaurea* gene-mutation probably occurred previously to 1919 or not.

Family 2052, in which *vetaurea* was first discovered, was the progeny of a typical specimen of *Oe. Lamarckiana*, and the single *vetaurea* specimen in this family was in all respects, except the color of the flowers, a typical pink-coned *Lamarckiana*. The other members of this family were all *rubricalyx*, being the F_1 of a cross between *Lamarckiana* and the characteristic homozygous alethal segregate from *Oenothera rubricalyx*, which I call *Oe. latifrons*. Only an accident of technique which resulted in a self-fertilization of the mother plant made it possible for the *vetaurea* specimen to appear in this family.

The parent of 2047, the other family in which mut. *vetaurea* has appeared, was itself a mutation in the cross-bred *Lamarckiana* family 198. It differed from *Lamarckiana* in having the bud-cones nearly free from red pigment, and the stems a clearer green, but finely speckled with red papillae as in *Lamarckiana*. The capsules were a little less well developed and slightly more divergent than in *Lamarckiana*. One of the two zygote lethals characteristic of *Lamarckiana* was also wanting in this green-budded mutant as shown by the fact that family 2047, produced by self-fertilization, split into (a) the parent type, namely, green-budded near-*Lamarckiana*, and (b) near-*decipiens*,

POT-GROWN ROSETTE OF FUNIFOLIA

The conspicuously revolute development of the basal portions of the leaves is characteristic of this mutant. Photograph by James P. Kelly. (Fig. 16.)

in the ratio 62 : 32,—almost exactly the 2 : 1 ratio expected in such a case.

Vetaurea AND *sulfurea* POSSIBLY ALLELOMORPHIC

There were some losses of plants in this family by death, and a small number, especially of the slow-growing *decipiens* type, failed to bloom. Of those which bloomed there were in the (a) group 40 yellow : 13 *vetaurea*, and in the (b) group two yellow: seven *vetaurea*. While these numbers are too small to allow one to place any dependence on their validity as a measure of the relative positions of the factors involved, it will be noticed that they assume the form of a linkage ratio, which gives a preliminary hint that the *vetaurea* factor is in chromosome I where the characteristic zygote lethals occur, and the amount of crossing over between the lethals and the *vetaurea* factor seems to be about the same as that between the *sulfurea* factor and the lethals. It will not be surprizing therefore if the *vetaurea* factor should be found to be allelomorphic to the *sulfurea* factor. The necessary steps have been taken to test this and many other problems which the presentation of this new unit-factor has suggested. An alternative hypothesis regarding the relation of *vetaurea* color to yellow and sulfur is also being tested.