ON THE DISTRIBUTION OF MUTANT CHARACTERS AMONG THE CHROMOSOMES OF *OENOTHERA LAMARCKIANA*

HUGO DE VRIES
Lunteren, Holland

AND

K. BOEDIJN
University of Amsterdam, Amsterdam, Holland

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During the last ten years the number of distinct mutant types of *Oenothera Lamarckiana* has increased considerably. One of us has determined the chromosome numbers for most of them, including those older ones, for which these figures had not as yet been ascertained. Moreover the fact that some mutant types are repeatedly produced by others has become very prominent, indicating some kind of genetic relationship. Outward features are often observed to run parallel with such connections; in other cases they are so much alike, as to give another trustworthy basis for the assumption of closer relations.

Starting from these facts, we have tried to arrange the mutant types into distinct groups, analogous to those proposed by MORGAN and his disciples for Drosophila. Unfortunately, it is in our case mostly impossible to determine dihybrid splitting figures, such as constitute the basis for MORGAN'S deductions. Differences in the ratio of growth of the pollen tubes, preferential fertilization of one of the kinds of egg-cells, in those cases where there are two or more of them, deviations in the partial sterility of pollen-grains and of seeds are among the main causes which tend to discard numerical data from our present considerations. But the distinctness of our results does not seem to suffer from this difficulty. We start from the numbers of the chromosomes, and bring those mutants, which do not deviate in this respect from the main species, into our first group. In doing so, we find that almost all of them belong to the ordinary types of mutations. They are mostly due to recessive characters, as, for instance, the dwarfs and the brittle races.

In a large number of the other mutants one of the chromosomes is doubled, bringing the total number of these bodies up from seven to eight

in the haploid cells, and from fourteen to fifteen in the somatic nuclei. Here, however, it is clear that the relations are not so intimate as to allow the combining of all these forms into one single group. Evidently there are some main mutations, from which the others may be derived, or to which they can be subordinated. These primary mutations have been described by one of us under the name of dimorphic mutants (DE VRIES 1916), since, after self-fertilization, their progeny mainly consists for one part of individuals of the parental type, and for the remainder, of specimens of the type of the original species, *Oe. Lamarckiana*. All of them are heterogamous, since their characters are not reproduced by means of their pollen.

Of these dimorphic mutants there are six main types. Three are old ones, having been observed since the beginning of the experimental cultures of *Oe. Lamarckiana* (DE VRIES 1901, pp. 273, 288, 300). They are called mut. *lata*, mut. *scintillans* and mut. *spathulata*. The three others have been described for the first time in 1916, in the article already referred to. Their names are *Oe. cana*, *Oe. liquida* and *Oe. pallescens*.

Among these six forms two are known to produce almost annually and in a high percentage another definite type, which, however, is distinct in the two cases. Mut. *lata* produces about 2 percent *albida* and mut. *scintillans* throws off *oblonga* in a still larger percentage. In some instances it reached 6 percent of the whole progeny (DE VRIES 1913, p. 314). The reverse process does not occur, and therefore *albida* must be considered to be secondary to *lata*, and *oblonga* to be derived from *scintillans*.

Albida and *oblonga* are, however, not dimorphic in the sense given above. They constitute constant races, but this constancy is due in part to the presence of barren grains among their seeds. They have two kinds of female gametes but only one kind of these is represented among their male sexual cells. From this very distinct character, they may be called "one-and-one-half" or "sesquiplex" mutants.

In considering the remainder of the 15-chromosome mutants it is to be noted that one of them, *Oe. candicans*, is also a sesquiplex type, but closely related to *Oe. cana*, whereas almost all the others are to be derived either from *Oe. lata* or from *Oe. scintillans*.

Semi-gigas types are known to have 21 chromosomes, and their derivatives vary in this respect with numbers going from 15 to 20. Our race of *Oe. Lamarckiana gigas* has 28 of such rods, as has been discovered by Miss LUTZ and GATES. These special types, however, must be excluded from the present discussion since in them the changes are not limited to

a single chromosome, but include, at least in their origin, all of them at the same time.

Returning to the fourteen- and fifteen-chromosome mutants we are led to distinguish the following groups:

A. 14-chromosome mutants.
   1. *Nanella.*
   2. Forms with homogeneous pollen and ovules.
      a. With normal fibres; *blandina, decipiens.*
      b. With brittle fibres: *deserens, tarda, fragilis.*
   3. Sesquiplex mutants: *simplex, secunda, compacta, elongata, favilla, linearis.*

B. 15-chromosome mutants.
   1. *Lata* group.
      a. *Semi-lata.*
      b. Sesquiplex mutants: *albida, flava, delata.*
      c. *Subovata, sublinearis.*
   2. *Scintillans* group.
      a. Sesquiplex mutants: *oblonga, aurita, auricula, nitens, distans.*
      b. *Diluta, militaris, venusta.*
   3. *Cana* group: *candicans.*
   4. *Pallescens* group: *lactuca.*
   5. *Liquida.*
   6. *Spathulata.*

With the exception of those mentioned under B 2 b, the chromosomes for all of these types have been counted. The homogeneous mutants of the first section do not arise, as a rule, immediately from the parent species, but through the intermediate of half mutants (DE VRIES 1919). These are, in the sequence given above: *problandina, erythrina, rubrinervis, scindens* and *simplex.* All these have 14 chromosomes. To this group belongs the *rubricalyx* of GATES, which is a half mutant with 14 chromosomes. Analogous to *decipiens* is the *latifrons* which is a homozygous alethal segregate, derived from *rubricalyx* by SHULL (1921, page 362).

Of the sesquiplex mutants, enumerated in the first section, *Oe. simplex* is the original type, the others having sprung directly from it. In the group of *Oe. lata* the mutants *albida* and *subovata* are old forms, whereas *flava, delata* and *sublinearis* are new derivatives from the main type. From *scintillans* the forms called *militaris* and *venusta* have sprung, but *auricula* and *aurita* have originated independently. In their external

features, however, they closely resemble *Oe. oblonga*. *Oe. nitens* is so like *Oe. scintillans*, that it has been described originally under this name (DE VRIES 1918, p. 13) and *Oe. distans* and *Oe. diluta* have been derived from it.

Full descriptions of the stature and characters of the new types will soon be given in "Flora" and the "Zeitschrift für Botanik."

From this review we conclude that there are three large groups of mutants and probably four small ones. Among the first, one has only mutants with the normal number of chromosomes, and their characters are mostly of a recessive nature. It is probable that this group includes also the factors which determine the difference between the *laeta* and *velutina* gametes. We will call it the "central" group. This gives for the other divisions the name of "lateral" ones. Two of them are large, consisting of several externally similar or genetically related races. The four remaining groups are very small, each including as yet only one or two types.

In his classical researches on Drosophila MORGAN has compared the groups of the mutants of this fly with the relative size of the chromosomes and concludes that the larger rods carry the factors of the large associations, whereas the smaller groups are located in the smaller chromosomes. Now if we extend this principle to our case, we are led to expect three large chromosomes and four small ones in the haploid nuclei, or three large and four small pairs after copulation.

Unfortunately, the size of the chromosomes in *Oe. Lamarckiana* and its derivatives is so small, and the irregularities in their reduction phenomena are so prominent, that until now no direct answer can be given to our question.

But one of the Californian species, which are most intimately connected with *Oe. Lamarckiana*, gives better results. RALPH E. CLELAND (1922) has described the reduction divisions in the pollen mother cells of *Oe. franciscana* Bartlett. In mid-diakinesis the chromosomes are arranged in rings, each ring consisting of one or more pairs, as shown on CLELAND'S plate XXVII, figures 25–29. Differences in size are easily seen and most clearly in figure 28. Three pairs are large, but four are evidently smaller. The three first ones are on one side and the small ones on the other, constituting two sharp groups. In clearness and distinctness these preparations far surpass those obtained by previous authors from other species and from mutant races.

Therefore, it seems permissible to apply the results of CLELAND provisionally to our question. If we do so, our three large groups of mutants

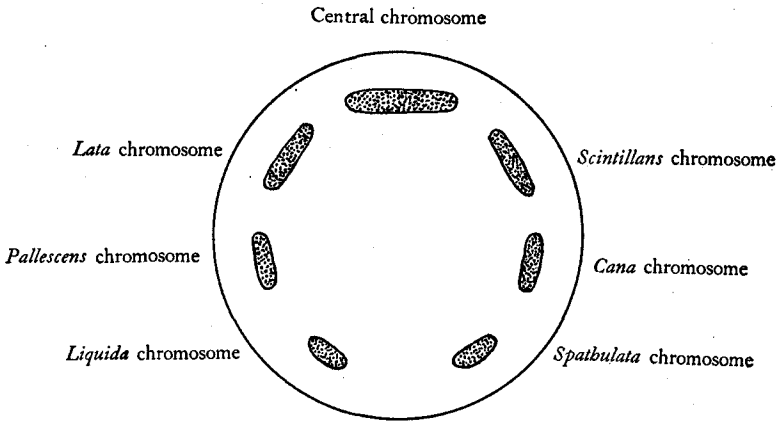

FIGURE 1.—Diagrammatic view of the seven haploid chromosomes in *Oenothera Lamarckiana*, to each of which, except the "central chromosome," is provisionally assigned one of the groups of 15-chromosome mutants.

obviously correspond, at least essentially, to the three large chromosomes and the four small groups to the four smaller chromosomes. We may then put the results of our investigation in the form of the following scheme (figure 1). In this scheme the position and relative size of the chromosomes have been drawn in accordance with figure 28 of CLELAND, but the axis of the figure has been turned a little so as to make it more clearly symmetrical. Of every pair only one rod has been reproduced.

Our central chromosome obviously corresponds to the chromosome I of SHULL (1921), which in the contrasting gametes of *Oe. Lamarckiana* carries the factors for the characters of *velutina* (I a) or those of *laeta* (I b). The new mutants *funifolia* and *pervirens* constitute also, according to the description of this author, members of the central group of mutant characters.

The lateral chromosomes have been given the names of their primary, dimorphic mutants, the sesquiplex and rarer mutants in each group being considered as of secondary importance.

Of course our scheme is only a provisional and in part an arbitrary one. But it is corroborated by the quite analogous results of BLAKESLEE with Datura. Many smaller arguments could be given to support it, as will be seen from the detailed description of our researches. We will here only adduce a single point, relating to the 21-chromosome types or *semi-gigas*. These proceed from *Oe. Lamarckiana*, with its two kinds of gametes, as

well as from *simplex*, all the sexual cells of which belong to the type of *laeta*. Now, whenever one of the lateral chromosomes mutates and is doubled, this does not seem to affect the sister chromosomes. But each time, when the central chromosome is doubled, all the lateral ones are affected in the same way, at the same time producing one or often a larger number of their possible mutations. "Very manifold groups of forms" (DE VRIES 1913 p. 333) may thereby arise, but their description must be put off till another opportunity.

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