CHAPTER 10

OENOTHERA

As was pointed out in Chapter 3, there was a growing interest in discontinuous variations in the 1890's. In 1901 there appeared the first volume of de Vries' monumental *Die Mutationstheorie,* in which he developed the idea that evolution occurs through discrete steps ("saltations" or "mutations") rather than by gradual changes accumulated by selection. This conclusion rested on a vast amount of data concerning many kinds of plants but was based more especially on the work of de Vries on the evening primrose, *Oenothera Lamarckiana*.

The members of this genus are American in origin, but several of them have escaped from cultivation in Europe, and grow in sandy or disturbed soil there, as they do in much of the United States and Canada. De Vries found a patch of Lamarckiana growing in an abandoned field at Hilversum in Holland, and noticed that two variant types were present. He brought all three types into his garden and found that the typical form produced a series of mutant types, generation after generation. Many of these new types bred true, and most of them differed from the parental form in a whole series of relatively slight respects. It is now known that this is because they differ from the parental form in many genes, and that Lamarckiana is a very unusual and special kind of multiple heterozygote. But to de Vries these new forms were essentially new species, and their sudden occurrence meant that selection had little or nothing to do with the origin of new species that differed from their parents in numerous ways. This was the mutation theory in its original form; it is ironic that few of the original mutations observed by de Vries in Oenothera would now be called mutations.

It seems likely that the properties of these new types were largely responsible for the emphasis placed by many geneticists on the multiplicity of phenotypic effects of single gene changes. It became the custom to emphasize the cases where such multiple effects occur—though surely if geneticists had approached their material without preconceived ideas, the striking thing would have been the relative scarcity of obvious multiple effects of single-gene substitutions.

It soon became evident that the genetic behavior of Oenothera is unusual. The short-styled type (brevistylis) of Lamarckiana was one of the Mendelian characters listed by de Vries in 1900, but it gradually became a puzzle in itself, since nothing else in the plant behaved in so orthodox a way.

The first examples of the new types to be explained were gigas, a tetraploid with 28 chromosomes instead of the usual 14, and lata, a trisomic with 15 chromosomes (Lutz, 1907, 1909). These led to a whole series of observations and experiments with other organisms, but they left unexplained the majority of the Oenothera mutant types, since these were found to have the 14 chromosomes of typical Lamarckiana.

The behavior of these 14-chromosome types when crossed to Lamarckiana, and the results of crosses between various distinct wild forms (biennis, muricata, and so on) were puzzling, sometimes giving "twin" hybrids (that is, two distinct types in F_1 from true-breeding parents), usually giving different results from reciprocal crosses, and usually producing hybrids that bred true. Bateson, and later Davis, suggested that Lamarckiana is really a hybrid—but this suggestion, while probably correct, did little to explain its anomalous behavior. Meanwhile de Vries published many data that seemed to show regularities but resisted all attempts at a systematic analysis.

The solution of the problems was really begun by Renner in a remarkable series of papers that were long disregarded, even by those of us who were actively trying to relate the published data to a scheme consistent with what was known elsewhere. This neglect of Renner's work was undoubtedly due to his use of a system of terminology which was and is very convenient for Oenothera but makes the papers unintelligible unless the special terminology is first learned. When it is learned, the papers are found to be written in a very clear and logical style.

The series of papers began in 1913 with one on fertilization and early embryology; it showed that a suggestion of Goldschmidt's (merogony) was incorrect. This was followed in 1914 and 1917 by a study of the embryos and seeds from Lamarckiana after self-pollination and after crossing with other species. These studies showed that Lamarckiana is a permanent heterozygote between two "complexes" called "gaudens" and "velans." After self-fertilization about half of the seeds contain inviable embryos. Half of these die at an early stage, and the other half at a later one. Renner concluded that these inviable seeds represented the gaudens-

gaudens, and velans-velans types, respectively, whereas the viable seeds were all gaudens-velans heterozygotes. In agreement with this was the fact that crosses (for example, to muricata) that gave twin hybrids gave fully formed viable embryos in almost all the F_1 seeds. Renner here developed the hypothesis of balanced lethals, though he did not use that term. He also suggested, especially in the 1917 paper, that such “mutant” types as nanella and rubrinervis arise from recombination between the two complexes.

In biennis, muricata, and suaveolens, the functional pollen is all of one kind, and the eggs are mostly of a different kind, so that crosses with these species yield reciprocal hybrids that are different. Renner studied the pollen in these species and in hybrids from them and showed (1919) that each produces two kinds of pollen in equal numbers, which are distinguishable especially by the shape of the starch grains they carry. Only one of these types is functional, as shown by the shapes of the starch grains in the pollen tubes in the styles, and in the pollen of their hybrids. Here was a direct demonstration of a pollen lethal and also a clear disproof of the idea of somatic segregation that Bateson continued to insist on in certain cases in Matthiola and in Pelargonium, where the pollen also fails to transmit some of the genes that may be recovered from eggs of the same individual.

The eggs, especially in muricata, only rarely transmit the complex that is transmitted by all the pollen, and Renner’s studies (1921) showed why this occurs. In Hookeri, which is homozygous, or in Lamarckiana, where the eggs are of two kinds in nearly equal numbers, he found that the uppermost (micropylar) megaspore of the four that result from meiosis is regularly the one that functions to produce the gametophyte. That is, it has an advantage due to its position. But in muricata the upper megaspore functions in only about half of the ovules; in the other half the basal of the four is functional. Evidently the “rigens” complex has an inherent advantage over the “curvans” one that usually enables it to function even when it occupies the less favorable position—although it never functions in the pollen. Here then, by study of the nature of the cells themselves, Renner succeeded in solving the problem of how the Oenothera species maintain their balanced condition—both the “homogametic” condition of Lamarckiana (where eggs and sperm both transmit both complexes) and the “heterogametic” one of muricata and similar forms (based on pollen lethals and megaspore competition).

These results left unexplained the nature of the “complexes,” which Renner interpreted as groups of linked genes, and he set about analyzing them in terms of separable components. It was soon apparent that the linkages are not constant. The dominant gene for red midribs on the leaves is completely linked to the complexes in muricata and biennis, but segregates independently of them in Lamarckiana. The various hybrids show one or the other of these kinds of behavior, but almost never an intermediate type with moderate linkage. In some of the hybrids, such as curvans-velans (from muricata by Lamarckiana), there is rather extensive recombination between the complexes, and Renner made use of such hybrids to dissect the complexes into their component parts. The most extensive account of these studies appeared in 1925. In this paper Renner concluded that if two genes are independent in any combination, they are in different pairs of chromosomes, and if these same two are closely linked in another combination, then in the second case the two pairs of chromosomes are not showing recombination. He suggested that the explanation was probably to be sought in the chromosome rings that Cleland had already described in Oenothera.

Cleland reported in 1922 that the 14 chromosomes of *Oenothera franciscana* do not form 7 bivalents at meiosis, but 5 bivalents and a ring of four. In 1923 he recorded still larger rings, including a ring of 8 and one of 6 in biennis, and a ring of 14 in muricata. He showed that alternate chromosomes in these rings pass to the same pole at the first meiotic division and suggested that this behavior might be related to the frequent linkage of characters that occurs in Oenothera.

Similar chromosome rings were observed in Datura by Belling, who in 1927 suggested that they were due to the past occurrence of translocations, so that two original nonhomologous chromosomes, with ends that may be represented as a.b and c.d, gave rise to two new chromosomes that between them carried the same genes but had the arrangement a.d b.c (or a.c b.d). He specifically suggested that the repeated occurrence of such translocations might give rise to the large rings of Oenothera. This suggestion was then followed up by Cleland and Blakeslee (1930) and by S. Emerson and Sturtevant (1931), who showed that it could be utilized to give a self-consistent scheme for the numerous configurations known, and that this scheme was also consistent with the variable linkage reported by Renner. With this result, the peculiar genetic behavior of Oenothera was at last brought into line with the general Mendelian scheme.

More recently these principles have been used by Cleland to build up a very extensive series of analyses of the chromosome makeup of a large number of strains collected over most of the United States, and by Renner and others to locate particular genes in particular chromosomes. The discovery of a “V-type” position effect in Oenothera by Catcheside will be referred to later (Chapter 14); the most recent advance in the unravelling of the genetic complications of the group is the discovery by Steiner (1956) that the egg complexes of many wild forms of the eastern United States carry self-sterility alleles of the oppositional type already known in the remotely related *O. organensis* (S. Emerson, 1938).