

REVIEW

OENOTHERA, CYTOGENETICS AND EVOLUTION. R. E. Cleland. Acad. Press, London, N.Y., 1972. 370 pp. £7.

This book is the story or most of the story, of the great *Oenothera* problem. It is also the story of the life of its author. For Ralph Cleland, who was born in 1892, ended his life when he finished writing the book in June 1971. To understand the whole business we need to go back even further than Cleland does, in fact to the death of Darwin in 1882. At that time there were a number of earnest Darwinians who believed that Darwin had led his followers astray and that they ought to be put back on the right path. First Weismann in Germany, then de Vries in Holland, and lastly Bateson in England, decided for their own different reasons on two connected steps. One was that Darwin's Lamarckism, his pangenesis, was false and must be rejected. The other was that Darwin's continuous variation and blending inheritance, which had led him to the Lamarckian error, must be replaced by discontinuity, by biological atomism, by mutation. Unknown to the others, of course, Mendel had shared these two opinions.

The first to be seized with the mutation idea was de Vries and it happened, we may guess, about the time in 1886 when he discovered plants of *Oenothera Lamarckiana* at Hilversum near Amsterdam, on the wasteland it always favours. And among them were his "mutants". His discovery ushered in a lifetime's work for himself, for Cleland and for many others. It also ushered in a greater train of events, a new age of experimental breeding of plants and animals, the rediscovery of Mendel and the development of genetics.

De Vries concluded from his mutants, some of which bred true, that mutation, whatever its cause or character, lay at the root of all hereditary and evolutionary processes, and when his *Mutation Theory* appeared in 1901 experimenters elsewhere began to repeat and extend his work, often using the seed he freely gave them. Then, as Cleland explains, three apparent flaws in his argument came to light.

One flaw appeared when an American investigator, Bradley Moore Davies, by a searching enquiry on both sides of the Atlantic, found that the Hilversum plants of "*Oe. Lamarckiana*" had come, not from Texas as a chain of seedsmen gratuitously pretended, not indeed directly from America at all, but from plants growing on the coast of Lancashire. Hence the importance of this stock lay not in its giving rise to new species, but rather in its having arisen itself as a new species in Europe. It had come, almost certainly, from a cross between two stocks, Virginian and Californian, whose seed had been brought together when ballast was discharged from ships reaching Liverpool from opposite sides of the American continent. It was a cross of a kind of which no natural example has ever been found in America but which, since 1850, has probably often occurred in Europe as a result of human intervention.

A second flaw had already been discovered by de Vries himself. For when he crossed different wild species of *Oenothera* he found they often gave, not a single uniform mendelian F₁, but "twin hybrids". It was as though, in Mendelian terms, one or both parents were heterozygous.

The third flaw appeared from the behaviour of the chromosomes. In these presumably heterozygous *Oenothera* species, instead of forming pairs at meiosis like most plants and animals, the chromosomes, so it was said, were joined, end to end, in a ring of fourteen. Neighbours went, as a rule, to opposite poles to give even and equal segregation. But not always, for some mutants had extra chromosomes: they were trisomics, numerically at least like those to be discovered in other plants and also much later in man. They were the trisomics whose particular character was to be neatly elucidated 30 years later by Catcheside.

From all this it became clear to many people (although hardly to de Vries) that the mutations of *Oenothera* were not in themselves the much wanted clue to a general theory of heredity and evolution. On the other hand, as the work developed, it also became clear to a few that no theory of heredity could afford to disregard *Oenothera*. Its aberrations had to be explained. But the explanation came only from a sequence of experiments and observations stretching over many years and many countries. How it all happened deserves to be carefully studied (with the help of Cleland) because much of it is still widely misunderstood.

The deeper meaning of the problem and hence the way to tackle it was discovered by Otto Renner at Munich between 1910 and 1920. And it was discovered obviously owing to Renner's unique understanding, both physiological and genetical, of the processes of plant development. Renner disregarded de Vries' cumbersome theory and terminology and proceeded on mendelian assumptions. He went on to examine the growth, the viability and the competition of pollen grains, embryosacs and embryos. In this way he was able to show that the species of *Oenothera* were hybrid in a novel sense. The differences were between complexes; these segregated as units without crossing over; and they were eliminated when homozygous.

It was these principles that caught the interest of Sturtevant and Muller engaged at the same time in the parallel elucidation of *Drosophila* where crossing over and segregation were bound up together. Renner's analysis gave a consistent account of *Oenothera*. It also threw light on new and far-reaching biological problems. It provided the first visible evidence of segregation at meiosis. It revealed new relations of nucleus and cytoplasm in the developing germ cells, relations quite unparalleled in animal embryology. But it did not seem to connect with *Drosophila*.

The connection was made through the chromosomes and it was made by Cleland. With species and hybrids he showed that each had a characteristic ring of chromosomes at meiosis corresponding in size with the size of the complex-unit that Renner had identified. The preparations Cleland had made he demonstrated in 1927 to the International Genetics Congress at Berlin. Cytologists, including myself, had often read unconvincing accounts of chromosomes united end-to-end in rings at meiosis. Now for the first time we saw them and saw that they were true.

Problems however remained, many problems. And they were different problems for different people. How different became clear from the papers published in the following five years, and also (privately) from the correspondence between Cleland and myself. To Cleland his discovery meant that *Oenothera* had rules for heredity and rules for chromosome behaviour, all of its own. They were different from those known, and rather well understood in peas and flies and grasshoppers and lilies, and elsewhere. For the chromo-

somes at meiosis they were the peculiar rules of "telosynapsis", a special manifestation of the "continuous spireme", which had to be discovered from observations and experiments with *Oenothera*. To me, however, it meant that we could now try to find how universal rules applied to *Oenothera*; how the specificity of side-by-side pairing or "parasynapsis", with its necessary and universal sequence of pachytene—crossing-over—chiasma formation—metaphase pairing—segregation—reduction, worked in this special situation.

How could these rules be applied? It was necessary to assume a condition that I called structural hybridity. Such a condition would result from an earlier interchange of segments. There was no novelty or difficulty in assuming one or two interchanges. The difficulty was in imagining a sequence of six interchanges with a network of genetic interactions, following one another and favoured at every step by natural selection. If this could be properly inferred it would in the first place allow us to explain *Oenothera* and all the work of de Vries and Renner; it would remove the inconsistency from our understanding of its chromosome behaviour and heredity. And, in the second place, what was much more important, it would allow us to see how evolutionary processes and mechanisms of heredity and reproduction worked on one another reciprocally in all sexually reproducing organisms; worked moreover by sequences of adaptive interactions of an interlocking kind which had never hitherto been visualised. This was the birth of the idea of the genetic system.

Accordingly, when Cleland's results appeared in the proceedings of the congress the following year, unexplained except by the word "telosynapsis", I wrote a short account of my interpretation of the *Oenothera* story. I assumed that a sequence of interchanges had promoted, maintained and enlarged hybridity. I then assumed that the success of the hybridity at each stage of its promotion was due to natural selection, a Darwinian principle which de Vries and his followers had been inclined to throw overboard along with Lamarckism. All the aberrations of *Oenothera* could then, I argued, be derived from these premises and would fall into place in the general scheme of genetics, chromosome theory and evolution.

Cleland was shocked by this intervention. For one unconnected with any kind of work on *Oenothera* to introduce into the argument *theoretical* considerations derived from the study of other organisms seemed to him at the time, and still seems to him, in writing this book after 40 years, unintelligible something like an act of treason. It is for this reason, I must suppose, that, with the best will in the world, here as always he refers to my interpretation of *Oenothera* as "Belling's theory" when he is confirming it, and as my theory when he is contradicting it. It was a distinction which alike surprised Belling, in 1932, when I discussed it with him and surprised me.

It was however from this distinction we can now see that *Oenothera* research developed. For it diverged, subject to the opposed assumptions of the investigators. His own side of these enquiries Cleland carefully describes. He himself followed the evolution of the species, in the subgenus *Oenothera*, as they spread across the United States after the retreat of the ice, interchanging their segments and developing their hybridity as they went.

The contrast between Cleland's point of view and my own became apparent to me by steps. The steps concerned two assumptions which I found necessary and explained in later papers. The first was about the positions of

interchanges. Here Cleland had taken his cue from Dr A. F. Blakeslee who in turn had taken his cue from what he imagined to be Belling's explanation of the trisomics in *Datura*; they had all assumed that interchange was the result of breakage and reunion at what we now call the centromere: Belling had spoken of "arms" so they all spoke of arms. For me however it was, *a priori*, uncertain where interchanges had taken place. But in 1930 I found that chiasmata were formed in *Oenothera* in interstitial segments demonstrating, as I argued, pairing and crossing over between the points of interchange and the centromeres. I could then be sure that the two did not coincide. At the same time, this figure-of-eight configuration was, secondly, showing that interstitial segments destined to become differential were the inherent property of heterozygotes arising from such interchanges; thirdly it was showing that these same chiasmata represented crossing over and secondary interchange necessary to explain the origin of half-mutants, mass-mutants and the rest (*J. Genet.*, 1931: 24, p. 456; 1936: 32, p. 344). The same type of configuration demonstrating the interstitial segments was later described by Sansome in rings-of-six in *Pisum* (*Cytologia*, 1933: 5: pp. 15-30).

Later work has clarified the distinction between the possible sites and modes of origin of interchanges. On the one hand, the study of both natural and experimentally induced interchanges shows that they may occur at all points in the chromosome but only rarely at the centromere. On the other hand, my own studies of meiosis later indicated that the centromeres of unpaired chromosomes at meiosis, are liable to misdivide giving rise to both interchanged chromosomes and iso-chromosomes. No one I suppose now doubts that the abnormal secondary and tertiary types of trisomic *Datura* arose from such misdivision in the unpaired extra chromosomes. That is why *Datura* proved to be misleading as a basis for the understanding of structural hybridity in ordinary diploid *Oenothera*.

The second step in divergence concerned the mode of development of heterozygosity. The alternative possibilities I represented in a diagram (*J. Genet.*, 1931: 24, p. 454). One assumed the separation of races homozygous for different interchanges which afterwards crossed to give rings. This had happened experimentally in *Datura* and was again the view that Cleland, following Blakeslee, had taken for granted. The other assumed that the interchanges occurred and accumulated under selection pressure within a population that was being forced towards inbreeding. Later experiments with *Campanula* (Darlington and La Cour, 1949, *Heredity*, 4, p. 221, table 3) together with the failure to find any interchanged homozygotes in *Oenothera* convinced me that accumulation with and indeed by inbreeding such as we expect on the edge of an advancing species was the only acceptable explanation. The abundant later work by Cleland described in this book shows just how the inbreeding and the heterozygosity were forced on *Oenothera* together as it moved eastwards across America. The same process has been demonstrated by James for *Isotoma* in Australia (*Heredity*, 1970: 25, pp. 53-77) and by John and Lewis in *Periplaneta* and *Blaberus* (*Heredity*, 1958: 12, pp. 185-197; *Genetics*, 1959: 44, pp. 251-267).

Last of all in the history of *Oenothera* came Renner's work on the plastids. Here Cleland renders particularly useful service, for never before have the plastid story and the chromosome story been set out in such detail side by side for their connections to be seen. The plastids make another lesson which, in the end, Renner and *Oenothera* taught the rest of the world. For the com-

plexes of the subgenus or macro-species *Oenothera*, are freely recombinable as units among all its inter-fertile components of North America, and the plastids likewise. But the plastids differ. And what are green plastids with the right nucleus are white with the wrong nucleus. Renner could therefore show for the first time the permanent genetic character of non-mutating plastids, and this opened up the field of plastid genetics as we now know it today. What we still don't know from Cleland's account is whether the individuality of the plastid is being used as a means of genetic isolation in *Oenothera*. For the chromosome mechanism at meiosis, with its localised pairing and crossing-over segments, had overridden the ordinary means of breaking up a species by random structural change and inter-sterility.

Some readers may find it difficult in this book to see the wood for the trees, especially the names of the trees. Others (with the help of the bibliography) will discover how Renner by his exquisite observations and manipulations in a mere 25 years disentangled some of the most daunting problems that have ever confronted an experimenter in genetics or in evolution. And we owe it to Cleland that he has here done his devoted best to preserve the record for the rest of us.

One thing more that we owe to this book, in what it says and in what it omits, is the contrast between three points of view and three methods of enquiry. One was expressed in the life-long purpose of de Vries: it was to explain the whole of Nature by the study of *Oenothera*. A second was expressed in the equally life-long more modest purpose of Cleland: it was to explain *Oenothera* (and nothing else) by the study of *Oenothera* (and nothing else). The third has been the purpose of many. It was first to explain *Oenothera* by the study of whatever was needed in the whole of Nature. And then to take what *Oenothera* had to offer and to use it in showing how things work elsewhere: whether in the sex chromosomes with their pairing and differential segments, or in other systems of polymorphism with their complexes or super-genes, or again in the general adaptive relations of reproductive mechanisms, breeding systems and chromosome arrangements. All this arguing back and forth is surely the way we have to go about our enquiries if we want to get anywhere in biology.

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