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CURRENT CHROMOSOME RESEARCH

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and
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PREFACE

We know the profound influence exerted by the chromosomes in development heredity and evolution but our confidence in their vital roles is tempered by the fact that we do not fully understand the chromosome either in its structure, in its behaviour or in its own evolution. Over 50 years of study have revealed much, but not all, and there remain ample areas for further profitable research. Those who devote themselves to the chromosome and its influences are usually aware of the deficiencies of knowledge; those who view the chromosome from a greater distance often do not and frequently abuse, misuse or mispresent it. Some conveniently ignore it. But for the experimental and theoretical cytologists the chromosome is central in the study of biology and the continuity of life. It is they who treat it with the respect it deserves.

Cytology seen as a science dealing with the chromosome as a visible, integrated structure, derives its information from the study of higher plants, animals and man all of whom possess chromosomes essentially the same in their structure, function and patterns of behaviour. It is therefore eminently sensible that, from time to time, those who study tradescantias, grasshoppers or humans should convene together to share their ideas and exchange their discoveries. Opportunities for such meetings have been provided in recent years by the Oxford Chromosome Conferences and their overseas offspring. The Conference at Kew was another such occasion differing from the previous ones in being designed principally for the many cytologists residing in Britain. In the event, a restricted number of researchers from elsewhere also attended and made important contributions to the meeting.

The Kew Chromosome Conference was inspired by the need to celebrate the centenary of the Jodrell Laboratory. Its success was certainly worthy of the traditions of that Laboratory and this in turn could inspire similar conferences in future years.

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DEMONSTRATIONS

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THE GREAT EVENTS IN CHROMOSOME EVOLUTION

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The centenary of the Jodrell Laboratory reminds us that in the year of its foundation Darwin published his "Effects of Cross and Self Fertilisation in the Vegetable Kingdom". This book was the fruit of a systematic study of the connections between inbreeding and outbreeding, fertility, sterility and reproductive process[1]. It was therefore the first great attack on a new problem, the problem of Genetic Systems.

But Darwin's attack was frustrated. He had left out two things which mattered most: heredity and the chromosomes. Yet while he was writing Flemming had seen the halving of the chromosomes into chromatids (in Fritillaria). And Hertwig had seen their doubling by the fusion of nuclei at fertilisation (in a sea-urchin). Here is a striking contrast. Darwin's "Origin" concerned organisms and was understood at once. But it took a whole century for the implications of these microscopic discoveries to catch the attention of the macroscopic world.

The greatest step was taken when Weismann saw that fertilisation and meiosis must go together. And that their connection was not only a matter of adding and subtracting (as is still taught today). It was also a matter of recombination, by a means which cytologists, Rückert, Boveri and Janssens, successively dragged out into the light of day.

This history was made clear from their opposed points of view by Morgan[2] and Wilson[3] at the time when Drosophila and the chromosome theory were being attached to one another. But when the combined theory brought us into the neo-Darwinian age, its origins had been forgotten. People were talking about chromosomes. But they were thinking about organisms. Many of them had never seen chromosomes except on paper. It was easy therefore for the new Darwinians to believe that such small things could carry heredity. But it was hard for them to believe that they could interfere with it. Yet in evolution this is what they most significantly do.

The solution of the chromosome problems was indeed troublesome. But it has shown that chiasmata are universally connected both with crossing over and with segregation. Weismann's recombination was therefore co-extensive with sexual reproduction.

Let us now take this solution back to Darwin's problems. We see that inbreeding and outbreeding must always be connected with fertility and sterility through what the chromosomes do at fertilisation and meiosis. The combination of the two in establishing sexual reproduction was therefore the greatest event in the evolution equally of organisms and of chromosomes.

It happened presumably through a sudden mutation affecting mitosis in a diploid cell some 3000 million years ago[4]. And it has survived for the reasons proposed by Weismann. It provided, he said "a source of individual variability, furnishing material for the operation of natural selection"[5].

This proposal was both a principle and a paradox. For the selection worked, not only on individuals, but on processes of fertilisation and meiosis which occurred before individuals or individuality as we understand them could have existed. And, having occurred, fertilisation and meiosis have been intercalated between individuals ever since.

Now, however, we may express Weismann's principle in another way. Individuality and continuity have been sustained together throughout evolution. They are the poles of our existence. The individuality arises from recombination organised through fertilisation and meiosis. The continuity arises from the structure of the chromosomes and the populations in which they maintain themselves. The paradox, we may add, arises from the properties of DNA which make these things possible[6].

This first great event in chromosome evolution inevitably dominated all the lesser events which followed it. The greatest of these, we may claim, was the invention of double fertilisation in a plant, a process first identified in the embryo-sac of Fritillaria by Sergius Navashin in 1898[7]. This discovery was soon widely confirmed in flowering plants and the next year a young botanist, Ethel Sargant, with singular pre-mendelian insight, pointed out its evolutionary significance. The half-hybrid endosperm, she suggested, would always be genetically adjusted to the nutritional needs of its twin, the fully hybrid embryo[8].

Now we can see that a number of connected changes took place in the common ancestors of the flowering plants 100 million years ago[9]. They lay in two parts of the newly invented flower:-

(i) The diploid style began to set a limit to the possibilities of fertilisation by haploid pollen producing diploid embryos; it was an upward limit to outbreeding and a downward limit to inbreeding. A single filter was at the same time excluding the wasteful consequences of incest and promiscuity[10].

(ii) The triploid endosperm began, first, to show a hybrid vigour proportionate to the needs of the embryo[11]. And secondly, it began to propagate for the embryo an environment genetically intermediate between it and its mother, an environment which was bound to extend the range of survival of embryos arising either from wide recombination or wide crossing.

Here was a system of many-sided flexibility. It would release a flow of hybridity which could be adjusted in any population to combine the greatest meiotic recombination with the least loss of fertility. To the original pre-Cambrian invention of meiosis had been appended, a new model which was to develop and exploit the effects of its predecessor with unexampled success. At the same time in the new system there was embodied an extension of the parental or genetic environment surpassing even the achievements of birds and mammals which were to follow it. Nothing surely could be compared with the new Angiosperm reproductive system before the Pleistocene invention of the human family[12].

The rapid success of this feat of genetic engineering was bound to ensure that no fossil trace of it will ever be unearthed. But what we see of its consequences today is enough to show that it changed the face of the earth and of all the life that lives upon it.

The other and lesser steps in chromosome evolution have been made by changes of process or structure. They are deviations of limited range and variable duration. But they work by rules which deserve attention. In the first place they are often, like the diffuse centromere, paralleled in remote groups. In the second place, they are all of them available, like gene mutations, for two alternative functions: for binding the species together by balanced polymorphism, or for splitting it asunder by intersterility[13].

Both of these effects are achieved by the restriction or even negation of the primary business of recombination. The structure-devices of inversion or interchange hybridity are the most obvious means. But the process-device of a control of meiosis restricting chiasmata and crossing over seems to lie at root of the great