
Meiosis in Perspective

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Phil. Trans. R. Soc. Lond. B 1977 **277**, 185-189

doi: 10.1098/rstb.1977.0010

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Meiosis in perspective

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Our understanding of meiosis springs from two suggestions made by Weismann in 1887. One was that meiosis would be found to compensate for fertilization in the life cycles of both sexes and all organisms. The other was that the development of sexual reproduction in evolution depended on the value of meiosis in exposing the results of genetic recombination to natural selection. In confirming these propositions we were bound to discover that the properties of meiosis appear both as the causes and the consequences of evolution: it is the hinge on which turns the evolution of breeding method, reproductive habit, life cycle and hereditary structure, that is the genetic system, in all sexually reproducing species of organism.

We have had three main fields of attack on our problem. First, there was the natural variation of meiosis including that of two-track heredity within the species: here, animals took the lead. Secondly, there was the experimental field – both with genetic controls such as polyploidy and the sterilizing mutations of mitosis as well as meiosis, and with physical and chemical controls: here, the higher plants and micro-organisms have given us our great opportunities. Thirdly, we have the widening field where physicochemical knowledge and genetic control converge and collaborate.

In all this work we have to be aware that meiosis works with chromosomes which always have the two functions of accomplishing evolution and of implementing its results in heredity. In consequence, the adaptation of meiosis is perpetually imperfect.

Meiosis, the subject of our discussion, lies at a cross-roads where processes of many kinds meet. They converge on it and diverge from it and to understand what the whole encounter means we need to bring methods and also ideas of many kinds together. The story begins with Oscar Hertwig's discovery in 1875 that fertilization, the basis of sexual reproduction, concerns the nucleus and therefore also the chromosomes. The ideas which have arisen from this discovery in the century which has passed have some of them made a great stir. Others have gone on their way to return like comets after many years. And others again have disappeared like the paper of Farmer & Moore in 1905 which left us the word meiosis and a few forgotten fallacies.

The idea from which all our work springs was, of course, Weismann's prediction that meiosis in both sexes must be the universal complement of fertilization. But even this had a chequered career. His statement to the British Association in 1887 was at once understood. But it carried with it a rider whose meaning has only gradually unfolded itself. The rider was to the effect that the sexual process had succeeded because it was 'a source of individual variability'. Recombination of the materials of heredity, which we may call *ids* or genes, germ plasm or chromosomes, allowed individuals in later generations to expose their variation to natural selection.

Weismann's sustained purpose behind this formula was to make a clean separation between Darwin and Lamarck. The idea was novel on the face of it. But behind the face of it were concealed more implications than behind any evolutionary idea other than natural selection itself. And these implications could be grasped only piecemeal as the study of meiosis slowly revealed the mechanism of recombination and the long sequence of its causes and consequences.

The first piece was picked up with its ancestry acknowledged, by Janssens when he suggested in 1909 that the four cells produced by meiosis were necessary because they were useful and useful because they were different. And they were different partly because the chromosomes had crossed over at chiasmata. Of the causes and consequences and even the structure of chiasmata Janssens was uncertain. But in the general genetic model which was Weismann's, he was correct. Fortunately so, since this was what Morgan took as the basis of *Drosophila* genetics.†

The second piece of Weismann's rider was recondite in a different way and for long it was unperceived. It was that natural selection must have favoured meiosis through the advantages it later conferred on its products and descendants. In other words natural selection must operate on variation in a continuous sequence of materials and processes in the cell through its effect on the future variation in organisms. The only individual, it seems, that is of no selective importance is that in which meiosis actually occurs.

Such an action is complex and indirect. What is more, it exposes a conflict of attitude between the many Darwinians who think of evolution in terms of organisms and those few (most of whom are perhaps in this room) who think of it also and equally in terms of chromosomes. Meiosis, I would say, requires us to admit that the effects of selection feed back in evolution to the control of all chromosome behaviour (Darlington 1932). It is only because the chromosomes are so rigorously constructed that they can carry the enormous weight of such a feedback mechanism.‡

We may describe the feedback effect in time as anticipatory or proleptic selection. Or we may describe it in a contemporary and spatial sense as group selection. But these separate dimensions merely hide the genuine selective connectedness of all the components of what I mean by the *genetic system*. Hereditary structure (DNA, genes and chromosomes), reproductive process (meiosis, fertilization, gestation and so on) and breeding habit (sexuality, mating behaviour, incompatibility and length of life cycle), all these are genetically controlled and are therefore bound to be, as we find, adaptively connected with one another.

In the systems which arise in this way the continuity of DNA and its interruption by the individuality of genotypes are not balanced. They have no fixed or lasting optimum. There is no perfect meiosis. As part of the system meiosis has an adaptive character. But in its adaptation long-range advantage is continually liable (as in human affairs) to be superseded by immediate and temporary advantage. Free combination, the continuous phase in evolution, may always give way to close linkage, permanent hybridity and even irreversible parthenogenesis.

Whether we accept these ideas in their totality or only little pieces of them, we find that they preclude (as Weismann intended) every tinge or taint of Lamarckian theory. Something else that we have to forgo, but in quite a different sense, is mathematical treatment. For the require-

† Janssens' words were: 'S'il se produit là quatre spores et pas deux, c'est qu'elles doivent avoir chacune quelque chose de particulier' (p. 391). In his address to the Genetics Congress in August 1932 Morgan had neglected to explain his connection with his antecedents. I therefore asked him in December of that year what value he attached to Janssens' work. He replied that Janssens as a Jesuit had thought in teleological terms, that is without scientific antecedents. Janssens, however, having cited Weismann and Boveri, had shown his basis to be in evolution by natural selection. He had, I believe, understood the theory of the problem more clearly than Morgan (cf. Darlington 1973).

‡ In this connection it is of interest that Alfred Russel Wallace in 1858 speaks of the governor of a steam engine as effecting what we should regard as selection. But he is of course using this classical cybernetic analogy in an organismal and not in a chromosomal sense. And he is using it to explain what we should call stabilizing rather than innovating selection.

ment of the calculator is to close the options. The business of genetic systems is to keep them for ever open.

When we discuss genetic recombination, owing to Galton and Mendel and their successors, mathematical treatment inevitably hypnotizes us and it is no doubt for this reason that the collision of ideas has for so long been avoided.

Let me give an example. Two-track heredity with two types of meiosis, chiasmate and achiasmate, with and without crossing over in the two sexes, has stared us in the face for sixty years.† But we have been misled. We have seen only the relations of the chromosomes to recombination in the species. We have seen the statistical effect of halving the frequency of crossing over. We have seen its trivial connection with inversion hybridity. Its effect by way of the whole genetic system has escaped us: only now can we recognize the value of using one sex-track to create and select variability in individuals while the other sex-track fixes and multiplies the resultant variation in lineages and populations (Darlington 1973).

Naturally the most serious collisions between those who study meiosis in the cell and those who study its results in organisms concern not far-reaching theories but immediate details.

When I met the late Dr Sturtevant in June 1932 I had said that the fourth chromosome in *Drosophila melanogaster* should have 50% of crossing over. Now Sturtevant was a great experimenter, the Columbus of chromosome mapping, and to him this was an unforgivable presumption: 'You are wrong', he said (in the vernacular); 'there is less than 1%.' I had believed that the chromosomes do not obey the laws of genetics: they make them. For Sturtevant and for Morgan the flies were the real things: the chromosomes were there to vindicate what the flies had revealed.

Since I had not seen the fly, let alone its chromosomes, it is not surprising that the discussion of meiosis including my views was omitted from the proceedings of the ensuing Genetics Congress. The barriers between chromosome studies and experimental breeding (and generally also between plants and animals and man) were and long remained impassable. The connection between them, asserted in theory, was disallowed in practice.

How far is this still the belief today? It seemed to me that, with the connection established between crossing over and chiasmata and chromosome pairing, our knowledge of recombination could be extended from ten species to ten thousand and by induction to the whole evolution of meiosis and the whole world of sexual reproduction. But, even today, I have no idea how far this view is accepted by those who teach genetics but have not studied meiosis. For today genetics is taught and learnt from textbooks whose authors have often learnt the subject, not as arising by hypothesis and induction, but as deduced from laws; not as a body of tentative, fallible and controversial statements, but as a body of indisputable facts; not as a road but as a destination. Indeed, just like the descriptive biology which we thought it had superseded (Darlington 1971).

In this discussion we need to remember the edges of fallibility because we are again bringing together widely different disciplines. Our inferences are bound sometimes to disagree where they overlap; particularly, I believe, in the overlap between what is microscopically visible

† My explanation of the absence of crossing over in male *Drosophila* as due to reciprocal chiasmata proved to be incorrect for the autosomes but, I believe, correct for the sex chromosomes. My hypothesis (1931*a*) was based on meiosis in a species of *Fritillaria* in which genus Noda (1975) has now found Japanese examples with the complete two-track meiosis better illustrated than in *Drosophila* itself (Darlington 1934). This coincidence may be said to have bridged (after forty years) the deepest abyss between studies of meiosis in plants and in animals.

and what is chemically detectable. Many years ago this conflict had already begun to cast its shadow over our descriptions of meiosis in a way that I may describe.

When I first broached the problem of meiosis I spoke of chromosomes 'dividing' (1931*b*, 1940). They did so before the onset of prophase in mitosis, after it in meiosis. I also spoke of the chromosome as 'single' or 'double'. I was referring to the *split* which is microscopically seen and not to the *reproduction* which has to be chemically recognized. This distinction of process and of method still, I think, holds although inevitably the two are connected. But now we find that, thanks to new inventions and new skills, reproduction or synthesis and division or splitting can be separated. Analytically and experimentally, they can each be taken to pieces (Darlington 1976).

When the logicians of the future examine these questions they will notice that the methods used in studying synthesis and splitting are different. The terms used in describing them are different. And the inferences derived from them may well be discordant. Today, therefore, we have to make many connections before we pass judgement.

The discordance of opinion, to give a practical example, is likely to be greatest in considering what I call *organellar* genes – those parts of the chromosome whose products are partly or wholly attached to them. The most demanding of these is the centromere. For here is a particle which differs from all the rest of the chromosome in the time and place not only of its synthesis and its splitting, but also of its visible activity. Its movements, which make it the focus of the chromosome map, can easily be seen to play different roles in mitosis and in meiosis. It operates moreover both by secretion and by movement, in the resting and in the dividing nucleus (Darlington 1957). And it changes in evolution by breakages and reunions, and above all misdivisions, which it can be seen to organize itself. It is almost an organism in its own right. But with all this knowledge visibly recorded its chemical structure has so far eluded us.

What has caught our imagination most about meiosis, ever since we first knew it, is its character, which is doubly paradoxical. Its first paradox is that, having arisen some 3000 million years ago, it has developed a prodigious diversity in itself; but by its basic uniformity it still betrays its common origin and the common function which selectively feeds back to preserve it. Its second paradox seems to lie outside the programme of this meeting but I may be forgiven for mentioning it. It is that meiosis throughout its history has been a continuing experiment in the use of a strict determinacy to generate uncertainty, the uncertainty on which the possibility of evolution has depended. It is this natural experiment to which we devote our studies.†

† It is worth noting that the uncertainty generated by recombination at meiosis has a creative effect which underlies some of the most practical and also some of the most contentious problems of the world today. For example, there is the issue between Fisher's and Haldane's assumption that selective advantages of alternative genes for individuals and their progeny may be estimated and my view that the present and future advantages of alternative genetic systems are always involved and are unquantifiable. There is also the issue between psychologists who estimate proportionate values to the effects of heredity and environment in determining the I.Q. of individuals in society and my view that all social environments have a genetic component which is again unquantifiable and makes such estimates meaningless. And, again, the issue between Keynes's assumption that the actions of the community in determining supply and demand are quantifiable in terms of average and aggregate values and Hayek's view that supply and demand depend on interconnected market relations between individuals and groups of an unquantifiable complexity.

In all these situations, which lie on the boundaries between science and the humanities, genetic recombination *fat* meiosis prevents accurate prediction. It allows us to understand the past but it prohibits our control of the future without constant reference to the changing empirical evidence.

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