

THE GENETICS OF *PARAMECIUM AURELIA*. By G. H. Beale. Cambridge University Press. 1954. Pp. 176. 12s. 6d.

The existence of genetic restrictions to mating in *Paramecium aurelia* was discovered by Sonneborn in 1936. Since that time he and his pupils have carried out a study of this group of organisms so fruitful as to react upon the whole development of biology. Now Dr G. H. Beale, one of Professor Sonneborn's former colleagues, gives us an account of the results.

The genetic study of *Paramecium* breaks new ground in two ways. It introduces old and established genetic principles on the new level of a unicellular organism. And it reveals on this new level new principles fundamental to the relations of genetics and physiology. This makes the task of presenting *Paramecium* genetics to the general biological reader almost as difficult and almost as important as the task of discovering it. At the beginning of such a presentation the writer has to decide what are the correct analogies between the very complex genetic system of the unicellular infusorian and those somewhat simpler or somewhat better understood systems that are known in the fungi and in the higher plants. He has to make this decision at the beginning because it governs the terminology that he uses for the systematics of the organism and for the elements of its genetic system with all their implications.

What are the terms used in *Paramecium*? In *P. aurelia* there are eight inter-sterile groups. In the past they have been described by *Paramecium* workers as *varieties*, but they are now known to be good species merely waiting to be described. Dr Beale gives the facts but does not apply them.

Within seven of these *sub-aurelian* species all individuals fall into pairs of alternative and parallel groups of a plus-and-minus type between which there is mating and within which there is no mating. What group a line or clone falls into depends on the properties of its macronucleus, sometimes in reaction with its cytoplasm. Now this system in its causation must be peculiar to organisms with a macronucleus. But in its evolutionary effects and perhaps in its physiological mechanism it is analogous with the incompatibility systems of higher plants and with the heterothallism of fungi. Like the second of these it has, on a false analogy, been described as "sex".

These groups are not described by Beale as incompatible groups but as "mating types". Why? Because, it is said, *Paramecium* undergoes a process of autogamy which is equivalent to self-fertilisation and we cannot have self-fertilisation and cross-incompatibility in the same individual. Now in its effects autogamy is certainly related to self-fertilisation. But not in its inherent character. It involves no conjugation of cells. It involves a union of identical haploid nuclei within one cell. It is analogous to the fusion of such nuclei in the parthenogenesis of certain higher plants and animals. Why then should we be surprised to find that it is consistent with self- and cross-incompatibility?

Symbols, by the way, are also important. The system adopted, or rather, retained, by Beale for these various genetic groups, however, is difficult for the beginner. And it is unnecessarily so. First, the "varieties" (or species) are labelled with arabic numerals. Secondly, the incompatibility groups (or mating types) are given roman numerals with a sequence of their own independent of the "varieties" and disregarding Sonneborn's plus-and-minus simplification. Thirdly, the stocks (which are not named under their "varieties") are given a mixture of arabic

numerals and capital letters. This confusing system arises from the gradual history of *Paramecium* genetics. But why not use the obvious and agreed simplifications?

There is another analogy between *Paramecium* and the higher organisms which does not concern terms or symbols but does concern the place of *Paramecium* in the methodology of genetics and also in our understanding of genetic systems in general. In *P. aurelia* there is, as we have seen, a combination of diploid incompatibility with haploid selfing. This means in effect that there is an alternation—a facultative alternation—of sexual generations of two kinds: one reproduces by autogamy and consists therefore of constant and absolutely homozygous diploid individuals, and the other reproduces by enforced cross-breeding. Such an alternation of self-fertilisation, which by a single stroke produces the purest of pure lines and cross-fertilisation producing heterozygosity, exactly answers to the formula discovered by Mendel for the crucial analytical experiment in genetics. Thus *Paramecium* by its nature and of its own accord has the capacity of carrying out with extreme precision the very experiment which the geneticist needs for defining its nuclear or Mendelian heredity. It is in part to this capacity for *in-and-out*-breeding that we owe the rigour with which it has been possible for the *Paramecium* school to separate the nuclear and cytoplasmic components of heredity.

Dr Beale describes the three main fields of cytoplasmic heredity in *Paramecium*: kappa, the antigens, and incompatibility. He is interested in showing that the kappa particles are unique. They propagate themselves in their hosts like viruses but they rarely or perhaps never exchange hosts by natural infection. They may therefore never have exchanged hosts in the past. Moreover, the substance paramecin which they produce, although it contains nucleoprotein, does not, as a virus would, propagate itself but disappears in its victims. Thus the kappa particles are not viruses. And the evidence is against supposing that they ever have been viruses.

In spite of their uniqueness, however, the kappa particles help to show us how the more easily classifiable particles in the cell live and move and have their being. Particularly they broaden our understanding of what the reviewer has called the *corpuscular* elements of cytoplasmic heredity. They make it clear that the genetic variations in size, stability, efficiency, temperature tolerance, rate of propagation and nuclear subordination shown by the plastids in plants can be shown by a corpuscle having quite different functions in the cell. These questions have been discussed by the *Paramecium* workers and Dr Beale might well have mentioned them.

The external reactions of the cytoplasmic systems responsible for the antigens and for incompatibility in *P. aurelia* are shown in regard to temperature, salinity, homologous antisera, enzymes and irradiation. Beale points out how such a range of responses in free unicellular organisms enables us to picture the process of differentiation in higher organisms, and the changing competence of their cells to respond to the external stimuli of organised development. But the importance of this example is surely enhanced when we find that there are alternative courses in the development of higher plants and that external conditions, especially temperature, will sometimes switch the balance of cytoplasmic determinants from one to the other. In *Tradescantia* (La Cour, *Heredity*, 3, 319) the difference between large and small pollen grains seems to be of this type.

And in the tomato, potato and pea (*cf.* Lewis, *Heredity*, 7, 337) the difference arises between type and rogue. Equally in *Paramecium* and in these plants we are dealing with alternative steady states and we are also dealing with what we still have to describe as the third level of heredity, the "undefined residue of heredity", undefined because it is non-corpuscular and susceptible to change during differentiation. This would also have been worth mentioning.

Many of the analogies between *Paramecium* and the higher organisms merely suggest new lines of enquiry. The mutual exclusiveness of cytoplasmic states in *P. aurelia* recalls the property of suppressivity shown in crosses between green and pale *Scolopendrium*. The breakdown of a cytoplasmic state when meiosis and nuclear fusion occur recalls the frequent failure of viruses to survive the sexual process. On the other hand the parallel antigenic polymorphism in the different "varieties" and the special functions of the macronucleus, these are properties so far peculiar to *Paramecium*.

Since this book is bound to interest many who are not generally concerned with genetics Dr Beale is wise to offer us some introductory remarks on the chromosome theory of heredity. He is not perhaps so wise in the choice of what he tells us. On page 1 he suggests that Mendel "ignored" the transmission of material in heredity. But on page 5 he quotes Mendel's own reference to the elements in the cells responsible for heredity. On page 1, again, Dr Beale argues that the hereditary materials in one organism "can under no circumstances embody the same atoms and molecules as were contained in the parents". This is a surprising statement. But supposing that we accept it what has it to do with *Paramecium*? On page 2 we learn that an "individual scarcely inherits any material possessions at all but merely some abstract pattern". Presumably *Paramecium* is a concrete pattern, its chromosomes and its kappa particles are an abstract pattern. On page 3 Beale continues with the idea that in the past it has proved "essential" to separate the hereditary material from the rest. Nevertheless it may be "unreal" to do so and it may not be essential in the future. On page 4 Beale reveals another difficulty: Weismann had "no real *proof* (sic!) that the chromosomes had any connexion with hereditary processes".

These remarks are a not very satisfactory recapitulation of the views expressed by Bateson forty-five years ago, views which so soon became untenable. Yet they are used to introduce *Paramecium*! They are on the first pages of a book in which Dr Beale himself interprets this organism on the assumption of an unimpeachable nuclear continuity, an organism in which spontaneous gene mutation has never been demonstrated, an organism therefore enjoying a molecular stability in the gene greater than that to be expected in a bar of iron.

Dr Beale makes another stumbling block for his readers when he suggests that it is only "hereditary characters studied *by the Mendelian methods*" which are known to be determined by genes (p. 7). We know of studies of the relation of balance, polyploidy, segregation in hybrids, fertility, induced mutation, continuous variation and polygenic inheritance in which the assumptions of breeding experiment and chromosome study have been combined. The methods used are not Mendelian. But do they not provide a large part of the strength of the chromosome theory and a larger part of the evidence of what the chromosomes and genes are

doing in heredity and evolution? And have they not in fact contributed to the understanding of *Paramecium*? Surely they have explained to us the varied properties of the polyploid macronucleus and the special consequences of irradiation.

These doubts and misgivings on fundamental questions have somewhat distorted the evidence and obscured the argument of this book. Dr Beale has tried to fit the revolutionary discoveries of the American geneticists into a framework for which they themselves have no use. His purpose is genuine, his methods are rigorous and often most fruitful, but his outlook seems to have required him to throw away some of the best of what his efforts have won.

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GENETICS BIOLOGICAL INDIVIDUALITY AND CANCER. By C. C. Little. London : Geoffrey Cumberlege, Stanford University Press. 1954. Pp. 111. 20s.

This book traverses the field of cancer research with a series of somewhat disconnected but often remarkable statements. The following example is worth quoting (p. 89) :—

“When a break in linkage occurs it is called *crossing over* because during mitosis a gene exchanges place with its counterpart gene in the other member of the chromosome pair to which it belongs.”

C. D. D.