

## GENETICAL SOCIETY OF GREAT BRITAIN

ABSTRACTS of Papers read at the HUNDRED AND TWENTIETH MEETING of the Society, held on 9th and 10th APRIL 1956, in the DEPARTMENT OF ZOOLOGY, UNIVERSITY OF EDINBURGH

### ACRIFLAVINE RESISTANT MUTANTS OF *ASPERGILLUS NIDULANS*

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Three independently obtained mutants, resistant to acriflavine and certain other substances, have been studied. In each mutant resistance is due to mutation in a single gene. Two of the mutant alleles, which confer different degrees of resistance, are semi-dominant. They are located about 23 units distal to the *w* locus and are presumably allelic. A cross involving these two alleles in repulsion gives 0.1 per cent. sensitives. A third mutant allele, unlinked to the first two, is almost completely recessive. This allele confers relatively slight resistance.

Degrees of resistance in haploids and heterozygous and homozygous diploids have been studied. The selection of haploid and homozygous resistant segregants from heterozygotes has provided a useful additional tool in the analysis of mitotic crossing-over and for the location of new markers.

### FUNCTIONAL RELATIONSHIPS BETWEEN THREE ADENINELESS MUTANTS IN *ASPERGILLUS NIDULANS*

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Three investigated adenineless mutants, out of five located very close to the *pab* region, represent three different sites of mutation. These three mutations bear the following functional relationships: two (*ad15* and *ad17*) are partially complementary—*i.e.* in the absence of adenine the diploid repulsion heterozygote shows intermediate growth between the haploid mutant and the wild type. A third (*ad13*) is allelic to both: the diploids *ad13/ad15* and *ad13/ad17* do not grow without adenine. As *ad13* gives prototrophs in crosses with either of the other two it seems unlikely to be a deficiency or a mutation involving both sites.

### MULTIPLE ALLELES AT A LOCUS CONCERNED WITH GLUTAMIC DEHYDROGENASE PRODUCTION IN *NEUROSPORA CRASSA*

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and

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A number of independently induced amination deficient, *am*, mutants are known in *Neurospora*. These strains require certain amino acids for normal growth and lack demonstrable glutamic dehydrogenase activity as a result of mutation at the *am* locus.

Several hundred backmutant wild types have been obtained from the *am* strains S.2929, 32213 and 47305 after irradiation with ultra-violet. There are significant differences in the backmutation rates obtained from different *am* strains.

In the 54 backmutant strains analysed, the mutant locus is within 1 cM of the *am* locus and all 54 strains recovered the ability to produce some glutamic dehydrogenase. Seven of the backmutants possess very low enzyme activity and one has been investigated in detail. This strain grows like a wild type, but possesses 5-10 per cent. normal enzyme activity. No *am* strains were recovered in 1084

ascospores from a low enzyme strain  $\times$  wild cross and 12 dissected asci show 2 : 2 segregation for high : low enzyme activity. Twenty asci from a low enzyme  $\times$  *am* cross show a 2 : 2 segregation for low : no enzyme activity. It is considered that low enzyme strain is due to intermediate allele, *am*<sup>1</sup>, although a closely linked suppressor is not excluded.

## EXTRA-NUCLEAR INHERITANCE IN A HOMOTHALLIC FUNGUS

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A strain of *Aspergillus glaucus* gives rise to a particular type of clearly distinguishable sector with a certain frequency.

The behaviour of the original and of the sector mycelia, tested in sexual and asexual propagation, discloses a situation not easily explicable in terms of Mendelian inheritance.

Apart from spontaneous sectoring at a low rate, the original type propagates true under all conditions. The rate of change is roughly  $5 \times 10^{-11}$  per micron<sup>3</sup> of mycelium.

The sector type propagates true when inocula involving large quantities of cytoplasm are used, *i.e.* blocks of mycelium or masses of sexual or asexual spores. But when sexual or asexual spores from the sector type are dilution plated (new colonies arising from single spores) they segregate into sector and original types. The segregations depend on the parent colony's substrate and other factors. Single haploid uninucleate ascospores of sector type generation after generation give rise to sector type colonies whose spores segregate.

A cross-graft technique has been developed using mycelia differing in morphological and biochemical markers. This technique shows that the determinants controlling the sector type reassociate vegetatively with the nuclei formerly present in the original type.

To explain the observations a genetic model based on extra-nuclear selfreplicating particles is proposed.

## THE GENETIC CONTROL OF METHIONINE SYNTHESIS IN SALMONELLA

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Transduction tests involving 32 independently isolated methionine-less mutants of *Salmonella typhimurium* showed that they could be divided into 5 groups. The number of transductions observed in tests between members of the same group is significantly smaller than in experiments involving members of different groups or when phage raised on wild-type bacteria is used.

The results are consistent with the assumption that each transduction group is equivalent to a gene locus and that the different members of a group are "non-identical alleles" and that the small number of transductions between members of the same group represents the infrequent recombination that takes place between pseudoalleles.

Syntrophism tests, growth responses to methionine precursors and chromatographic analysis of culture filtrates show that complete correspondence exists between the grouping based on transduction tests and the grouping by biochemical tests.

The high frequency with which bacteria carrying two auxotrophic markers can be transduced to prototrophy using phage raised on wild-type bacteria indicates that the methionine loci are linked to several loci controlling the synthesis of cysteine and tryptophane.

## EXPERIMENTS ON GENETIC ASSIMILATION

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It has been suggested by Waddington that selection of an environmentally-induced character produces a genotype which tends to condition the spontaneous appearance of the character. The process has been termed the Genetic Assimilation of an acquired character.

In a number of cases selection of a phenocopy has led to genetic assimilation. Further selection of the assimilated characters without treatment has produced almost true-breeding stocks. Investigation of the genetic basis of these characters indicates that a major gene and penetrance modifiers may be involved in each case, thus suggesting the importance of incompletely penetrating genes in determining the potential direction of assimilation. There is evidence that assimilation has been the result of the lowering of the threshold for expression of a character in the normal environment owing to an increase in the population mean during phenocopy selection.

HOST EFFECT ON THE SIZE OF IMAGOS DEVELOPING FROM  
TRANSPLANTED OVARIES (*DROSOPHILA MELANOGASTER*)

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Two inbred lines of *Drosophila melanogaster* produced by selection for size were used in these experiments: line ES<sub>4</sub> of small size and line LZ<sub>5</sub> for large size, the latter carrying the marker *w*. Ovaries from the "large line" were transplanted at the third instar larval stage into "small line" larvae of the same stage. When the operated larvae gave rise to hatching imagos these were mated to males of the "large line." Two groups of offspring were obtained from these matings (scored by the eye marker gene), namely hybrids of the two lines and homozygotes of the LZ<sub>5</sub> line. Measurements (thorax length) of these as well as of control hybrids and LZ<sub>5</sub> were made.

The statistical analysis of the data provided evidence that (a) there is some influence of the host on the size of the LZ<sub>5</sub> individuals developing from the transplanted ovaries, making these offspring somewhat smaller than the control LZ<sub>5</sub>, but (b) the effect is very small.

## "RECOVERY" FROM X-RAY MUTATION

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Experiments on the frequencies of sex-linked lethals in first-day and second-day progenies of X-rayed *Drosophila* males suggest that in the testes of irradiated males spermatozoa may "recover" from X-ray induced breaks and point mutations.

THE PRODUCTION OF SEXUAL ISOLATION IN  
*DROSOPHILA* BY SELECTION

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A population consisting of a mixture of ebony and vestigial flies was allowed to mate freely, and was carried on by selecting as parents for the next generation the flies which were either ebony or vestigial, *i.e.* the offspring of matings of like with like. The proportion of cross-matings gradually fell. The significance of such processes for evolutionary theory is discussed.

## AN EXPERIMENTAL STUDY OF THE EFFECTS OF INBREEDING AT DIFFERENT RATES ON SIZE IN *DROSOPHILA MELANOGASTER*

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Selection against homozygotes should lead to the retention of more heterozygosity in slowly inbred than in rapidly inbred lines carried to the same theoretical inbreeding level.

To test this, a number of lines of *D. melanogaster* have been inbred at different rates by sib-mating,  $\frac{1}{2}$ -sib mating, etc., and mean size and viability, and the variance and heritability of size were estimated at stages when all lines had reached roughly the same inbreeding level.

Mean size and viability first began to decline after about 50 per cent. inbreeding, and declined most rapidly after about 70 per cent. The phenotypic variance of size declined most rapidly in the early stages, and did not decrease further after about 60 per cent. inbreeding. The heritability of size declined more slowly than expected on simple theory, in the later stages of inbreeding, and there was a suggestion that less genetic variability was retained in the more rapidly than in the less rapidly inbred lines.

## ACCLIMATISATION TO HIGH TEMPERATURES IN INBRED AND OUTBRED *DROSOPHILA SUBOBSCURA*

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Three inbred lines of *D. subobscura*, and the three types of  $F_1$  hybrid between them were reared at two temperatures, 15° and 25° C., and the time for which adult flies could survive at 33.5° C. in dry air recorded.

Individuals which had been kept at 25° C. either as larvae or as adults survived for much longer than those kept at 15° C. throughout. Two kinds of temperature acclimatisation can occur, a long-lasting "developmental acclimatisation" in individuals kept at 25° C. until emergence and subsequently at 15° C., and a short-lived "physiological acclimatisation" in individuals kept at 25° C. as adults only.

There were no consistent differences between the capacities for physiological acclimatisation of inbred and outbred flies, but outbred flies showed a significantly greater extent of developmental acclimatisation than did inbred ones. Those genotypes which showed the greatest extent of developmental acclimatisation were also the least variable when raised at a given temperature.

These results confirm the hypothesis that organisms which show a greater capacity for regulation during development, as expressed by greater constancy of adult phenotype, are also capable of greater adaptive modification of phenotype in response to changed conditions.

## THE ROLE OF MUTATION IN THE MAINTENANCE OF GENETIC VARIATION

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For the first time, evidence is now accumulating from different sources on the rate of production of new quantitative variation, both spontaneous and induced. The units of measurement have to be in terms of variance rather than of rates at individual loci. Such information is of great value in the discussion of the maintenance of variation in natural populations. For abdominal bristles, the spontaneous rate observed is sufficient to be an important factor in this connection. X-rays appear to give a definite increase in the mutation rate but it is as yet too early to discuss in detail the magnitude of the increase.

## GENETIC AND DEVELOPMENTAL HOMEOSTASIS

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Six lines have been run for ten generations from a wild stock of *Drosophila melanogaster*, two selected for high, two for low sternopleural number and two controls. Bilateral asymmetry of sternopleurals was used as a measure of developmental homeostasis and increased with selection, but did not increase in the controls.  $F_1$ s between the pairs of selected lines and also between high lines and low lines had asymmetries characteristic of their parents. These results support the view that homeostatic mechanisms deteriorate in selection lines but do not support the view that this is related to increasing homozygosity. It seems more likely that directional selection itself picks out genes for low developmental homeostasis. Other results to be reported agree with this, but they do not support the view that developmental homeostasis as measured is a significant cause of genetic homeostasis.

## CYTOLOGICAL ANALYSIS OF TRANSLOCATIONS IN THE MOUSE

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Twelve X-ray induced autosomal translocations in the mouse have been studied cytologically. The work was carried out in four steps: (1) cytological confirmation of the presence of a translocation in a semi-sterile strain, (2) analysis of double translocation heterozygotes establishing cytological independence of genetically independent linkage groups, (3) pachytene analysis of single translocation heterozygotes and (4) where two translocations involved the same linkage group, determination by deduction which chromosome carries this group. The following linkage groups have been localised in the following chromosomes: II in 9, III in 14, V in 17, VIII in 18, IX in 16, XI in 15 and XIII in 19. The genetical part of the work has been done by Dr T. C. Carter, Dr M. F. Lyon and Miss R. Phillips, and has been published by them.

## LITTER SIZE IN MICE: STUDIES ON SELECTION, INBREEDING, AND CROSSING

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The response to two-way selection for number born alive in first litters indicates a realised heritability of about 15 per cent. Selection was effective in both directions, but the improvement was very slow; the mean increased from 7.5 to 8.5 in 14 generations. Inbreeding reduced the mean by 0.5 for each 10 per cent. of inbreeding coefficient. Crosses were made between the best three out of twenty lines at  $F = 0.84$ . Litter size in the cross-breds averaged 9.5. The gain by this means was thus double that by selection and was achieved in a shorter time.

## THE DEVELOPMENT OF VESTIGIAL-TAIL IN THE MOUSE

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Newborn mice homozygous for the recessive gene for vestigial-tail (*vt*) have either no tail at all or, at most, a short stump. The anomaly can be traced back to the  $9\frac{1}{2}$  day stage of embryonic development. In the tail buds of vestigial embryos, there is a reduction of the tail gut which is somewhat variable. There is always a massive overdevelopment, both relatively and absolutely, of the neural tube in the

tail which, on its ventral aspect, grows solid excrescences and ultimately divides into 2-4 branches. Normal mouse embryos, between the ages of  $9\frac{1}{2}$ -11 days, have a hitherto undescribed ventral thickening of the tail ectoderm; this originates from the cloacal membrane, whence it spreads to the tail tip; in 10-days-old embryos the distal part of the thickening has lost contact with its source and resembles in structure the apical ectodermal ridge of the limb buds. That it may have a similar function in regard to tail growth is suggested by the fact that this thickening is greatly reduced in vestigial embryos. The tail is smaller than normal in 10-days-old embryos; a constriction at its base develops in 12-days-old embryos and by the 13th day the final situation is reached.

## CYTOGENETICS OF A MOUSE TRANSLOCATION

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Male mice heterozygous for Snell's translocation T(5:8)*a* form quadrivalents in only 8 to 30 per cent. of first spermatocytes, all the remainder having 20 bivalents. The quadrivalents are invariably rings with 4 (exceptionally 5) chiasmata at diplotene. There is evidence that the failure of association always occurs in the distal (non-centromeric) arms. The maximum amount of recombination to be expected in these arms is therefore 15 per cent. But Snell reported more than 30 per cent. recombination between *b* and *a* (*a* marks the break); hence *b* must lie in a centromeric arm. He also showed genetically that *b* and *pa* are in opposite arms; hence *pa* also must be in a centromeric arm. The centromeres are very nearly terminal in all mouse chromosomes. It follows that the centromeres must be at the *Sd* end of Group V and at the *b* end of Group VIII.

The disjunctional arrangements at early anaphase lead to the expectation that about 40 per cent., and certainly not more than 50 per cent., of sperm will be viable. Yet new tests confirm Snell's report that fertility of male heterozygotes exceeds 60 per cent. of normal. Possible explanations of the discrepancy will be discussed.

## THE POSSIBLE EFFECT OF OUTCROSSING ON THE EVOLUTION OF CHROMOSOME NUMBERS IN ANIMALS

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Beatty and Fischberg found 3.4 per cent. heteroploid, mainly triploid, eggs amongst the  $3\frac{1}{2}$ -day-old embryos in crosses of the inbred lines A, C<sub>57</sub> and CBA of *Mus musculus*. The percentage of heteroploid eggs from matings within an inbred line was negligible. This difference, which is statistically significant, suggested that heteroploidy is due to outcrossing and could be the first sign of an incompatibility between sperm and egg of individuals with different genetic constitution. If so, one might equally expect heteroploidy to occur in the offspring of crosses between individuals of small isolated populations of one species and to a greater extent amongst the F<sub>1</sub> of species crosses. This phenomenon could in fact link up with the 100 per cent. haploid false hybrids occurring in the F<sub>1</sub> of crosses between certain forms of animals. It is further suggested that, since the first step of this process of increasing incompatibility between sperm and egg occurs in population crosses, it may be a factor in the evolution of chromosome numbers in animals; for here distant crosses are rare. Preliminary crossing experiments with newts of different populations and of different species lend support to this hypothesis.

## BLOOD GROUP GENE FREQUENCIES IN IRELAND

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The gene frequency maps for the ABO blood groups will be explained in terms of the known invasions, settlements and population movements of the last 1000 years. The Anglo-Norman settlements in the east and south and the James I plantations in the north are clearly reflected in these gene frequency maps.

The frequency of Rhesus negative people is higher in the east than in the west of Ireland.

Against this general background an analysis of data of about 10,000 people living in the city and county of Dublin will be discussed. A significantly higher proportion of the people living in the country regions are group A than in the city. The explanation of this may be that the city has received more emigrants from western Ireland, where the frequency of group A is low, than has the surrounding country. The city has been sub-divided into about 200 areas and the data of people living in these areas have been analysed to decide whether there is a pattern of frequencies within the city. An analysis of the data when divided into occupational groups will also be mentioned.

## SOME RECENT BLOOD GROUP DISTINCTIONS BETWEEN NEGROES AND WHITES

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## I. WITHIN THE MNSs AND DUFFY SYSTEMS

Three blood transfusion compatibility problems in which we have recently been involved have disclosed some new racial antigenic differences.

All European blood samples so far tested have the antigen S or s or both. Two allelic genes *S* and *s* provide a perfectly adequate genetic background for the Ss part of the MN system in Europeans. The blood of some negroes (less than 1 per cent.) has neither the antigen S nor the antigen s. We suppose that such people are homozygous for a third allele *S<sup>u</sup>* not found in whites.

All European blood samples so far tested have the antigen *Fy<sup>a</sup>* or *Fy<sup>b</sup>* or both and two allelic genes provided a sufficient genetic background to the Duffy system. Surprisingly, about 70 per cent. of New York negroes have neither antigen. The simplest genetic explanation is that in the negro there is a third allele, *Fy*, not found in whites, with a frequency of about 82 per cent.

## II. WITHIN THE RH SYSTEM

The antigen V is present in the blood of about 40 per cent. of West Africans, 27 per cent. of New York negroes and about 0.5 per cent. of white people: the antigen belongs to the Rh system. The gene *V* can be part of some *cde* and some *cDe* chromosomes; its precise place in the system is not yet clear.

The blood of 77 per cent. of New York negroes (and over 90 per cent. of West Africans) discloses itself as non-European by being V+ or by being *Fy(a-b)*.

## FUNCTION AND ORGANISATION OF GENETIC MATERIAL

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Chromosomes are the carriers of certain functions which are revealed by genetic and biochemical analysis. The evidence suggests that these functions are carried out by transfer of surface specificity to large molecules. A model of the organisation of the material composing the chromosomes must account for this transfer as well as for stability and variability. This is possible if the chromosome itself contains specific surfaces. Under special conditions such a system may be duplicated.

AN IMPROVED METHOD OF SELECTIVE BREEDING  
IN POULTRY

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In a typical poultry flock a number of sires are each mated to a number of dams and each mating produces several offspring. Individuals may thus be classified by dam families (full-sibs) or sire families (half and full-sibs). It is shown that, theoretically, for improving traits of low heritability, selection of female breeders on the average of the sire family to which they belong may be markedly more efficient than the orthodox methods of selection on individual merit or full-sib average. Such a feature may prove of importance in the large class of poultry populations where trapnesting facilities are limited, since selection for such traits as egg production may be carried out on the basis of pen records with sire families housed as units.

The value of the method declines with increasing heritability but under all circumstances maximum theoretical gains are offered by an index which gives particular weighting factors to each type of family average and individual merit. Even up to heritability values of 50 per cent. maximum weight is to be attached to sire average, less weight to dam average, and least of all to individual performance.