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DEPARTMENT OF GENETICS

C. B. Davenport, Director

GENERAL STATEMENT

The progress of genetics since the establishment of this Department 23 years ago continues unabated and new vistas are continually opening. At the same time new contacts are being made with cytology, experimental and physiological embryology, and with biochemistry. Genetics, reared in the house of morphology, has gone forth to associate with other branches of biological science.

Perhaps the leading advance of the year with us has been in the subject of mutation, or the origin of inheritable variations. This topic was early recognized by Darwin and others as the problem that lies at the very heart of evolution. The distinction between "variation" of the older authors and "mutation" has come to be associated with size; but this is unfortunate, since size has nothing to do with the matter. Properly, as used by modern geneticists, a mutation is nothing but a variation that has the quality of being hereditary or genetical. Any variation, however large or small, that is inherited is, by this modern definition, a mutation. If we know how mutations arise, then we understand the genetical basis of evolution.

One advance of the present year relates to the experiments on Cladocera which have been continued, by Banta, in parthenogenetic reproduction here for 650 generations. Probably in no other multicellular organism has the succession of generations been followed so far in genetically constant germinal material. As this germinal material has been carried through the generations it has undergone changes. In the breeding lines, at intervals of between 5 and 35 generations, obvious changes have occurred that have permitted the investigator to raise a new strain of the organism, one or more of whose qualities varied around a new mutative center. These mutative changes did not occur at definite seasons of the year; they seemed rather associated with the interval elapsing since the last mutation; yet the interval is by no means a constant one.

The inference as to the cause of this mutation that seems most justified is that, without special external inciting agents, the germ plasm (chromosome complex) of the Cladocera is undergoing changes in the direction that is being followed by the investigator (and very likely in others, as well), and which may be accumulated by a selective agent (in this case the investigator) until they acquire an important increment.

Simply by waiting a sufficient time, the investigator finds the desired mutations to his hand in the form of special bodily types. The individuals with their peculiar traits are of interest because they constitute an index of mutations that have already occurred in the germ-plasm. The germ-plasm that has mutated makes itself known, so to speak, by the peculiar way in which the soma develops.

From this point of view it follows that, strictly, the individual has an ontogenetic development, but not a phylogeny; it is the germ-plasm that has

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a phylogenetic development. The course of ontogenetic development is determined (apart from environmental factors) by germ-plasmic, phylogenetic changes. It is because we can not see the changes directly in the germ-plasm that in speculating on the "phylogeny" of any species we arrange its relatives in a series that is most probably in accord with the sequence of mutations in the germ-plasm (chromosomes). Evolution is no longer the tracing of the origin of species, but of the origin and succession of germinal mutations.

The second marked advance relates to the architecture of the germ-plasm. The theory of the gene has been fully elaborated, and its general relation to bodily development has been traced. And for some time we believed that the genetic unit for the various traits had been found in the gene. But, gradually, it is becoming clearer not only that the genes do not play a particular and exclusive rôle in the development of any character, but also that the genes are themselves complexes in much the same way as atoms are complexes of electrons. It may well be that these components of genes do not differ qualitatively, but only in their number, to make the different genes; this matter is still speculative. But the doctrine of the compound nature of the gene has been experimentally derived.

The conclusion as to the compound nature of the gene rests on several lines of evidence. First, the long-established principle of multiple allelomorphism, according to which several states or degrees of the same trait occupy the same locus in the chromosome. A good example is afforded by the recessive, sex-linked, mutant eye colors: white, tinged, buff, eosin, cherry, blood, also the wild-type red eye in Drosophila. Similar series are found in the albinism of mammals, and in other traits. The evidence is good that each of these sets is due to a mutation of the same gene. This implies a complex nature of the gene, incompatible with the theory of its elementary constitution.

Second, the facts of inheritance of variegation of leaves and floral parts are best harmonized on the view that the gene is changeable during somatogenesis, owing to its composition out of many, more elementary, units that vary in number.

Third, and this is the contribution of Demerec, mutations at their inception frequently affect a large proportion of the progeny and in a variety of grades. As a result of selection in successive generations the mutation tends to become fixed and to occur in a nearly constant proportion of the population. This multi-mutating condition is most readily accounted for on the ground of a compound gene which shows a varying number or proportion of elements.

A third advance is in the cytology of genetics. Metz has found that during sperm formation in the fly Sciara the maternal and paternal chromosomes do not come together in pairs and then segregate at random in the usual fashion, such that any sperm may have representatives of both kinds, due to chance assortment. Instead, no intimate pairing occurs, and the evidence indicates that the maternal chromosomes all pass into the cell which produces the sperm, while the paternal homologues segregate from them by means of a monocentric mitosis, and then are cast off. (Genetic proof of this for one chromosome pair has been obtained.) Consequently, the sperm fails to transmit traits that were in the male gametes carried by the earlier generation. This is a mechanism that has not hitherto been described in genetics; it may lead to the discovery of still other possible types of cytological behavior.
Still another advance lies in the accumulating evidence that in *Datura* non-homologous chromosomes may show a mutual attraction, so as to form "sets" of three chromosomes that have not the same genes. Also, pieces of non-homologous chromosomes apparently may unite to form whole chromosomes. These aberrant unions complicate the interpretation of the progeny of a given mating.

Finally, reference may be made to the increasing evidence, based largely upon the facts of variegation, that somatic mutation is, in certain cases, the cause of a definite somatic pattern. And the hypothesis may be entertained that the clear facts of variegation are a diagrammatic representation of a widespread process in development. The changes in form of the developing organism may be, in part, due to regular ontogenetic changes in the germ-plasm that are of the nature of somatic mutations.

The second main division of the work of the Department of Genetics deals with the processes, controlled by the germ-plasm, which result in the development of the individual with its somatic characteristics. Only a beginning has been made in this field. Its cultivation involves studies in the physiology of reproduction and development and a knowledge of the individuals that fall by the side of the developmental path prematurely, as compared with those that reach a more mature stage. It involves the development of the gametes, the conditions under which the zygote is formed, the growth of the individual, and the special activators that stimulate it. Particular attention is being devoted to development as a sequence of chemical processes, since the influence of the chromosomes upon development can be completely interpreted only in physico-chemical terms. Much attention is being paid also to the non-chromosomal factors that modify the course of development, especially to the effect of external agents in modifying the work both of the genes and of the chromosomal complexes which are directing development from the inside. One of the most significant of the lines of the newer work is that which demonstrates the chemical basis of the difference between the sexes. In so far as this difference is controlled by the sex-determining chromosome, we must believe the chemical nature of that chromosome to be in the last analysis responsible for the fundamental chemical difference between the sexes. Truly, endocrine glands play an important rôle in the control of development; but their activity, in turn, is influenced by hereditary factors. This conclusion is confirmed in the existence of the high and low thyroid strains of pigeons that have been produced in this Department. Consequently we are led to the conclusion that these endocrine glands are among the most important agents utilized by the chromosomes for the carrying out of their work. In the special group of mammals where 5 per cent or more of the period of rapid development is spent in the maternal body, receiving hormones from it, a special study is being made of the effect of these hormones upon development. Any such effect, though one or more genetical factors may be involved in it, is determined primarily by factors outside of the chromosomes of the developing individual. This complication is, doubtless, responsible for difficulties in explaining some mammalian traits on a Mendelian basis.

Finally, progress is being made in the analysis of the inheritance of special traits in race horses and man; and other practical applications of heredity to the American population have not been neglected.
The Director has been studying problems in human development, normal and abnormal, and has been working on the modification of development by special treatment in mice. Dr. A. F. Blakeslee, Assistant Director in the Station for Experimental Evolution, has continued his work on breeding Daturas to discover their mutations and get a chromosomal interpretation of them. He has collaborated with Miss Satina on the chemical basis of sex-differences. Dr. H. H. Laughlin, Assistant Director, Eugenics Record Office, besides conducting the heavy correspondence of that Office, has continued his studies on the influence of immigration and deportation on the quality of the American population. He has also directed a research on heredity of racing capacity in thoroughbred horses.

In other researches on the germ-plasm we have the operations of Dr. A. M. Banta on parthenogenetic lines of Cladocera that show repeated somatic mutations, on their sexual reproduction, and on the calling forth of males. In these studies he has been assisted by Miss Thelma Wood and, during the summer, by Mr. L. A. Brown and Mrs. George Snider. Dr. M. Demerec is working on mutations in Drosophila and Delphinium, especially on the topics of multi-mutating genes and variegation and the light they seem to throw on the compound nature of the gene. Dr. C. W. Metz is working out the chromosomal behavior in an anomalous inheritance in Sciara; and, with Miss Moses, is continuing his studies on chromosomes of Drosophila. Dr. Belling's protracted illness has interfered with the carrying out of some of our Datura program. Despite his illness he has continued his investigations.

In the field of physiology, of that development which is, in large part, directed by chromosomes, Dr. E. C. MacDowell has completed his study of the effect of alcohol on the sex ratio and is entering the field of prenatal deaths in mice and of the relation of X-radiation to the production of abnormalities. Dr. Oscar Riddle is measuring the effects of different endocrine secretions on metabolism and the reproductive cycle with special reference to sex. The sex differential is being investigated by Dr. Riddle with the collaboration of Mr. W. H. Reinhart; and also by Miss Satina and Dr. Blakeslee. Also, Dr. Banta's researches in parthenogenesis and male production in Cladocera touch on this field.

In the field of human heredity and development Dr. Banker has continued his studies of family capacity for learning as evidenced by school records. He has utilized the extensive records of the Huntington Schools for this purpose. Dr. Estabrook, in the mountains of Kentucky, is continuing his study of the genetical factors that have determined the special mental qualities of, and their distribution in, this population.

Our experimental breeding-pens of mice have been in charge of Miss Elizabeth Lord, who has collaborated in much of the experimental work. The pigeon houses have been in charge of Dr. Riddle and Miss Frances Burns. The eugenics archives have been in charge of Dr. Elizabeth C. Muncey until her retirement in January and since that time of Miss Grace Burns. The computing room has been in immediate charge of Miss Catherine Carley, who has been engaged in statistical service for many of the researches and has continued the computations upon and tabulation of the anthropometric data. The greenhouses and gardens have been in charge of Mr. Morrison.
Among the visitors at the Department may be mentioned Professor Frederick Breinl, of the German University of Prague, who did some statistical work on correlation between the developmental abnormalities that are held to depend on abnormal endocrine functioning.

Dr. John T. Buchholz, of the University of Arkansas, spent some weeks at the Department studying pollen-tube growth.

Dr. K. George Falk transported his laboratory from the Harriman Research Laboratory to this Department during the early summer, and researches on changes of enzymes during development were carried on by Miss Helen Noyes and Mr. Lorberblatt, using fishes and mice. Dr. Falk and Mr. Lorberblatt also developed a simplification of the Manoilov sex-reaction.

Professor Masuharu Tange, of Kyushu Imperial University, Fukuoka, Japan, cooperated with Dr. Riddle on the effects of follicular hormones on the development of pigeons.

Dr. J. N. Couch, a holder of a biological fellowship of the National Research Council, worked at the Station for Experimental Evolution during the year. He investigated the sexuality of the water molds, in the conduct of which work he was in close contact with Dr. Blakeslee.

**DETAILED REPORT ON CURRENT INVESTIGATIONS**

**THE GERM-PLASM**

**Cladocera**

Progress has been made in the elucidation of the real nature of germinal mutation by Banta working with the "water fleas," Cladocera. He has bred these, now, for 650 generations, or nearly thrice the number of generations allotted to man on earth by the ecclesiastical chronologists. During this period there has been continuous parthenogenetic reproduction. Each germ-cell of the female grows and develops into new eggs which become enveloped in a covering, nourishing organism, the female soma of the following generation. The eggs that this female is nursing after a few days grow and develop into more eggs, covered in turn by a new nourishing organism, the female soma of the third generation, and so on. The form of this soma is precisely determined by the chromosomes (germ-plasm) of the egg from a piece of which it has arisen; the other pieces forming more eggs—those of the "next generation." Thus the form, structure and behavior of the soma are an index of the constitution of the germ-plasm.

This germ-plasm remains unaltered through the generations, merely doubling in each cell-generation. It undergoes no "reduction" in the number of chromosomes, such as occurs in sexual reproduction; it does not fuse with other (foreign) germ-plasm, as happens in sexual reproduction. The germ-plasm should go through the "generations" unchanged, and, correspondingly, its index (the soma) should remain constant and invariable. And so it does, ordinarily; the somas of the successive generations of Cladocera are exceedingly similar.

But now occur the interesting exceptions. Banta has traced a line with a peculiar germ-plasm, as indicated by the fact that the outline of the front of the head is slightly excavated. The amount or depth of the excavation is variable. This "excavated-head" line has been continued for 85 generations and an attempt has been made to break it up into 2 lines. The following method has been used: The amount of excavation fluctuates (doubtless
partly on account of the complexities of ontogenetic development). One germinal line (A) was continued on the ground that it was producing the deepest excavations—above grade 0.50; another line (B), on the ground that it was producing the shallowest excavations—below 0.50. In line A, after about 35 generations, the fluctuations began to occur around an obviously new and higher center, namely, at 1.20. In 5 more generations the center of fluctuation had arisen to 1.60, and after 75 generations from the beginning to about 2.00. Thus new centers of fluctuation appeared after two intervals of 35 generations and one interval of 5 generations. The center was elevated about 0.40 or 0.50 points at each rise. In line B the results were less marked. In one case a reduction of the fluctuation center from 0.60 to 0.25 occurred after about 27 generations; in another case a reduction from 0.75 to 0.25 in 7 generations from the beginning.

The interpretation that is put on the appearance of these new centers of fluctuation is that the germ-plasm has undergone mutation just previously to their appearance. The time, nature and degree of the germinal mutation is made known by the change in the soma whose development is controlled by the germ-plasm. In general, one may say that mutations are of approximately equal size—varying from 0.3 to 0.5 point at a time. Possibly this uniformity is apparent rather than real, for a change of less than 0.20 point would probably not be recognized as a mutation; and a change of over 0.60 point might be regarded as due to two mutations occurring in quick succession. The mutations occur at unequal intervals, of from 5 to 35 generations.

Next, it is to be noted that the mutations occurred without reference to season, conditions of nutrition or any other assignable change in the environment. The most probable conclusion is that the germ-plasm, while extraordinarily protected from alteration by external agents, is, at more or less regular intervals, undergoing a change. This change appears to be "spontaneous," or dependent upon causes inherent in the germ-plasm itself. Larger changes are built up by selection. The selector is a person who watches carefully for evidence that the germ-plasm has undergone a change in the desired direction and breeds from that germ-plasm.

That the mutations found in the Cladocera—whether in lines bred for reactivity to light, or for sex-intergradedness, or for excavated head—are real inherited mutations has just been tested by Banta. After some years of failure he has succeeded in securing fertilized eggs and, indeed, rearing "hybrids" between the wild or normal strains and mutant strains. There were obtained 135 young from a cross between females of wild stock and males of the mutant line; also 70 of the reciprocal cross. In addition, he secured 34 sexually produced young from normal × normal and 17 from mutant × mutant matings. The study of these young showed (as set forth in a later section of this report) that the new mutations were inherited in Mendelian fashion, and, consequently, that a gene mutation is involved.

MULTI-MUTATING GENES

In respect to the nature of mutations, the observations of Demerec are of importance. While genes are extraordinarily stable, resisting all attempts (except perhaps one) to change them experimentally, they change (mutate) relatively frequently from some uncontrollable cause. Demerec has been working with a plant (Delphinium) and an insect (Drosophila), in each of which there have been found multi-mutating genes.
DEPARTMENT OF GENETICS

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REDDISH IN DROSOPHILA

As described in last year's report, reddish is an allelo morph of yellow and mutants in females, but only when they are heterozygous with yellow or its wild allelo morph. A constant reddish has been obtained from the mutating line. Reddish in a cross between the mutating and constant lines does not mutate. A new reddish (reddish-2) has been found by Miss Moses. It arose independently of the first reddish, is phenotypically indistinguishable from it, is allelomorphic to it.

Reddish-2, however, does not mutate. But when reddish-1 is crossed with constant reddish-2 the heterozygous females do mutate. In this respect reddish-2 differs from the constant line of reddish-1.

MINIATURE WING IN DROSOPHILA

This new sex-linked character is allelomorphic to the already known miniature -1. Miniature-a (as it is called) mutates in all stages of development; in males as well as females; in germ-cells as well as in somatic cells. Somatic mutations produce mosaics; i.e., in the wings of flies carrying miniature-a more or less of the wing may show areas that have mutated back to the normal or wild type. Miniature-a may mutate back to wild type; if the mutation occurs in the germ-cell or early in somatic-cells, wild individuals are produced. Wild-type flies that have originated from miniature do not regularly mutate back to miniature. The frequency of mutation back to wild differs in the various lines. By selection almost constant lines of miniature-a have been isolated; other lines yield close to 100 per cent of wild flies. Without selection the multi-mutative property of miniature-a genes tends to disappear. Unselected lines with a high frequency of mutation to wild tend to lose the miniature character; those with low frequency of mutation tend to become constant miniature.

Thus, the mutation of reddish-1 is limited to the reduction division in heterozygous females, while miniature-a mutates at all stages of development. Miniature-a is, then, directly comparable with some plant variegations, for example, Delphinium.

DELPHINIUM

In the larkspur, Demerec has now identified 6 multi-mutating genes. Of these, 3 produce variegations in leaf chlorophyll and 3 in flower color. In some of these a study was made of the frequency of somatic mutations. The method used is thus described by Demerec:

"It was assumed that each dark-colored spot originated by an independent mutation of the gene for light color to the gene for dark color. If the mutation occurred early in the development, many cells are produced from the mutated one, resulting in a large dark spot; and if the mutation occurred later in the development fewer cells are formed from the mutated one, giving a spot of smaller size. Size of the spots can, therefore, be used in determining the time when mutation occurred. Since, on the average, each cell has an equal chance to divide, it was assumed that each succeeding cell generation would double the size of spots. Since with each cell generation the number of cells is, on the average, doubled, the chance for the mutation to occur in any of the cells is also doubled. Based on the above assumptions, calculations were made as follows: Spots were measured, counted and classified according to size, each class being twice as large as the preceding one to allow for the doubling of the size of the spots due to the doubling of the number of the cells
with each cell generation. To allow for the increased chance of the mutation occurring in later cell generations, because of the larger number of cells present, the total number of spots in each class was divided by a divisor which was increased in geometric proportion for each succeeding class.

"In figure 1 are presented the results of measurements on the frequency of mutations of three multi-mutating genes for a period of six cell-generations during the later part of the development of leaves, or sepals and petals respectively. The curve number 1 represents the frequency of mutation of a gene for chlorophyll variegation (variegated-3). From that curve it can be seen that the frequency of mutation continued approximately the same during the period of measurement. The frequency of mutation for another gene for chlorophyll variegation (variegated-1) is given in curve number 2, which shows that the frequency increased appreciably in the last measured cell generation, i.e., at the end of the development of the leaf. The same was true for the frequency of mutations of a gene for flower-color variegation, which is shown in curve number 3. The upper leaves and flower, when compared with lower leaves and flowers, gave identical mutation curves, indicating that the increase in the frequency of mutations observed in curves 1 and 3 is determined by some factor connected with the development of the leaves, or sepals and petals, rather than with a factor concerned with the development of the whole plant."

**Sciara**

In the last report of this Department the aberrant chromosomal relations of the fly *Sciara*, as discovered by Metz, were described in some detail. Many of the difficulties that appeared in that report have been cleared up during the current year. Also an improved technique has been devised for the flies, and a survey has been made of about a dozen species for the purpose of selecting those most favorable for breeding experiments and chromosome studies.

The findings of Dr. Metz that elucidate the chromosomal peculiarities of *Sciara* are shown in the comparison of a typical, primary spermatocyte, or
reductional division. On the one hand, and that of Sciara on the other, shown in Table 1.

Table 1.—Comparison of reductional spermatocyte division in typical forms and in Sciara.

<table>
<thead>
<tr>
<th>Cell structure or function</th>
<th>Typical division</th>
<th>Sciara coprophila.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maternal and paternal chromosomes</td>
<td>Undergo synopsis</td>
<td>Do not synapse.</td>
</tr>
<tr>
<td>Appear in prophase</td>
<td>As bivalents</td>
<td>Singly.</td>
</tr>
<tr>
<td>Equatorial plate</td>
<td>Present</td>
<td>Absent, chromosomes scattered at various levels.</td>
</tr>
<tr>
<td>Spindle</td>
<td>Bipolar</td>
<td>Unipolar (monaster).</td>
</tr>
<tr>
<td>At reduction</td>
<td>Bivalents divide and one component of each goes to each pole.</td>
<td>Half of the single chromosomes go to one pole and half to the other.</td>
</tr>
</tbody>
</table>

"These features," continues Metz, "are shown schematically in the accompanying diagrams A–F. Ten chromosomes are shown here. Presumably four of these come from the mother and six from the father. The latter include four like those from the mother, and in addition the two large "sex-limited" chromosomes found only in the males. These two may be disregarded, for the moment, since they always go together toward the 'pole.'

"Interest attaches here, especially, to the fact that all the chromosomes are oriented with respect to one astral center or centrosome and are connected with it by 'spindle' fibers; yet part of them, instead of going toward this center or pole, move directly away from it. In so doing they travel backward, with the point of fiber attachment posterior instead of anterior. Their paths are radii from the pole, and hence are at first divergent instead of convergent. Later they are intercepted by the cell wall (or possibly by cytoplasmic obstructions) and made convergent, so that eventually the chromosomes come together at a point opposite the astral center or pole. They are then cast off bodily in a bud, as described in our last report. The other group of six chromosomes goes toward the pole in the ordinary way and needs no special comment.

"It appears, then, that four of the chromosomes are picked out, so to speak, from the group, and carried away from the others. These four chromosomes show by their form and behavior that they are being subjected to two forces. One of these is represented by the 'spindle' fibers and acts in the direction of the pole or astral center. Its action is localized at one point on the chromosome—the point of fiber attachment. The other force acts in just the opposite direction and apparently acts on the whole chromosome, carrying it bodily away from the pole in spite of the retarding action of the spindle fiber force. This force acts as if it represented a repellant effect of the astral center or pole, rather than the attraction of something on the other side of the cell (e.g., the cell wall), for when an obstruction is encountered or when the periphery is reached the chromosomes do not stop, but are merely deflected, and keep moving till they reach the point farthest from the pole."

Every sperm-cell after reduction has 6 different chromosomes (of which 2 kinds are limited in occurrence to the male cells) while every egg presumably has 4 chromosomes (somatic cells have 8). In the fertilized egg there should be then 10 chromosomes (4 pairs + 2) and all should produce males—which is not true. Consequently since there is no parthenogenesis, the 2 male-limited chromosomes must be dropped out in forming the female zygotes. Where the dropping out occurs Metz can not yet say certainly. Genetic evidence from the species which give unisexual progenies makes it appear probable
that "the female is responsible for the sex-ratio and, hence, that the elimination or retention of the sex-limited chromosomes is determined by the egg." Nothing like this is known in other organisms. Clearly there are numerous new problems here for study.

In studying the mode of inheritance of a mutant character Metz has found a type that is correlated with the aberrant chromosome behavior. Metz reports on this matter as follows:

"The character is a wing-modification called truncate. Its history and mode of inheritance are summarized as follows:

"It was first seen among the offspring of a pair mating. These offspring were all males—since we are dealing here with a species which gives unisexual progenies. Fifty-five were truncate and sixty-three 'normal' or 'wild-type,' approximately a 1:1 ratio. This and other later results indicated that the character was a dominant, but critical tests showed that it was recessive, the ratios being due to the peculiar type of inheritance involved.

"When the latter was analyzed it was found that the genetic behavior of females was of the ordinary type, or approximately so, and that the peculiarities were due to the male. The male inherits equally from both parents and exhibits the somatic characters expected on this basis, but it transmits only the factor (gene) derived from the mother, not that from the father. If the mother is truncate the sons transmit only truncate—I. e., they breed as if they were homozygous truncate—regardless of the constitution of the father. Likewise, if the mother is heterozygous for truncate those sons which receive the truncate gene breed as if they were pure truncate. These features are shown in Table 2, which represents the descendants of reciprocal crosses."

A factorial analysis of these matings shows that heterozygous males transmit only the maternal gene. It should be noted that the character truncate is not sex-linked, but is transmitted equally to both sexes, hence we are not dealing with sex-chromosome behavior.

Table 2.—Descendants of reciprocal crosses in Sciara.

<table>
<thead>
<tr>
<th>Truncate ♀ × Normal ♂</th>
<th>Normal ♀ × Truncate ♂</th>
</tr>
</thead>
<tbody>
<tr>
<td>F₁: All normal.</td>
<td>All normal: F₁.</td>
</tr>
<tr>
<td>F₂: Normal and truncate.</td>
<td>All normal: F₂.</td>
</tr>
<tr>
<td>Parents: F₁ ♀ × trun. ♂</td>
<td>Backcrosses of F₁ flies to truncate:</td>
</tr>
<tr>
<td>Offspring: nor. and trun.</td>
<td>F₁ ♀ × trun. ♂: Parents:</td>
</tr>
<tr>
<td>Parents: F₁ ♂ × trun. ♀</td>
<td>Nor. and trun.: F₁ ♂ × trun. ♀: Offspring:</td>
</tr>
<tr>
<td>Offspring: all trun.</td>
<td>All nor.:</td>
</tr>
<tr>
<td>Backcrosses of normal F₂ flies to truncate:</td>
<td></td>
</tr>
<tr>
<td>Parents: F₂ ♀ × trun. ♂</td>
<td>F₂ ♀ × trun. ♂: Parents:</td>
</tr>
<tr>
<td>Offspring: nor. and trun.</td>
<td>All nor. or nor. and trun.: F₂ ♂ × trun. ♀: Offspring:</td>
</tr>
<tr>
<td>Parents: F₂ ♂ × trun. ♀</td>
<td>All nor. or all trun.:</td>
</tr>
<tr>
<td>Offspring: all nor.</td>
<td>Offspring.</td>
</tr>
</tbody>
</table>

"Translating these results into terms of chromosomes, and considering the chromosome pair carrying these genes, it is evident that the male transmits only the chromosome from his mother. All the sperms, therefore, should carry this chromosome, and the corresponding chromosome from the father should be eliminated, or else we must assume that the sperms carrying the paternal chromosome are non-functional. In the latter case, we would expect a random segregation of chromosomes in the maturation divisions,
while in the former segregation should be of a selective and constant type rather than at random.

“As has been noted above one of the distinctive features of chromosome behavior in these flies is the absence of the usual mechanism which should give random segregation in spermatogenesis. From the chromosome behavior in the first spermatocyte division it was postulated that the maternal chromosomes were segregated from the paternal ones, and that one group was regularly cast out. The genetic results provide a confirmation of this, at least as far as one chromosome pair is concerned. But the process is just the reverse of that expected; i.e., it is the paternal rather than the maternal chromosomes which are eliminated. It is not certain that this applies to the other three chromosomes, although it seems reasonable to assume, tentatively, that it does. If so, then the two sex-limited chromosomes, which are known to be paternal in origin, go with the maternal chromosome toward the pole in the first spermatocyte division (see figure 2), while the other paternal chromosomes are cast out. Work is under way to test this hypothesis by following the inheritance of factors in other chromosomes than that considered above.”

**FIG. 2.**

**DROSOPHILA**

The study of the chromosomes of this genus has been continued by Metz. In all, 27 species of the genus and 6 species from related genera have been studied. Especially has spermatogenesis been studied comparatively. The following new conclusions are drawn by Metz.

“Homologous chromosomes undergo synapsis in the telophase of the last spermatogonial division and apparently remain in intimate association during the growth stages.

“The sex-chromosomes remain relatively condensed and attached to, or included in, the nucleolus during this period.

“Preceding and during the first spermatocyte division the sex-chromosomes exhibit characteristics of form and behavior such as to suggest that the Y-chromosome remains relatively passive or inert, while the X-chromosomes
undergo changes more like those of the autosomes. Their behavior also suggests that instead of undergoing an intimate side-by-side conjugation, or synapsis, the elongate X becomes attached to the compact Y in only one or two (or at most in only a few) places. This, in turn, suggests that Y is 'empty' or 'inactive,' save for certain regions which contain materials homologous to those in X, which agrees with the genetic evidence indicating that Y is relatively 'empty' of genes, as compared with X.

"No evidence of the leptotene and diplotene stages, seen in many insects and other animals, is found here. This may bear a significant relation to the fact that there is no genetic 'crossing-over' in the males among these flies. It is, however, merely in agreement with the genetic evidence, and can not be considered as throwing light on the mechanism of crossing-over. The material is not sufficiently favorable for the latter purpose.

"Both maturation divisions exhibit the usual general features of chromosome behavior, with typical and regular distribution of the chromosomes to the spermatids. In some species, however, numerous deeply staining non-chromosomal bodies may be present whose superficial resemblance to chromosomes might lead at first sight to a misinterpretation of the figures."

**Datura**

The study of the mutations of the germ-plasm of *Datura* and the associated phenotypical conditions has been made by Dr. Blakeslee, in charge, Dr. Belling, cytologist, Gordon Morrison, gardener, and Miss Maria N. Hilliard, assistant.

**List of Primary and Main Secondary Types**

Since *Datura stramonium* has 12 chromosomes, 12 primary types, each due to a different extra chromosome, are expected. Last year we reported that only 11 of them had been identified, but that a weak type, that had arisen from the 3n × 2n cross, was being investigated, as possibly the missing twelfth primary. It proved not to be, but by somatic characters and breeding behavior was identified as of the double mutant type "buckling-ilex." Since in all these years no primary mutant type has appeared with the extra member in the twelfth chromosomal set, the conclusion is drawn that such a condition so unbalances the zygote that it is lethal to it.

**Table 3.—List of primaries and their secondaries in Datura, arranged by size of chromosome in the trisomic set.**

<table>
<thead>
<tr>
<th></th>
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<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Rolled</td>
<td>Rl.</td>
<td>Sugarloaf, Polycarpic</td>
<td>Largest.</td>
</tr>
<tr>
<td>2</td>
<td>Glossy</td>
<td>Gs.</td>
<td>Smooth</td>
<td>Large.</td>
</tr>
<tr>
<td>3</td>
<td>Buckling</td>
<td>Bk.</td>
<td>Strawberry, Maple</td>
<td>Large.</td>
</tr>
<tr>
<td>4</td>
<td>Cocklebur</td>
<td>Ck.</td>
<td>Wedge</td>
<td>Large.</td>
</tr>
<tr>
<td>5</td>
<td>Elongate</td>
<td>El.</td>
<td>Undulate</td>
<td>Large.</td>
</tr>
<tr>
<td>6</td>
<td>Echinus</td>
<td>Ec.</td>
<td>Mutilated</td>
<td>Large medium.</td>
</tr>
<tr>
<td>7</td>
<td>Microcarp</td>
<td>Me.</td>
<td>Scalloped</td>
<td>Large medium.</td>
</tr>
<tr>
<td>8</td>
<td>Reduced</td>
<td>Rd.</td>
<td>Dwarf</td>
<td>Small medium.</td>
</tr>
<tr>
<td>9</td>
<td>Poinsettia</td>
<td>Pn.</td>
<td></td>
<td>Small medium.</td>
</tr>
<tr>
<td>10</td>
<td></td>
<td></td>
<td></td>
<td>Small.</td>
</tr>
<tr>
<td>12</td>
<td>Ilex</td>
<td>Ix.</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The extra-chromosomal types in the diploid series, so far as determined, arranged in order of size of the extra chromosome, are as shown in Table 3,
DEPARTMENT OF GENETICS

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the primaries being printed in capitals; followed by their secondaries in italics. The sizes of the chromosomes are based on measurements made by Belling.

In addition to the above, there is the group of Spinach and Divergent, which are evidently interrelated, but whose relation to the primary \( (2n + 1) \) types has not been traced.

If two mutant types that Blakeslee has found this season in line 1-A pedigrees are the secondaries Maple and Undulate, as they appear to be, all of the \( (2n + 1) \) types listed above trace their ancestry to the same haploid which is the origin of line 1-A. Barring new mutations in the haploid, or occurring since their origin from it, the members of each chromosomal set in all these mutant types should be identical in gene composition.

The group consisting of the \( (2n + 1) \) types, Nubbin, Pinched, and Hedge (discussed in Year Book No. 24, p. 23), has been further studied by Blakeslee, who reports as follows:

"As a preliminary hypothesis to explain the morphological peculiarities and breeding behavior we have suggested that, in Nubbin, the Rolled set consists of the following members: one, a normal Rolled chromosome, which, in terms of its two halves, Sugarloaf and Polycarpic, may be written \( (Sg - Py) \), one, with the Mutilated part of the Echinus chromosome joined to the Polycarpic part of the Rolled chromosome, which may be written \( (Mt - Py) \); and one with the Sugarloaf part of Rolled joined to the Strawberry part of Buckling or \( (Sg - St) \). The mutant type Pinched would then be, in respect to its Rolled set, \( (Sg - Py), (Sg - Py), (Sg - St) \), while Hedge would have the formula \( (Sg - Py), (Sg - Py), (Py - Mt) \). Such an arrangement of the chromosomes in the Nubbin group seems almost inevitable to explain the morphological peculiarities and breeding behavior, but without a more detailed cytological study than has yet been possible it is unwise to consider it as more than a provisional hypothesis.

"In previous reports we mentioned the occasional appearance of \( (2n + 2) \) Globes with two extra chromosomes in the Globe set. Judging from the chromosomal counts, which show two extra chromosomes, and from the fact that the new mutant throws a very large proportion of the corresponding \( (2n + 1) \) type, as does also the \( +2 \) Globe, we apparently have now in our cultures a \( (2n + 2) \) Reduced.

"Since the last report two or three new types of \textit{Datura} have been found which have not yet been studied cytologically and which have not yet given recordable offspring.

"Of considerable interest is the occurrence of a new type of sectorial chimeras. Polycarpic, the \( (2n + \frac{2}{2}) \) secondary of Rolled, has several times given rise to two kinds of bud-sports. One type of branch resembling a normal diploid may be assumed to have lost the Polycarpic chromosome. The type of branch which is more delicate in growth than the Polycarpic plant from which it arose has been called Etiolated and may have arisen by a dropping out of one of the normal Rolled chromosomes. It has not yet been possible to determine the cytological relations; but, in bud-sports involving chromosomes from another set, it has been possible to judge of the chromosomal changes from the breeding behavior. Ten Poinsettias and 5 plants of its secondary Dwarf were kept in the greenhouse well into the winter. Two of the Poinsettias produced each a single branch with the appearance of a normal diploid. One of the 5 dwarfs had a branch which differed in leaves and capsules from a typical Dwarf. All these plants had come from a cross between a homozygous dominant and the double recessive, white-curled,
which is a linked factor-complex represented in the Poinsettia chromosome. They all started out, therefore, with a single white-curved chromosome, in addition to the two other chromosomes in the same set not carrying the genes for white or curled. In all three cases, the off-type branches gave only dominant offspring in contrast to the typical branches, which showed segregation in their progeny. Attempts are being made to induce bud-sports again in similar forms and to discover if there is any significance in the fact that in the cases discussed it was always the double recessive chromosome which was eliminated."

**DOUBLING OF CHROMOSOME**

A cold chamber with automatic temperature control has recently been installed, in which we hope to be able to study the effects of temperature changes upon the production of chromosomal types. As Blakeslee has previously reported, he has succeeded,

"by the application of cold, in inducing pollen abortion and the formation of giant pollen-grains and, in 4 out of 5 such experiments, has apparently increased the number of chromosomal types in the offspring of plants subjected to roughly controlled low temperatures. As a preliminary to a more detailed study of the effects of cold upon the types of offspring, Miss Watt has investigated the relative time of the reduction divisions in the formation of male and female gametophytes respectively. She has found that reduction in the stamens occurs when the bud is about 5 to 7 mm. long, while reduction in the ovary occurs considerably later, when the bud is about 20 to 30 mm. long. Since extra chromosomes are rarely carried by the pollen, induced chromosomal changes must be brought about in the egg-cells to show in the offspring, and our failure to obtain an increased number of mutant types in one of our earlier cold experiments may have been due to removing the plants from the cold before the time of reduction in the ovaries. In *Echinus*, the pollen grains that contain the extra chromosome are practically devoid of starch. Mr. Cartledge is testing by iodine the giant pollen-grains which occasionally are formed in this mutant to see whether the doubling of chromosomes has taken place before or after reduction in the pollen mother-cells. So far, the work seems to indicate that doubling of chromosomes in pollen may occur both before and after reduction. Since our last report, we have additional evidence, from tetraploids which have arisen from heterozygous parents, indicating that doubling of chromosomes in these cases has occurred after reduction. The fact that pollen of a tetraploid will not function in ovaries of diploids and the fact that we have never discovered a spontaneous triploid in our cultures, lead us to the belief that the doubling of chromosomes which brings about tetraploidy in *Datura* has taken place in the zygote."

**BAD POLLEN PRODUCERS**

"It has been previously reported that two kinds of white Daturas are found in nature. The gene for the A-white is located in the Poinsettia chromosome and behaves normally in inheritance, while the B-whites give abnormal ratios with both Poinsettia and Rolled. From a study of the chromosome of Wiry, a form that arises from parents heterozygous for B-whites, Belling has suggested that in the B-whites a segmental interchange has taken place between the non-homologous chromosomes, Rolled and Poinsettia. This hypothesis seemed to be confirmed by the production of the 50% abortion expected in pollen and ovules in the F1 generation when certain B-whites were crossed with Line 26, a form from Cuba, which had been shown to be an A-white. Further tests of this Line 26, however, have shown that F1's between it and most of our other lines (whether A or B whites) show 50% abortion—in other
words, that Line 26 is a ‘bad pollen producer.’ An attempt is being made to reconcile the hypothesis proposed with the lack of pollen abortion expected in F₁'s between B-whites and other normal lines, since it appears to be the best hypothesis so far available to account for the peculiarities of the B-whites.

“A rather extensive series of crosses between the main lines in our collection shows a number of points to be bad pollen producers. So far in this group we have a line each from Cuba, the Bronx (New York), New Jersey, and the island of Madeira. Crosses of these lines interspecific have given F₁’s with good pollen, a fact which leads to the belief that in the bad pollen producers so far identified we are dealing with the same genetic difference. This summer we have in the field both F₁'s and F₂'s from the cross between the Primary mutants of Line 1 and normals of Line 26 and should be able soon to determine whether the hypothesis of segmental interchange between non-homologous chromosomes is a possible explanation for the 50% abortion of pollen and ovules in F₁'s between bad pollen producers and other lines. So far as the pollen counts being made by Mr. Cartledge have gone, the results suggest that possibly both the Echinus and the Microcarpic chromosomes from Line 26 may be responsible for the production of abortion in the hybrids.

“If, as appears to be the case, both the B-whites and the bad pollen producers are due to chromosomal changes, we have an opportunity in these types of studying chromosomal evolution which has taken place in nature.”

GENE MUTATIONS IN DATURA

“A few new gene mutants have been discovered from material sent us from our own collections, or from spontaneous mutations. A dominant gene, ‘Bronze,’ responsible for increased pigmentation at base of leaves, has been located in the Glossy chromosome by the method of trisomic ratios. By the same method we hope to be able to locate a number of other genes before the end of the summer.

“Spontaneous gene mutations are relatively rare in Datura. Of the three useable mutants so far secured in our main Line 1, two first appeared as recessive segregates from two plants which were the offspring of a haploid. The heterozygosity of each of these two parents was most likely due to a mutation which had affected a single gamete of the haploid. The number of parents tested for heterozygosity is too small to conclude that mutations are more frequent in haploids than in diploids, although a considerably fewer F₁’s from haploids have been tested than parents less closely related to haploids. The occurrence of any mutations in a haploid, however, is of some theoretical interest in indicating that the phenomenon of gene mutation may be independent of heterozygosity, which by some has been considered a cause of their occurrence.”

GAMETOPHYTE SELECTION

Professor John Buchholz has continued his researches of past years into the differential fertilization of Datura ovules by pollen-grains containing n and (n + 1) chromosomes respectively, such as are found in the pollen of (2n + 1) mutants. He has sought to increase the percentage of Globes transmitted through the (n + 1) pollen, by the method of limiting the number of pollen-grains placed on the stigma, so as to reduce competition. It appears that the largest percentage of Globes is obtained if fewer than 600 pollen grains are used. The optimum is between 450 and 500 grains; with these numbers 10 per cent or more of Globes may be produced. With 700 to 900 grains competition is so severe that the (n + 1) grains fertilize below 3 per cent of the ovules. If fewer than 350 grains are employed, the capsules are small and many (2n + 1) zygotes are eliminated.
As to pollen-tube growth, it appears that at 18° C. the pollen-tube reaches a maximum rate of growth at 2 hours after the beginning of germination and maintains that rate. The rate of growth of the pollen-tube depends on temperature, so that if the rate at 10° is taken as unity, that at 16.5° is 2; at 22° is 3, and at 30.5° is 4. A maximum growth-rate of 5.55 mm. per hour is attained at 33°, above which temperature growth begins to decline.

When on Datura stramonium pollen of D. meteloides is placed the pollen-tubes grow 2 mm. per hour at 18° C.; but the egg forms no proper embryos. The pollen of D. stramonium on D. meteloides grows so slowly (about 0.8 mm. per hour) that the tube can not reach the ovary through the long style before the latter falls off. This cross is thus entirely sterile.

**Configurations of Chromosomes in Non-Diploid Sets**

Dr. Belling has continued his analysis of the interaction of chromosomes where more than the typical pair are involved to the set. He reports as follows:

*Configurations of trivalents and of quadrivalents*—"The five usual configurations of trivalent in the triploids, and the eight configurations of the quadrivalents in the tetraploids, are those which would occur if the chromosomes were united by their homologous ends; the two ends of any one chromosome being different in this respect, and each of the n classes of chromosome being different at both ends in the kind of attraction. Thus in Datura there would be 24 such attractions, normally all different. All of the configurations demanded by this hypothesis were found; and configurations not corresponding to the hypothesis were not found, either in the triploids, in the primary (2n + 1) forms, or in the tetraploids. (There were three apparent exceptions out of the hundreds of configurations studied; but alternative explanations were available for these.)"

"The frequencies of each of these configurations showed that there was a greater likelihood that two homologous ends of two chromosomes should unite than that three or four should meet at one point. That is, either the attraction of two ends was partly neutralized by their union (at the thin thread stage), so that they did not attract a third chromosome end so strongly; or the combination of two homologous ends was more stable than that of three or four. This was also shown by the number of separate single chromosomes not united with any other (cases of non-conjunction), being larger in the triploids than in the diploids (where they are scarce), and larger still in the tetraploids.

"There are no less than five criteria by which, in a first-metaphase group of bivalents, trivalents, or quadrivalents, it may be shown to which pole of the cell any particular chromosome is proceeding. These criteria may also be applied to secondary (and to tertiary) 2n + 1 forms. In this latter case the expected numbers of primaries and secondaries in the progenies can be calculated beforehand, and estimates can be made of the mode of inheritance (diploid or triploid) in the trivalents."

*Parallelism between certain configurations of plant chromosomes and crossing-over in Drosophila*—"In the long chromosomes of certain diploid plants, at the late prophase and first metaphase, it has been found that homologous chromosomes are often joined at the ends (as is exclusively the case in Datura), and also at the median (or nearly median) points of constriction. In addition to such junctions, the homologous chromosomes are often connected at one other point (near the center, or nearer one end) where they seem to cross. Less often they are connected at two such crossing-points, at different places
in different configurations. Rarely there is an apparent triple junction. According to the estimates already made, the cases where there is no junction, except at the ends or the point of constriction, may be not far from half the number. Also, the number of cases of two junctions is about one-fifth of the total. These phenomena seem parallel, qualitatively and quantitatively, to the single, double and triple crossing-over in the X-chromosomes of Drosophila melanogaster."

The attachment of non-homologous chromosomes in certain $2n + 1$ forms—

"Attraction between non-homologous chromosomes in Datura has been proved in one form of $2n + 1$ mutant, namely, $Wy$. Here one chromosome of the same size as the extra chromosome of $Pn$ (No. 9) is sometimes combined, in the trivalent (open V, or ring-and-rods), with the two large chromosomes, like the extra chromosome of $Rl$ (No. 1); or is sometimes combined in an open V with the two other chromosomes of the same size as itself, No. 9.

"$Wy$ has three No. 9 chromosomes, as has also $Pn$. But $Wy$ differs in many respects from $Pn$. Hence one of the No. 9 chromosomes must be different in $Wy$ and $Pn$. Since this altered chromosome of $Wy$ unites both with chromosome 1 and with chromosome 9, it may be considered as having exchanged a terminal segment with chromosome 1. Since $Wy$ has arisen several times from $Pn$ crossed with a $B$ strain of diploid Daturas, but from no other $Pn$, it seems there is something in the $B$ Daturas which causes this abnormality. If in the $B$ Daturas segmental interchange has occurred between the non-homologous chromosomes 1 and 9, at the origin of the strain in the past (as it doubtless occurred also in one species of Stizolobium used in species crosses in Florida), then the altered chromosome 9 would have a terminal segment, perhaps a half, replaced by an equal terminal segment of chromosome 1; and vice versa for chromosome 1.

"This hypothesis accounts for the appearance of $Wy$ and also for the abnormal ratios given by $Rl$ and $Pn$ after crossing with $B$ whites.

"It was thought at first that the $F_1$ of normal diploid Daturas and the $B$ strain was semi-sterile. But it was found that this semi-sterility was confined to the descendants of one abnormal plant. If the exchanged portions of the two non-homologous chromosomes contained genes vital to pollen and egg-cells, the $F_1$ would be semi-sterile, as in certain Stizolobium crosses; but this is not necessarily the case. The hypothesis fits the facts at present known, and permits several deductions, some of which may be readily tested.

"A similar hypothesis seems to extend to $Hg$, where an altered chromosome 1 unites both with the 1 bivalent and also apparently with the 6 bivalent. $Nb$ also seems to show a similar attachment of non-homologous chromosomes.

"These mutants are of interest also since they appear to show a possible origin of plants mutually 1/2, 3/4, 7/8, etc., sterile (when crossed), in a species, as a result of varietal chromosomal mutations."

Differences and likenesses between plant and animal chromosomes at the reduction division—"In plants of Uvularia which had been forced in February and March there were found, in 1924, an abundance of stages between the metaphase and anaphase of the reduction divisions. These appeared to demonstrate that in the single or double rings the chromatids were interlaced at the junctions; that in the horizontal rings or V's one of the chromatids from each lateral half went to one pole and one from each half to the other; that in the vertical rings or V's both chromatids from the upper half went to one pole and both from the lower half to the other pole; that the two opposed spindle fibers regularly drew out a loop from the points of constriction, and that this constriction remained visible throughout the metaphase and ana-
phase; that crosses in the early anaphase were due to partial separation of the homologues, leaving two decreasing median arms; that oval configurations with two axes of symmetry (when the constrictions were subterminal) were due to separation of the homologues of a horizontal truncated A, except at the ends. These last two points, doubtless, differ from the phenomena in insect chromosomes, as described by Janssens, for instance."

"Chromomeres and spirals—"The metaphases of the reduction division have been observed in about 30 species of flowering plants, the fixation in the pollen mother-cells being usually perfect. Chromomeres are often readily visible at the metaphase and anaphase of the reduction division, especially in *Tradescantia*, *Datura*, and *Hosta*. When feebly stained, the margins of the chromomere seem to show up, so that something resembling an irregular, single or double spiral may be traceable. The chromomeres, on close examination, seem themselves divided; so that accurate counting is not easy. By the use of pressure, however, even the X-shaped second metaphase chromosomes may be seen to be composed of chromomeres. Chromomeres can be seen, near the limit of best microscopical vision, even in the first metaphase chromosomes of the haploid *Datura*. If the fixation is not perfect, the chromomeres may run together, as a post-mortem change."

"Perfect and imperfect fixation of chromosomes in pollen mother-cells and young pollen-grains—"With iron-aceto-carmine, the fixation of many pollen mother-cells takes place in a few seconds, as shown by the commencing reddening of the chromosomes. In small cells, such as those of *Datura*, the 45 per cent acetic acid (strong enough to blister the fingers) has only a few microns of cytoplasm to penetrate, as well as one more or less permeable pectin-holding cell-wall. Large pollen mother-cells, such as those of *Canna*, with abundant cytoplasm, take longer to fix; but if properly manipulated, fixation may be perfect. On the other hand, young pollen-grains at the stage of the first metaphase may have a somewhat cuticularized wall, as in *Datura*, and the solution does not penetrate them quickly enough to give the best fixation.

"A number of anthers of different flowering plants have been tested in the usual chronic acid, osmic acid, or platinic chloride fixatives. Perfect fixation was never obtained for paraffin sections of the whole anther. On the other hand, the same fixatives gave perfect fixation with the endosperm chromosomes of *Lilaceae*, at the stage when the nuclei are in a single sheet of cytoplasm without cell-walls. In this case the embryo sac was cut open before putting it in the fixative, as Strasburger, apparently, first recommended.

"When smears are made of pollen mother-cells or young microspores, fixed and then stained in the usual way on the slide and preserved in balsam, there often seems to be more or less shrinkage of the chromosomes, especially in the pollen-grains, as compared with iron-aceto-carmine preparations of the same plants."

EXPERIMENTAL MODIFICATION OF THE GERM-PLASM

In striking contrast with the frequency and large size of mutations that arise spontaneously in the germ-plasm is the difficulty of securing a modification of the genes of the germ-plasm by the action of any external agent. In earlier reports of the Department, genetic abnormalities have been described that occurred in strains of mice that had been subjected to X-rays (Little and Bagg). The matter seemed to call for reexamination, and this is being made by MacDowell, cooperating with Bagg of the Memorial Hospital. First of all, it has appeared necessary to establish the minimum sterilizing dose. The study was limited to males, since the testes could be exposed to the X-rays without harm to other organs, and more frequent breeding tests obtained from them.
Dr. MacDowell reports:

"We now have data on three sets of four litter mates. These were first tested for fertility, then treated with exposures of 3 to 20 minutes and then every week mated with a new set of six young females that had been tested for fertility. In order to protect the other organs from the heavy dosage, a lead screen was used and each animal, under ether, was strapped in position with the scrotum exposed.

"One male exposed for ten minutes and two for five minutes bred at once after the treatment and continued to sire large litters for the three months the matings were continued; the longest interval between irradiation and copulation resulting in pregnancies was 11 days.

"Two males were exposed for ten minutes. One of these showed no effect of the treatment, giving as large and as frequent litters as the males with the lighter doses. The other one in the first week after the treatment gave three pregnancies; one of these resulted in no young at birth and two resulted in one young dead at birth. These same mothers had given first litters of 5, 6 and 7 young. After this first week no pregnancy was given for two months, at the end of which time full fertility returned.

"Six males, exposed for fifteen minutes each, gave pregnancies in the first week that resulted in small litters averaging 1.9 young per litter, while the same mothers gave first litters averaging 6.2 young. Two of these males gave a pregnancy in the second week as well. After this all were sterile. Two were tested through seven months, and four have so far been tested one month with no return of fertility.

"One male exposed for 20 minutes gave no detectable pregnancy and no young in all the seven months of testing.

"From this it appears that a dose of 15 minutes may be expected to reduce the fertility at once and to induce sterility within two weeks, while a dose of 10 minutes is close to the border-line and may show the same effect or none at all. If the scrotum of a mouse can be exposed directly for ten minutes without showing any effect upon fertility, it is not surprising that our earlier experiments, in which a total of one minute of exposure divided into five daily treatments applied dorsally, failed to reveal any genetic modifications. Furthermore, these results question any causal relation between this same exceedingly light dosage and the inherited abnormalities reported by Little and Bagg."

**PHYSIOLOGY OF REPRODUCTION AND DEVELOPMENT**

Genetics is no longer just the science of the laws of heredity, nor the system of dependence of inheritance upon chromosomes, or their genes. Inheritance will first be understood when it can be shown how the chromosomes do their work of directing the course of development. That they work by chemical means it is impossible to doubt. In the coming era of the study of differentiation in development, biochemistry will play a leading rôle.

For the present our contribution to the problem of development is largely concerned with ovulation, with growth processes, with inter-uterine deaths and with the chemical basis of the sex differential.

**Ovulation in Mice**

One approach to this subject has been the effect of alcohol upon the germ-cells and development, a line that is being followed especially by MacDowell. He had shown that female mice treated with fumes of alcohol for 45 minutes each day did not differ from the controls in any of the criteria for reproduc-
tion—length of oestrus cycle, as determined by vaginal smears, number of corpora lutea per pregnancy, as determined by counts made through an incision into the body-wall, number of young born alive and born dead, total amount of prenatal loss. The results of these experiments led to the use of an increased dosage of alcohol such that a condition of deep anesthesia was produced at each treatment, the time required to produce this result varying with age, strain, and weather. The extreme times were 30 minutes (at 4 weeks) to 120 minutes. Only one male and one female were rendered infertile by the treatments, in which every imaginable difference (except alcohol) was controlled. Some of the final results of this investigation are reported on by MacDowell as follows:

**ACTIVITY OF THE OVARY**

"Based on the number of corpora lutea, the ovaries of treated mice are fully as active as those of their untreated sisters. Neither in the beginning of their reproductive life after 20 to 40 treatments, nor late in their reproductive life after 6 to 8 months of treatment, is there any indication that the alcohol cut down the number of corpora lutea. On the other hand, there is found a distinct tendency for the corpora lutea from the treated mothers to average higher per ovulation than the controls in the same parity. This result may be associated with the tendency of alcohol to diminish the blood-supply to the skin, resulting in visceral hyperemia. However much the alcohol may cut down the number of young born, this is not due to a reduction in the activity of the ovaries.

**TIME BETWEEN LITTERS**

"Aside from the vicissitudes of taking a large number of mice down into deep alcoholic intoxication each day, the number of pregnancies studied from control mice was soon found to be exceeding those from treated mothers. This led to a special study of the age at the time of first births and the time between subsequent births. The treated and control females in each unit experiment at four weeks were given a male already tested for fertility, so the age at the first birth was significant of the female. As all young were removed from their mothers on the day of their birth and the mother remated at once, the time between litters is also significant. This study showed a clear-cut delay in the birth of the first litters from treated mothers, as well as longer intervals between first and second, and second and third litters; in later litters the difference between the treated and control mothers dwindled. The exact cause of this delay is not yet ascertained. To test the hypothesis that the difference in the number of corpora lutea produced by the two groups of females might be merely an expression of the differences in age at the corresponding birth due to the treatment delaying conception, the following study was made."

**RELATIVE INFLUENCE OF PARITY AND AGE UPON THE NUMBER OF CORPORA LUTEA**

"In last year's Year Book (p. 49) reference was made to the problem of separating the effect of age upon the number of corpora lutea per ovulation from that of the number of previous pregnancies. A more complete analysis is now available with larger numbers and the primary classification based on parity instead of age. That is, the corpora lutea counts for all first litters are arranged according to the age of the mother at the births of the litters; the averages of the different age classes are practically equal. The counts for second litters so classified and averaged are also equal, but higher than first litter and so for third, fourth and fifth litters. That is, for a given parity, the corpora lutea counts for the different age groups average about the same,
but as the parity is increased all age groups increase, until the maximum activity of the ovary is reached about the fifth or sixth litter. These results lead to the conclusion that the previous reproductive history up to the fifth litter makes more difference in the number of corpora lutea than the age of the mother. This may be explained in terms of the suspension of ovulation that occurs during pregnancy; every pregnancy means two or more fewer ovulations than in an unmated mouse, and each of these rest periods may result in accelerated ovulation until a maximum number is reached. Hence it is concluded that the difference between the corpora lutea counts from treated and control mothers of the same parity can not be due to the difference in the ages of the mothers."

**TREATMENT AT TIME OF OVULATION**

"The procedure adopted at the outset of this investigation was to suspend the alcohol treatments between the day of the operation for counting the corpora lutea and the birth of the young. In 65 per cent of the cases this period was from 5 to 7 days. But during these last days of gestation, the final stages of ovigenesis are accomplished for an ovulation that takes place soon after birth; besides this, at the time of ovulation a new proliferation of cells from the germinal epithelium initiates a new set of ova, some of which will reach maturity at a later ovulation. It thus appears that the alcohol was being omitted at the most critical period of the ovarian cycle. The experiments were, therefore, divided into two series; half of them would continue as at first and half would be given alcohol throughout pregnancy with the exception of the day of the operation, but not excepting the day of birth. These experiments led to the conclusion that the administration of alcohol throughout pregnancy yields results of the same nature and only questionably different in amount from the omission of this treatment at the end of pregnancy. This result supports the opinion that whatever the effect of the treatment in general upon the number of the corpora lutea, it is probably indirect and not specific."

**OVULATION IN PIGEONS**

Ovulation in birds involves relatively larger changes in metabolism than in mammals, since the bird makes all nutritive provision for the embryo during the few hours of ovigenesis, while mammals feed it through weeks of gestation. Riddle and his collaborators are investigating these changes. Just as the suprarenals hypertrophy and the blood-sugar increases at this time, so does the blood calcium. The calcium is, indeed, doubled in females (but not in males) at the ovulation period; and this demonstrates extraordinary activity at this time of the parathyroid glands. Following the ovulation of the second egg this excess of calcium gradually diminishes to normal proportions. Also, early in the preovulation period a notable increase of both fat and phosphorus appears to occur in the blood. The final data will, it is expected, enable us to compare the metabolism of fats and phosphatides in males and non-reproducing females.

In cooperation with Professor Masahura Tange, who was a guest of this Department during six months, tests were made of the effect of injections of placental and follicular hormones upon the acceleration of puberty and growth and activity of the oviduct in birds. There was some evidence that oviducal hyperemia is induced by these hormones, but the results were less striking than those obtained in mammals. Enlargement of the spleen was unfailingly induced.
To test the possible influence of the bursa Fabricii upon reproduction, this gland was removed by Riddle and Tange from 8 males and 12 females that were reared to maturity. The bursectomy shows no effect upon rate of growth nor age of maturity. It has been earlier shown by Riddle that as the bursa begins to atrophy the rate of growth of the gonads increases. In herons examined in Florida by Riddle the bursa is retained during one or two years and these species do not mature until their third year.

**RIGHT AND LEFT GONADS IN BIRDS**

Additional evidence was gathered during the year by Riddle that “in many, or most, species of birds those conditions that repress testis growth are more effective in the right testis than in the left.” Two feral male birds (an oven-bird and a wood-thrush) showed a rudimentary left and right testis respectively. Nevertheless, the seminal vesicle on the rudimentary side was fully formed, indicating that its size is not determined by its function merely, but probably largely by the secretions of the functional testis (of the opposite side).

Studies made by Riddle in Florida showed that the regression in size of the testis, following the breeding-season, occurs quite as readily in a hot climate as in a cool or temperate one. Riddle has now made observations on the condition of the testis in 100 species of feral birds belonging to 28 families.

**GROWTH IN MAMMALS**

One of the most obvious of the developmental processes is growth of the body, as a whole. Hardly less important is that of the different parts of the body. While the importance of nutritive conditions in controlling the velocity of growth is not to be overlooked, on the other hand, each species, or race, has its standard adult size. Even the rats of Osborn and Mendel, which grow with such unexampled speed, do not much exceed the weight of slower-growing rats fed on a less highly selected diet. Adult body size and the general laws that it follows in the individual of the species is a genetical character. Studies in growth of man and lower mammals have been made by Davenport. Misses Allen, Gould, March, Newman, and Scudder have participated in the observations and computations.

Additional anthropometric data of children have been secured from the Orphan Society of Brooklyn, and these data, together with others already on deposit at the Eugenics Record Office, were utilized in an analysis of growth. The study of “Human Metamorphosis” was published in the “American Journal of Physical Anthropology.” Development of stature and weight were traced in both sexes; also relation of stature to span, sitting height, and chest-girth were analyzed for a stock chiefly of Northwestern European origin. A paper on the human growth curve, with special reference to growth cycles, was read before the National Academy of Sciences in April. Standard growth curves for human females were published as a schedule of the Eugenics Record Office.

Abnormal human growth is being followed in humans, especially in mongoloid dwarfs, in continuation of work begun some years ago at Letchworth Village. Further studies have been made by Davenport on human dwarfs in collaboration with the State institutions at Laconia, New Hampshire, Columbus, Ohio, Gainesville, Florida, Gracewood, Georgia, and Newark, New York.
The studies on the production of dwarf mice by operations on their mothers have been continued with the cooperation of Professor Swingle. For comparison with the growth of normal mice there were weighed repeatedly (by Miss Newman) 48 litters of controls and 66 litters of mice from mothers that had been thyrocauterized.

**Prenatal Mortality**

In the studies on the effect of alcohol upon reproduction especial attention was paid to prenatal mortality. It was found by MacDowell that——

"the prenatal mortality normally increases with the parity—a result that illumines the reduction in fertility so generally found in mammals after the early reproductive peak is passed. For each parity, from the first to the sixth, the prenatal mortality is increased by the alcohol treatment of the mothers. The differences in order of parity in percentages are 12.6, 8.5, 5.5, 11.5, 11.6, 11.1. This completes the demonstration that alcohol treatment of the mothers cuts down the reproductive output by losses after ovulation rather than by cutting down ovarian activity.

"Another considerably larger set of data (over 800 litters and corpora counts) on prenatal mortality has been obtained in a series of experiments originally planned to test the conclusion of Stockard that in guinea-pigs the treatment of the fathers increases the prenatal mortality as much as the treatment of the mothers. Instead of treating the mothers, in this series half the fathers were treated and each mother mated for alternate litters with a treated and control male. The differences in prenatal mortality from treated and control fathers in different subgroups is between 1.0% and 0.1% and in no case statistically significant. On the other hand, a clear difference in prenatal mortality is found when the litters from the two strains of males are compared.

"It is concluded (1) that the nature of the sperm influences the amount of prenatal mortality; when the sperm are genetically very similar to the ova (inbreeding) the prenatal mortality is higher than when the sperm and ova are dissimilar (crossing) but the amount of this reduction in the mortality depends on the strain from which the male came; (2) that the extreme alcoholization of the males failed to produce any significant modification in the prenatal mortality of the young, either in the beginning of the treatments or after many months. This is considered to indicate that the germ-cells of the mouse are resistant to alcohol and to fall in line with the finding that alcohol does not impede the maturation of ova."

**Abnormal Development**

In the alcoholization experiments upon mice several abnormal young were found in the first generation derived from the treated animals. The question arose, in how far is the alcohol responsible for these abnormalities. The statistical fact is that, in the series of alcoholization experiments where the mothers were treated, abnormalities of different sorts appeared in 0.83 percent of the young of the treated mothers and 0.65 percent of the young from control mothers. Also, different strains showed different types of defect; thus, one strain showed defects of the eyes (but this strain was characterized by this defect before the experiment was begun), another of the jaws (otocephaly), and another of the feet (talipes).

"In the series of experiments with the fathers treated, out of 2,082 young from treated fathers 9 were abnormal, and out of 2,087 young from the control fathers 9 were abnormal. Only two of these (one tailless and one abnormal footed) came from the four experiments in which the fathers were from the
Dilute Brown strain; all the rest came from the four experiments in which fathers were Bagg Albino.

"Although the young in all these cases were F₁ hybrids from unrelated lines, the number of abnormalities, as in the inbred matings, is influenced by the strain and not by the alcohol.

"It is of interest to note that all the types of abnormalities shown externally by the abnormal race that originated in the X-ray experiments of Little and Bagg have been found in these experiments. They could not be distinguished by the somatic appearances, but there is good evidence that the genetic basis is different and, indeed, complicated.

"By selecting abnormal eyed parents the proportion of eye defects has been increased in one branch to over 30% of all young born. Normal parents will throw the abnormality and abnormal parents will throw normal young. In crosses with an entirely unrelated line and using unselected normals from the first strain, the abnormality has appeared in four cases in the F₁ generation. Two of these have been inbred and in both of the branches so started the abnormality has reappeared, but in one the frequency is much higher than in the other line. There is, as indicated, no evidence that alcohol had anything to do with inducing these abnormalities; and this doubt extends to the abnormalities secured by Bagg and Little in their X-ray line of mice."

**SEX**

Since sex (and the train of associated sex characters) is generally believed to be chiefly determined at the moment of fertilization, it is one of the earliest determined traits of the zygote. Indeed, in the parthenogenetic strains of Cladocera whether there shall be males or not is probably determined before the time of maturation.

**Male Induction in Moina**

Further progress by Banta and Brown in inducing males experimentally has been made. The importance of low temperature in determining the result, reported last year, has been confirmed this year.

**Pseudo-Sexual Eggs in Daphnia**

A report on sexual-like eggs of *Daphnia* that develop parthenogenetically, and which were discovered by Banta, has been made by Dr. Franz Schrader of Bryn Mawr College, who has examined their cytological conditions. It appears that the pseudo-sexual eggs have the full complement of 24 chromosomes, which is the somatic number for the particular strain of *Daphnia* studied. This is the same number as that found in the parthenogenetic or summer egg.

**Chemical Differentiation of the Sexes**

In this topic several studies have been made. In those on green plants and mucors Blakeslee has had the assistance of Miss Satina, whose salary has been met by an appropriation from the Committee of the National Research Council for Research on Sex Problems. It appears that the plus (female) strains of mucors have a greater power of reduction of selenium and tellurium than the minus strains. Many races of *Absidia blakesleeanus* and *Circinella spinosa* were tested and found to vary in vigor of reaction to the tests for sex.
In green plants, also, a difference appears to the reaction of juices of plants of the two sexes to various tests. Thus alcoholic extracts of the leaves showed the female to be on the average more yellowish and the male more greenish. Catalase gave a stronger reaction with female than male leaves. Reduction of KMnO₄ and of methylene blue were stronger in the females. The Manoilov's reaction generally gave the violet reaction with the extracts of female plants. *Parastitella*, which is a mucor that is parasitic on other mucors, also gave the male and female reactions, like the other mucors.

In pigeons, Riddle, with the collaboration of Mr. Warren Reinhart, is applying the Manoilov sex reaction. Special attention is being given to cases and conditions in which the test gives reversed reactions, to the relative strength of the reaction obtainable from a wide series of organs or tissues in one and the same animal, and other points.

**RACE DIFFERENCES IN THYROID GLANDS IN PIGEONS**

An attempt has been made by Riddle to establish races of pigeons characterized some by large, others by small size of the thyroid gland. In consequence of certain special procedures during the past five years it has come about that now we have high thyroid and low thyroid races of ring-doves, and perhaps also of the common pigeons. The basis of selection for thyroid activity was sometimes indirect, as when made on the basis of reproductive abnormality; for there is a close relation between thyroid activity and reproductive activity. The selection was often based on direct knowledge of thyroid conditions in the family, since the thyroids of all birds have been, during the past 5 years, weighed at autopsy. At the same time, possible effects of age, season of year and disease were considered. Meanwhile, the diet, degree of confinement and amount of sunlight have been standardized in such a way as to minimize the variability of these factors.

There were selected for close inbreeding young from parents whose thyroids were known to be abnormally small or abnormally large. Thus, in one strain in 3 generations the weight of thyroids increased, on the average, from 20 mg. in the offspring to 27 mg. In a strain selected for decreasing thyroids the weight fell from 14 mg. to 11 mg. in 4 generations. Two strains or races of ring-doves with large thyroid glands and at least 2 races with small thyroids seem to have been well established. Through 3 or more generations a great majority of the healthy individuals of these races have shown thyroids characteristically large or small in accordance with their race. It is believed that these are the only "thyroid races" that have been experimentally produced.

Just the races with high or low thyroids are poor breeders. It is the races of intermediate thyroid size that are most highly fertile and produce the most viable young.

In cooperation with Dr. F. G. Benedict, Director of the Nutrition Laboratory, Riddle is securing data on the basal metabolism of races of pigeons that deviate widely from the normal thyroid size. The necessary measurements are being made by Miss Edith Banta. The apparatus permits of the measurement of the basal metabolism of 3 birds each day. Among the apparatus is one equipped with a heating and insulating device that permits the birds to be subjected to external air of any desired temperature.
As stated above, Banta has succeeded in hybridizing clones of *Daphnia* differing in respect to the degree of "excavation of head," from the wild type (unexcavated) to an extremely modified type. A summary of his results, so far as success in hatching the young goes, is given in Table 4.

**Table 4.—Results of matings among "wild" and mutant "excavated head" forms.**

<table>
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<tbody>
<tr>
<td>A. &quot;Wild&quot; ♀ × &quot;wild&quot; ♂</td>
<td>228</td>
<td>34</td>
<td>15</td>
<td>31</td>
<td>91</td>
</tr>
<tr>
<td>B. Mutant ♀ × mutant ♂</td>
<td>116</td>
<td>17</td>
<td>10</td>
<td>12</td>
<td>70</td>
</tr>
<tr>
<td>C. &quot;Wild&quot; ♀ × mutant ♂</td>
<td>373</td>
<td>135</td>
<td>36</td>
<td>112</td>
<td>84</td>
</tr>
<tr>
<td>D. Mutant ♀ × &quot;wild&quot; ♂</td>
<td>192</td>
<td>70</td>
<td>36</td>
<td>60</td>
<td>86</td>
</tr>
</tbody>
</table>

As Table 4 shows, the mating of two mutant lines gives the least fertility; that of two wild lines next least; while cross-matings, in reciprocal fashion, give a relatively high fertility. This low fertility of the mutant stocks is accounted for, by Banta, on the ground that they carried lethal or sublethal mutations.

The method of inheritance of "excavated head" is shown in Table 5.

**Table 5.—Inheritance of "excavated head."**

<table>
<thead>
<tr>
<th></th>
<th>No. individuals tested.</th>
<th>No. bearing excavated head.</th>
<th>No. bearing sex intergrade.</th>
<th>Mendelian expectation.</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. &quot;Wild&quot; ♀ × &quot;wild&quot; ♂</td>
<td>27</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>B. Mutant ♀ × mutant ♂</td>
<td>6</td>
<td>3</td>
<td>3</td>
<td>4½ to 1½</td>
</tr>
<tr>
<td>C. &quot;Wild&quot; ♀ × mutant ♂</td>
<td>109</td>
<td>53</td>
<td>31</td>
<td>54½ to 64½</td>
</tr>
<tr>
<td>D. Mutant ♀ × &quot;wild&quot; ♂</td>
<td>57</td>
<td>24</td>
<td>23</td>
<td>28½ to 28¼</td>
</tr>
<tr>
<td>C's and D's followed longer</td>
<td>39</td>
<td>16</td>
<td>20</td>
<td>19½ to 19¼</td>
</tr>
</tbody>
</table>

"The approach to the expected 1 to 1 ratio is fairly good in the hybrid groups, for both excavated head and sex intergrades.

"Hybridization was also carried out between wild stock and the sex-intergrade lines. The sex-intergrade character has rarely been manifest in the individuals hatched from sexual eggs; but its genetic presence is shown by their production of parthenogenetic offspring showing the character. It is a matter of record that sex-intergrade offspring frequently do not appear among the early broods of a mother. It was impossible to follow all these mothers of hybrid origin far enough to learn conclusively just how many of them genetically possessed the sex-intergrade character, and it is certain that more than 31 of the 109 wild type ♀ × ♂ mutant ♀ hybrids would have shown the character if they could have been followed farther. Of 28 such hybrids, which were followed throughout their reproductive history, 13 showed the sex-intergrade character among their offspring. This and other evidences not readily introduced in brief lend weight to the interpretation that the real ratio is again 1 to 1 and that sex-intergradedness, like the excavated head character, is due to a dominant heterozygous factor in the parent mutant stock."
ACCESSORY FACTORS INVOLVED

"It seems probable that in addition to the principal factors involved in the inheritance of this excavated head character there are also accessory factors (possibly 4 or 5) affecting the extent of the manifestation of the character."

"The results of sexual reproduction throw further light on this subject. A level for the excavated head character at least one step below the lowest level obtained in the low-selection strains is strongly suggested. Perhaps, then, the excavated head character at the lowest level reached in the selection experiments was still controlled by the principal factor and one accessory factor. Further, the large number of hybrid strains which show a mean grade around 0.30 to 0.40 suggests that this is another genetic level for the character.

"An analysis along similar lines seems to fit the facts for the inheritance of the sex-intergrade character, so that it too seems to be influenced by accessory factors.

"The excavated head and sex-intergrade characters are inherited independently—approximately one-fourth of the hybrids (between stock having both mutant characters and wild type stock) bearing neither character, one-fourth bearing both characters, and one-fourth bearing each but only one of the two characters.

"The apparently typical Mendelian behavior of these mutant characters, which we had previously followed through several modifications in parthenogenetic inheritance, when carried through sexual reproduction seems to bring our studies on inheritance in parthenogenesis into harmony with the very extensive studies that others have made on bi-parental inheritance in other animals and in plants."

MAIZE

Studies on albinism in maize have been continued by Demeree in cooperation with Professor R. A. Emerson, of Cornell University. These have established the presence of at least 13 genotypically different factors for albinism. It has been found, also, that a large proportion of albinos are determined by duplicate and some by triplicate genes.

THE THOROUGHBRED HORSE

This extensive investigation conducted by Dr. Laughlin is rendered possible by the continued generous support of Mr. Walter J. Salmon. Six assistants and statisticians are employed on this investigation. The principal purpose of this research is to discover as definite rules as possible of inheritance of certain constitutional qualities of the running horse. The most important of these are age of mature performance, weight-carrying ability, stamina or distance-going ability and speed.

BIOLOGICAL HANDICAP

The accurate determination of the biological handicap is fundamental to the study, as that number represents the racing merit of the horse or his standing in the group of thoroughbreds. Laughlin has worked out a method of securing this value by relative standing of the propositus in relation to other horses whose handicaps have already been determined.

RELATION BETWEEN DISTANCE AND SPEED

In making this determination the basis of speed is taken as "the mean number of seconds per furlong in the American record for 2 furlongs, i. e., 10.62 seconds. With this as a standard, the increased number of seconds per
furlong was computed for each particular number of furlongs in American speed records. In this particular series of records, age, sex and weight carried were not considered, because the whole breed, regardless of age, sex and weight carried, is striving for speed, and when a record is broken, which is, of course, rarely, all subordinate conditions are most apt to be at the optimum. In analyzing speed records, if we let \( y \) equal the number of furlongs run, and \( x \) equal the mean time per cent increase per furlong, when the basic unit \( 1.00 = 10.62 \) seconds per furlong, we find that \( x = 10 (0.088296 \cdot \log y + 1.9763) \). While in general this has proven to be a successful measure of the effect of distance upon speed, it is clear that each individual horse is not a duplicate in distance-running ability of the best of the breed as a whole."

**Relation between Weight and Speed**

"This determination is proving much more difficult than the determination of the relation between speed and distance. A number of records are in process of analysis and efforts are being made to eliminate the factors which obscure the most direct effect of weight upon speed. This, too, when found for the breed as a whole, will have to be modified to fit the weight-carrying abilities of the individual horse.

"In actual racing, the range of weight carried and distance run by an individual horse in a single season are not great enough to supply the series of data desired for the more definite determination of the influence of weight upon speed; therefore, experiments are planned to test the speed of selected horses under a wide range of distances and of weights carried."

**The Futurity Index as a Predictor of Speed and Breeding Quality**

"During the year the Futurity Index was further developed and put to a more extensive test as a particular pre-indicator of racing ability and breeding quality. The elements which enter into this index are the racing abilities of the nearest blood-kin of a selected horse, or of a prospective foal, based on data securable at the time of the mating of the sire and dam of the particular foal."

There is also a close correlation between the Futurity Index and the Breeding Index found later in the offspring.

The relation of Futurity Index to Near-Kin Index is so close that even when the series of grades of the Futurity is divided into a scale with 6 divisions the Near-Kin Index increases in each division with increasing value of the Futurity.

**Twinning in Sheep**

In the autumn of 1925, No. 3795 was again used as sire to the flock of sheep. There were born 21 lambs to 14 ewes, or an average of 1.5 per ewe. This is a further reduction in the average number of young born to a mother. The still-borns increased in number. The ram has been replaced by one of the late Alexander Graham Bell's flock of high twin production.

**Human Genetics**

**Heredity in Aristogenic Families**

The work of analyzing the scholarship records of the Huntington schools, with the aim of throwing light on inheritance of the elements of scholarship, was continued during the year by Banker. He has spent much time on devising better methods of interpreting school records than those now in use. This preliminary work has involved a laborious amount of statistical research.
During the year Banker has published an analysis of age distribution in the grades as a measure of mentality. He has worked out for each school grade the chronological age at or above which the pupil is presumptively feeble-minded or border-line; also the chronological age at or below which the pupil is one of "superior intelligence" as defined by Terman. He concludes that achievement increases with a diminishing increment as the intelligence quotient increases.

A study was made by Miss Grace Allen of the families of 48 children having intelligence quotients of between 133 and 190. This is a group which has been the center of studies made by Teachers College, New York City. The results of Miss Allen's findings were published as Bulletin No. 25 of the Eugenics Record Office. The fathers of the children showed 12 times the average rate of graduation from college. The mean intelligence quotient of sibs was 127. All, except 1, of 21 tested cousins had IQ's of between 120 and 185; but one untested family had five subnormal cousins. The fecundity of the parents is low; 0.8 of a reproducing child to each parent. The life expectancy of the grandparents and the physical development of the children are exceptionally good.

**Heredity in Cacogenic Families**

The studies of Estabrook in the Southern Appalachians are giving general conclusions of importance. He reports as follows:

"These studies indicate that in isolated and unproductive regions of the Southern Appalachians there is a great tendency for the more energetic individuals to move on, leaving the less energetic and incapable in the more undesirable regions. Further research indicates that these energetic individuals who have started out for new homes keep on moving until they finally find an environment which is best suited to their inherent capacities. This leaves stranded in the less favored sections of the Southern Appalachians a group of people with little energy and low mental and physical capacity for action. Their mental level is below that of the population found in more favorable areas. The economic level of many of these people is retarded not only by the untoward conditions of the environment, but also by the fact that the individuals themselves are of mediocre intelligence and activity. The field work carried on in the Ozark Mountains in Arkansas and in the Pacific Northwest on migrant families from Eastern Kentucky and Tennessee tends to strengthen this conclusion.

"It has been noted in previous reports that Leslie County in Kentucky was settled in the year 1800 by about 50 families which came mainly from Virginia and North Carolina. The general history of these families shows that there has been a high birth-rate, that the family groups are large, and that much intermarriage took place between these groups and that there were but few matings from stocks outside the area. There has been much migration in some families and little in others.

"The people left in the isolated areas in the Southern Appalachians are not particularly energetic. The more active, few in number, produce only for their own needs and a little surplus for sale for profit. The greater majority produce little and live at a very low economic and sanitary level. The schooling in this whole area has been negligible and illiteracy is quite the rule in the older generations, and while the last two, in general, have been taught to read and write, actually little use is made of this training. Mental tests made in the schools in this area show none with an intelligence quotient above 100, the great majority have an I. Q. of about 75. A large
number of individuals are found who seem incapable of assimilating academic training beyond the fourth grade. A number of distinctly feeble-minded persons have been found.

The children of Leslie County who have attended one of the schools for mountain children number 142 during the past 30 years. One-half of these are now in the county, one-fourth in other mountain counties, a fourth have left the area. A study has been made also in Owsley County, Kentucky, which was settled by the same stocks as located at Leslie County and at about the same time. The terrain is less rough, the valleys are wider and hence the county is more adapted to agriculture and general development. Though this county has only half the population of Leslie County, it has at the same period sent 500 students to the mountain school just mentioned. In this county, just because it appeals to a higher class of persons, there remains a much larger number than in Leslie County of active, energetic men and women who have been held by good homes, productive farms, and fairly normal economic conditions. This continued residence of the best stock results in the greater success of the students at the mountain school; for 70 per cent of them subsequently do well, as compared with 25 per cent of the students from Leslie County.

The migrants from the South Appalachians have been traced at two points in the United States—the Ozark Mountains in northwestern Arkansas and the Pacific Northwest, especially the Willamette Valley in Oregon. The Ozark mountaineers settled in 1820 and later from the mountain people of Eastern Tennessee and Kentucky. They found in the Ozarks a region similar to that they left. A section of the more ambitious strains from the Alleghenies has resulted in a more intelligent, industrious and progressive stock. A later migration from eastern Kentucky to the Ozarks in the late eighties was of a less progressive stock. There remain on the ridges much the same poor economic and social level as there did in the Southern Appalachians.

GENETIC CONSTITUTION OF THE AMERICAN POPULATION

Economic Population Complex

Progress has been made, by Laughlin, on his tabulation of the data on area, population, literacy, wealth, births and deaths, and emigration and immigration of the principal emigrant exporting and immigrant receiving countries. It is expected that this tabulation will throw light upon the extent to which migrations are affected by economic and other conditions.

Deportation

The survey of deportable aliens in State and Federal custodial institutions begun last year by Laughlin now includes returns from 687 institutions, containing 482,535 inmates. Of these, 19 per cent were reported as foreign born and 3.28 per cent of them were reported as deportable. The non-deportable were mostly (31,584) resident in the United States for longer than 5 years, a smaller number (14,671) having been naturalized. 3,317 were inmates from causes arising since admission to the United States, and the remainder unclassified. Some data have been gathered concerning parenthood of inmates after discharge from institutions.
In connection with the topic of deportation of aliens to their home countries, statistics were gathered on the return of public charges by one State to the State of which they are citizens. These statistics indicate the development of a principle of considerable eugenical significance, namely, the tendency to require the nation, State or community that produces a socially inadequate individual to care for him.

**EUGENICAL STERILIZATION**

Inasmuch as the Eugenics Record Office has been looked to for information on eugenical sterilization, since the publication of Laughlin's book on the subject, we have continued to gather statistics on the topic. These statistics have been published during the year by the Eugenics Society of America.

A collection of about 700 initial-case histories of persons who have been sterilized has been made. The calls for these data have been considerable, and it is hoped, as soon as funds may become available, to follow up these histories for the purpose of determining the physiological and psychological effects of sterilization.

**ADMINISTRATIVE RECORD**

The archives of the Eugenics Record Office have been maintained and indexed. As of June 30, 1926, the books in the archives amounted to 1,858; field reports to 63,570; special traits file (A & S), 28,850; records of family traits 9,435; special inventories (during 1925-26), 2,309; index cards, 1,208,000. Some 27 schools and colleges cooperated by sending in family records.