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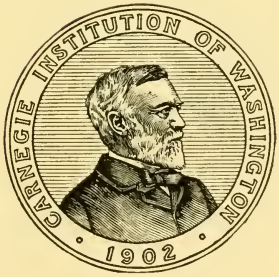

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DEPARTMENT OF EXPERIMENTAL EVOLUTION.*

C. B. Davenport, Director.

Among the principal advances of the year have been the demonstration of the fact that the sex-behavior of pigeons can be altered by injections of extracts of the germ glands; the first proof that an apparently pure race may really be "heterozygous" (*i. e.*, mixed) in one sex; and clear evidence that marked aberrations may be associated with a detectable chemical differentiation of the cell-sap, and that development of the egg-embryo is accompanied by important demonstrable changes in chemical constitution at different stages. The exact method of inheritance of depressions that lead to suicide, and the sex-limited nature of inheritance in certain types of nomadism and alcoholism in man have been worked out, a useful hypothesis of the origin of plural determiners secured, a first insight gained into the evolution of the chromosomal complex (continuing work started at Columbia University, under Dr. E. B. Wilson), and further experimental evidence obtained of the reality of the selective nature of elimination.

STAFF.

The Director continued his work on heredity in poultry, sheep, goats, and cats and brought the work on canaries to a close. His major work has been the study of data obtained by the aid of the Eugenics Record Office. From July 17 to October 20 he was absent on a journey to Australasia on the invitation of the Government of New Zealand (as one of an American party of about 12) and of the British Association for the Advancement of Science. He gave public lectures on the work of the Station and on heredity at Auckland, Wellington, and Christchurch, New Zealand, and examined some of the results of the sheep-breeding experiments at Canterbury, especially the so-called "half-breds" and "Corriedales." He also inspected one of the flocks of Leghorn fowls that has an average yield of over 200 eggs per hen. Conferences were held with sheep-breeders, biologists, and government officials on matters of genetics and an effort is to be made to establish a chair in genetics in the University of New Zealand. At the Sydney (Australia) meeting of the British Association he read a paper on "Heredity of Emotional Traits," and later he gave a public lecture at the rooms of the Royal Society on "Heredity and Eugenics." He also made some observations on the aboriginal Australian, both "full blood" and "half caste," at Brewarrina.

Dr. G. H. Shull has passed the entire year at Berlin in order to complete the Burbank manuscript. He carried on experimental work at the greenhouses of Prof. Dr. E. Baur of the Landwirthschaftliche

*Situated at Cold Spring Harbor, Long Island, New York. (For previous reports see Year Books Nos. 3–12.)

Hochschule. During the summer Mr. H. H. M. Bowman made detailed observations on Dr. Shull's cultures at Cold Spring Harbor. Dr. J. A. Harris spent two months with Mr. Lawrence, assistant, at the Desert Laboratory, Tucson, Arizona, applying the methods of determining osmotic pressure of vegetable saps from the depression of the freezing-point as developed by Dr. Gortner and himself.

Dr. R. A. Gortner cooperated with Dr. Harris and Dr. Banta and continued his exceedingly interesting work on the chemical changes that accompany individual development. Dr. Gortner received an excellent offer of an associate professorship at the University of Minnesota, and the Laboratory has sustained a severe loss in his departure. During the five years of his connection with this Station he issued 37 contributions from the laboratory of which he had charge and advanced greatly our knowledge of the chemistry of animal pigments, the processes of pigmentation, and individual development.

Dr. A. M. Banta continued his studies on cave organisms and explored, for material, certain caves of Indiana and, in early October 1914, the caves of the Schoharie and Cobleskill Valleys in Central New York, known as Howe's Cave, Ball's Cave, and Becker's Cave. Dr. G. C. Bassett, who was a guest of the Laboratory from July 1913 and later was temporarily appointed to continue his work on the effect of alcoholism in rats, has received a call to the University of Pittsburgh. His work will be continued by Dr. E. C. MacDowell.

In accordance with plans matured last year Dr. Oscar Riddle transferred the Whitman collection of pigeons and the new stock to this Station in November and he began work here December 1, and his assistant, Miss Spohn, on January 1. His work is to complete the editing of the Whitman manuscripts for publication. Incidentally he is continuing certain researches that are necessary for the full treatment of one of the subjects upon which the late Professor C. O. Whitman had begun work. Mr. Charles W. Metz has been appointed to act as cytologist and is making studies on the behavior of chromosomes (the germ-plasm of Weismann) in the vinegar flies, *Drosophila*—a genus which assumes particular importance because of its use for experimental breeding by Professor T. H. Morgan, of Columbia University, and his pupils.

REPORTS ON INVESTIGATIONS IN PROGRESS.

SEX.

Studies on sex still constitute an important part of the year's work, although Dr. Blakeslee and Dr. Goodale are no longer with us and Dr. Shull's work has, during his absence in Germany, been directed into other lines. The chief work on this subject is that of Dr. Riddle.

Sexual Differentiation of Pigeon's Eggs, Oscar Riddle.

Over a year ago Dr. Riddle showed that, in pigeons, which usually lay two eggs at a time, commonly one male and one female, eggs destined

to produce males are smaller, and have higher water-content and smaller energy-content, than those that produce females. This conclusion he has repeatedly confirmed at this Station. Especially has he been able, by the use of the bomb calorimeter, to demonstrate that eggs destined to become males contain less stored energy than eggs destined to develop into females. Whether the difference in energy-content (however it may have arisen) is the cause of the difference in the eventual sex or whether it is induced by a certain difference in the unfertilized egg which determines the difference in storage metabolism is uncertain. There is reason for thinking that the ova of birds are of two kinds, those destined to produce males and those destined to produce females, and there is also evidence that the former contain a sex chromosome which the latter lacks. This difference in the chromosomal content of the eggs destined to be males and females, respectively, may therefore be the cause of the difference of energy-content of the two kinds of eggs. This is a matter for further study.

With the aim of determining whether a modification of the amount of yolk stored in the egg can control the sex of the resultant chick, Dr. Riddle has spent some time (partly in collaboration with Dr. Bassett) in trying to induce such a modification. One result secured is that when the female pigeon is subjected to alcohol vapor it lays smaller eggs than normal. Other substances used (phloridzin and urotropin) have caused a reduction in the fertility of the egg, but have not markedly altered its size.

The foregoing studies are of interest because of their relation to a normal determination of sex in the egg-laying of pigeons. If, as Whitman first pointed out, certain somewhat distantly related species of pigeons be crossed and if the eggs be taken away as fast as laid, so as to induce the pair to continue to lay fertile eggs, then in the beginning of the season (*i. e.*, in the spring) both eggs of a clutch will produce nearly or quite exclusively males; the last eggs laid in the autumn will be nearly or quite exclusively females; while in the transition period the first egg of the clutch usually produces a male and the second a female. Of course, one can not say that the experiment has induced any change in the sex-fate of the eggs; it may possibly be that the distribution of the male and female eggs in the ovary is such that this result necessarily follows from the forced heavy reproduction of the mother. Dr. Riddle holds an alternative hypothesis, and an attempt will be made to decide between them.

Modification of Sex Behavior in Pigeons, Oscar Riddle.

A very remarkable fact, in addition to those stated in the preceding paragraph, is that when two full sisters from such series are hatched from the two eggs of a single clutch the first hatched behaves in copulation as though it were a male. Also females hatched early in the season (the period when most males are produced) are more masculine

in behavior than are their own sisters hatched late in the season. Dr. Riddle has succeeded in some cases in reversing the sex-behavior. Thus, if extracts from the ovary of a pigeon be injected into those females that are behaving like males they come to behave like females. Contrariwise, if testicular extract be injected into those females that are acting like females they come to act like males. The full significance of this result is still obscure. The sex-behavior of a bird is probably determined by internal secretions from its sex-glands carried to its central nervous system. On this hypothesis the quality of the internal secretions of the ovaries of birds that act like males must be different from those of birds that act like females. The effect of the injected extract may perhaps be regarded as superior to that induced by the natural secretion of the ovaries.

Sex-linked Inheritance in Lychnis, G. H. Shull.

The series of studies on *Lychnis*, which exhibits certain characteristics that render it critical for the study, has been continued by the use of a narrow-leafed mutant that depends upon a sex-limited defect. The original narrow-leafed plant was a male which when crossed with broad-leafed females produced broad-leafed males and broad-leafed females; but when these were bred together they produced (in F_2) broad-leafed and narrow-leafed progeny. The narrow-leafed progeny were all males, but the broad-leafed progeny were partly males, partly females. Thus the narrow-leafed condition shows itself in F_2 only in males, though half of the females carry the determiner of narrowness in half of their eggs, as experiment proved. All of these broad-leafed F_2 females were crossed with the narrow-leafed males, and it was expected that in F_3 many narrow-leafed females would appear from the union of sperms carrying both the female character and the determiner for narrowness with eggs of the same constitution. It was an unexpected and baffling result that practically no narrow-leafed females occurred. This unexpected failure to produce narrow-leafed females in the F_3 was experimentally shown to be due to the absence or inefficiency in the narrow-leafed males of sperms carrying the determiner for femaleness, for crosses between these same narrow-leafed males and homozygous broad-leafed females resulted likewise in only a rare production of females. There is a theoretical reason for believing that the mutation first occurred in a male-bearing sperm and that a large section of the species (if not all of it) is characterized by sperms defective in regard to the broad-leaf determiner. Such defect could appear *somatically* only after an *egg* had also lost its determiner for broad-leaf, as the narrow-leaf is a recessive character. In support of this conclusion, a broad-leafed male and a broad-leafed hermaphrodite, both from points in the United States far from the home of the original mutant, were tested and were found to be heterozygous for the defect; that is, they

carried the defect in their germ-cells, but had never been able to reveal it up to that time in their progeny because all of the female germ-cells previously fertilized by their pollen had carried the determiner for broad-leaf. The fact that an hermaphrodite crossed with a heterozygous female exhibited this defect in its offspring completely confirms Dr. Shull's conclusion that his hermaphrodite mutants in this species were originated through a mutational change in the *males*. This important experiment supports the view, suggested long ago by de Vries, that many heterozygous individuals may carry a defect in their germplasm, even as a racial character, and this character may never express itself in the progeny because it has never got into the germ-cells of the opposite sex. In this paper a much-needed revision of sex-formulæ is undertaken which, it is hoped, may simplify and standardize current usage.

VARIATION.

The problem of variation of organisms still remains unanalyzed and little progress had been made in its treatment. At this Station this summer (1914) we have made a systematic search for striking variations in the field, we have studied the relation of variations in a plant to their position on the plant, and we have compared the chemical composition of varying organs or plants to learn how far the chemical differences that accompany morphological variations can be detected. Finally, we have made a beginning on the task of inducing hereditary variations at will—that is, altering the germ-plasm.

Mutations in Nature, H. H. M. Bowman.

During July and August 1914, Mr. Howard H. M. Bowman was assigned to the work of looking for striking and probably inheritable variations in plants near the Laboratory, with the aim of locating material that might be used for future studies in variation. In this search he was successful, since he recorded such variations, mutations, and aberrations in 66 species. He also recorded the condition of each leaflet for 393 seedling *Fraxinus* (ash) of known pedigree from ascidiate (pitcher-leafed) and non-ascidiate ancestry. The results will be used in Dr. Shull's study of this remarkable mutation.

Periodicity in Abnormality in the Passion Flower, J. A. Harris.

In *Passiflora* (the passion flower) the fruit shows a great number of abnormalities, mostly proliferation and allied phenomena. A comparison of the number of abnormalities in plants grown in normal soil and in soil to which a considerable proportion of bone-meal had been added showed no difference in the proportion of abnormal fruits, but established the fact that the proportion of abnormalities in the fruits

of any plant decreases as the plant becomes older. A similar periodicity has been described in other species, but usually in such cases the proportion of abnormal fruits *increases* with the age of the plant. The interpretation of the result is still uncertain.

Chemical and Morphological Differences, J. A. Harris and R. A. Gortner.

Dr. Harris and Dr. Gortner have undertaken studies on chemical differences associated with those of a morphological character. It appears that in a species (*Lagerstræmia indica*) with dimorphic anthers, the larger red anthers lose water more rapidly upon evaporation than the slightly smaller yellow ones, a correlation that has a certain ecological bearing. Attempts were made to detect a chemical difference in the juices of apples and pears of varying size and fertility; the conclusion reached is:

"We have, however, been unable to demonstrate any sensible differences in the osmotic pressure, mean molecular weight, or electric conductance of the saps of nearly ripe fruits of different sizes or producing different numbers of seeds. However, between the tissues of the normal capillary whorl constituting the wall of the fruit of *Passiflora gracilis* and those of the *tetramerous, abnormal whorl* forming the teratological mass, *i. e.*, the secondary fruit sometimes found within the otherwise normal fruit, there is unquestionably a *differentiation in physico-chemical properties of the expressed juices*, as follows: The specific gravity, specific electrical conductivity, osmotic pressure, and ratio of the electrical conductivity to the depression of the freezing-point are distinctly *higher* in the saps extracted from the tissues of the wall than in that expressed from the abnormal mass. Thus the *electrolytes form a relatively smaller and the non-electrolytes a relatively larger proportion of the solutes in the sap of the teratological tissue.* Apparently the mean molecular weight of the solutes of the sap of the included mass is higher than that of those extracted from the wall."

These matters are discussed in detail in a paper now ready for the press. To facilitate the calculation of molecular weights and osmotic pressure in saps from observed depression of the freezing-point, Doctors Harris and Gortner prepared for publication two extensive tables.

Modification of the Germ-plasm by Alcohol, G. C. Bassett.

The problem of inducing changes in the germ-plasm has been attacked by subjecting organisms to the action of alcohol vapor. This is a method which Stockard has already employed with success in demonstrating that after having been subjected to the vapor of alcohol the capacity of germ-cells for producing viable offspring diminished. Dr. Bassett has sought to find if any inheritable effect of such alcoholization of a parent upon intelligence of its offspring might be detected. Unfortunately, after having elaborated the method with great care, he was obliged to abandon the experiment. Its continuation is now in the hands of Dr. MacDowell.

Abnormalities in Development Resulting from Centrifuging Eggs, A. M. Banta and R. A. Gortner.

As a by-product of some chemical studies, interesting abnormalities in developing embryos of frogs were induced which are worth recording, though they have no obvious significance for heredity. Dr. Banta and Dr. Gortner "centrifuged" some embryos of *Rana sylvatica* at the blastopore stage, subjecting them to 1,350 times the pressure of gravity for 2 minutes, and an accessory tail-like appendage developed in all of the survivors—usually one accessory tail, but occasionally two to four. The accessory tails were scattered along the mid-ventral region and had a typical tail-like structure. In some "centrifuged eggs" of the salamander, *Ambystoma*, the front end of the head, sometimes back as far as the gills, failed to develop. The interest of this observation lies in the demonstration that the hereditary determiners for development work out their destined end only when maintained in certain proper spatial relations. When displaced by the centrifugal machine they influence the production of their appropriate organs in abnormal positions. By reducing the abnormal pressure a point is reached where the determiners are not displaced and, hence, no abnormal development occurs. The limit serves, in a way, to measure the relative strength of hereditary and environmental forces in the given case of development.

BIOCHEMICAL PROCESSES IN HEREDITY.

Chemistry of Ontogeny, R. A. Gortner.

Development is a series of chemical processes which is directed by the presence of certain determiners that afford the hereditary control. A beginning has hardly been made upon the study of the chemical changes that accompany the morphological changes of ontogeny, yet this problem is of the greatest importance for evolution. For, just as the changes in form exhibited by an organism during ontogeny give some idea of the successive forms of the ancestors of the individual from the earliest to more recent times—and thus epitomizes the course of evolution of the species—so the chemical changes during ontogeny may well be considered to epitomize the evolution of the chemical characteristics of the species. And as there is much reason for thinking that the morphological changes have depended upon the chemical, it is obvious that the proposed study is of the greatest importance for evolution. The earlier experiments of Dr. Gortner on this subject were described in last year's report. Dr. Gortner continued this work by comparative analyses of the eggs and the newly hatched larvæ of the giant salamander, *Cryptobranchus alleganiensis*. The total dry weight diminishes by 1.6 per cent, due to loss of carbon dioxide and water, for the total nitrogen does not change. There is a gain of fats to the extent of 14

per cent over that in the egg. The greatest loss is from the protein fraction, some of which has gone into the fat. Dr. Gortner concludes:

"There is considerable evidence that the nitrogen ratios in the protein fraction are not fixed quantities, but that some amino acids are more necessary for the development of the embryo than are others, and as a result there is a continuous breaking down and recombining of the resulting radicals into new compounds. For example, the gain observed for arginine B, although small, is probably significant. It seems probable that there is, in the eggs of *Cryptobranchus*, a carbohydrate nucleus, either free (glycogen) or combined in the form of a glycoprotein, and that during the process of embryonic growth this carbohydrate is broken down to carbon dioxide and water, with a consequent liberation of energy for the 'Entwicklungsarbeit;' but the breaking down of the carbohydrate proceeds more rapidly than the needs of growth demand, with the result that the surplus energy is stored as fat."

Inhibition of Pigmentation, A. M. Banta.

In the last two reports attention has been called to our work in preventing the formation of black pigment in the little salamander, *Spelerpes*, by phenols. This year Dr. Banta used the same method with young larvæ of the giant salamander, *Cryptobranchus*, and got practically the same results. When small amounts of these inhibitors to the oxidation of tyrosin (a process which forms black pigment) are put into the tissues of the developing larvæ before pigmentation begins, the onset of pigmentation is markedly postponed and the pigment produced is much reduced in amount. Because of the toxicity of the inhibitors it is impossible to state how long these modifications would persist, for the larvæ, even though kept in the solutions for only 8 to 15 days, do not develop beyond the stage when the stored food in the egg is all utilized.

A Toxin of Bread Molds, R. A. Gortner and A. F. Blakeslee.

In last year's report the discovery (made in the course of studies on sex of molds) of a powerful toxic agent in the bread mold, *Rhizopus nigricans*, was alluded to. The full paper has now been published. The toxin has no effect when taken into the alimentary tract by a rabbit, whereas it is fatal to rabbits when injected intravenously in even so small an amount as 1 to 275,000 parts of body-weight, being one of the most poisonous organic substances known.

Modifying Effects of Cave Conditions, A. M. Banta.

The material in the cave and vivarium has been brought through with greater success than in any previous year. To the species previously maintained here have been added the blind cave-fish, *Amblyopsis spelæus*, and an additional species of salamander, *Ambystoma opacum*. During the present season large series of wood-frog tadpoles

were reared in the light and in the dark. Those developing in the vivarium were fairly black, as tadpoles of this species normally are, while those reared in the cave had very little pigment except in the eyes, and were so transparent that the heart and larger blood-vessels in the head and tail regions were visible externally. These larvæ and larvæ of the common spotted salamander, *Ambystoma punctatum*, when reared in the dark, have so little pigment that they resemble the cave-fish in the soft pinkish-white general body-color and in the reddish appearance of the heart region due to the large amount of blood showing through the transparent tissues. Again, this season many *Ambystoma punctatum* have been reared in the cave. One is struck by the relative lack of pigment in most individuals of this species developing in darkness. It requires close scrutiny to detect any pigment whatever, except in the eye. In every case, however, as the period of transformation approaches, the light individuals begin to develop pigment and by the time transformation is completed even the lightest individuals, though kept in the dark all the time, have developed a normal pigment complement. The *Ambystoma opacum* larvæ reared in darkness developed a reduced amount of pigment as compared with those reared in daylight, but the reduction is not nearly so large as with *A. punctatum*. *Spelerpes bilineatus* larvæ reared in darkness show only a comparatively slight reduction in pigment development. Species and, to some extent, individuals, show a marked difference in the amount of pigment reduction produced by developing in darkness. *Ambystoma punctatum* is very susceptible to the effect of darkness and develops very little pigment. *Ambystoma opacum* is much less influenced by the lack of light, and *Spelerpes bilineatus* is only slightly influenced.

Considerable numbers, both of the cave form and of the outside form, of the amphipod *Eucrangonyx gracilis* have been kept in the cave and in the vivarium. The cave form has no pigment except in the eyes, while the outside form has the normal amount of pigment for a crustacean. Young of the outside form, made to develop in the cave and consequently never exposed to daylight, have nevertheless formed body pigment in some cases and in others have no pigment except in the eyes. The young are only two-fifths grown and all may yet develop pigment. None of the series kept in the cave and derived from ancestors living outside caves has developed even approximately as much pigment as individuals of like size kept in daylight.

The work upon a comparison of the light and tactile reactions of the cave form and the above-ground form of this amphipod was completed while in Indiana in February. The results show conclusively that the cave form is considerably more reactive to tactile stimulation than the outside form. A definite measure for this difference in reactiveness was used and the results were obtained in precise terms. On the other hand, the cave form is somewhat less reactive to photic stimulation

than the form not living in caves. This difference is small but fairly constant. In general, so far as the evidence has been obtained, cave animals are *less* reactive to photic stimulation and *more* reactive to tactile stimulation than their near relatives living in other situations. This was notably true of the common *Asellus* and its eyeless and pigmentless cave relative, *Cœcidotea*, with which Dr. Banta experimented several years ago. The slightly modified cave form and the outside form of *Eucrangonyx gracilis* showed the same differences, but in a much smaller degree.

As a by-product of these studies a paper has been prepared by Dr. Banta and Dr. Gortner on an albino *Spelerpes* which was found while collecting and saved for purposes of breeding, but which died before reaching sexual maturity. It was an orange-yellow colored individual possessing the normal amount of yellow pigment, but without any black pigment in skin, eyes, or connective tissue. Aside from the albinic axolotl, it is believed to be the only recorded case of an albino urolele living in the open. Numerous albinic subterranean uroleles are, however, known.

HEREDITY.

Heredity of Some Emotional Traits, C. B. Davenport.

A large amount of time during the past two years has been spent in an analysis of family histories obtained by trained investigators. These histories comprised families with some greater or less criminalistic tendencies. As stated in my last report, the traits of more or less periodic outbursts of hysterical temper and uncontrollable eroticism are inherited as positive or dominant traits. Also, it now appears that a family tendency to periodic depression accompanied by a suicidal tendency is inherited as a negative or recessive character. Especially striking has been the result of study of cases of dipsomania and allied forms of alcoholism on the one hand and of nomadism or wanderlust on the other, which quite certainly prove an hereditary factor which is inherited as a sex-linked one. Data are also presented demonstrating the inheritable basis of inhibition or "moral control." The whole work, which is now ready for the press, is entitled "The Feebly Inhibited," and gives a first clear insight into the hereditary basis of conduct.

Heredity of Certain Mutations, C. B. Davenport.

Further study of the "bare-neck" poultry supports the view, expressed in my last report, of the dominant nature of the factor that prevents feathers from growing on the neck of these fowl. A brief note on this subject, with photograph, appeared in the Journal of Heredity for August. The case is important, since it is another clear example of a morphological defect that is inherited as a dominant.

Duplicate and Plural Determiners, G. H. Shull.

Dr. Shull's discovery of a clear case of duplicate determiners in the triangular capsules of *Bursa* has led him to consider generally the whole matter of aberrant heredity of this type. He distinguishes as "duplicate" determiners those which, when separated from each other, produce characters so like that they can not be distinguished from one another, while the term "plural" determiners (the more inclusive term) comprises two or more genes which independently produce a character or modify it in any way whatever which does not destroy its identity. A useful attempt at an explanation of the origin of duplicate determiners is then offered, according to which one of a homologous pair of chromosomes containing a determiner (D) becomes displaced in its synapsis, uniting with a chromosome that lacks D. Thus *two* synaptic pairs come to possess the determiner D, though in a simplex condition; and consequently the determiner, henceforth, behaves as duplicate. A similar result would follow if a determiner alone crossed from one synaptic pair to another. The consequences of the hypothesis are followed out in an important paper.

Cytological Studies on Heredity, C. W. Metz.

At this Station, from its inception, we have appreciated the importance of the study of chromosomes as "bearers" of heredity, and we originally had a laboratory of cytology. A vacancy having arisen (through the resignation of Dr. Gortner) we have secured the assistance of Mr. Charles W. Metz, who began work in June and who reports as follows:

"Prior to coming here in June I was engaged in a comparative study of the chromosomes in the Diptera, with especial emphasis on the genus *Drosophila*. This study brought to light a remarkable series of chromosome groups in the Drosophilas, which series was not only very interesting in itself, but showed that the material was exceptionally favorable for study through hybridizing, and through genetic work on individual species. For the latter reason, several species were bred extensively and attempts were made at crossing. The cytological results of these studies were published as 'Chromosome Studies in the Diptera: I. A preliminary survey of five different types of chromosome groups in the genus *Drosophila*' (Journal of Experimental Zoology, July 1914). Further breeding work was carried on with *Drosophila ampelophila*, in studying the inheritance of the 'apterous character.' The results of this study are in press in the American Naturalist.

"Since coming here in June I have been carrying on the cytological and genetic work which I already had under way, but on a much larger scale, and in addition I have been breeding the beetle *Bruchus quadrimaculatus* extensively. Of course much of my time has been occupied with securing equipment, getting the laboratory into good working condition, and organizing the investigations. No attempt has been made to complete any investigations, owing to the shortness of the time and to the fact that a good deal of the equipment has only recently arrived. The organization of the Laboratory is now almost complete and several lines of study have been considerably advanced, some of which are

nearing completion. Much time has been devoted to securing and preparing material for study during the winter. This has involved the dissection and cytological preparation of hundreds of specimens. Many preparations have been completed and studied, with numerous interesting results. In addition many thousands of flies have been bred and studied for genetic purposes. A more detailed account of these studies follows.

"Most of the cytological as well as the breeding work has centered in the genus *Drosophila*, because it offers an unusual combination of favorable characteristics, most of the species being comparatively easy to breed and exhibiting striking specific differences in their chromosomes. In addition to the 12 species reported in the above-mentioned paper, several others have recently been studied. All but one of these fall into the general scheme proposed for the others. One species, however, is remarkably unlike the rest cytologically, and is of exceptional interest because it is favorable for a study of the maturation and prematuration stages in the *male*, a condition greatly desired because of its bearing on previous breeding experiments in *Drosophila*.

"The cytological work on *Drosophila* falls into three divisions: One is concerned chiefly with the relation between the chromosome groups of different species. Thus far about 18 species have been studied with the following results: Each species has been found to possess a characteristic group of chromosomes. These chromosomes are arranged in pairs, which differ from one another in size, form, and behavior in such a way that they may be readily distinguished. Thus the individual chromosome pairs in any species may be separately identified and followed. This fact has made it possible to compare the different specific chromosome groups with one another, chromosome by chromosome, with the result that individual chromosome pairs have been homologized throughout the series, and that the different groups have been found to make up what appears to be a definite evolutionary series, in which the various steps can be clearly followed. The results demonstrate beyond any doubt the real existence of the phenomenon of chromosome pairing, an association of homologous maternal and paternal chromosomes; and they add very substantially to the accumulating evidence of the individuality and continuity of the chromosomes—all of which facts have a very direct bearing on the relation between chromosomes and heredity.

"The second phase of the cytological work depends entirely on the breeding results—*i. e.*, whether or not species-hybrids are secured. Since the crosses have not yet been obtained, no advance has been made here. This is the most important aim of my *Drosophila* work, and although only negative results have been given thus far, I am very hopeful of ultimate success, even though considerable time and effort may be required. The result depends largely upon how many species can be secured, especially species from distant localities. The opportunities are unique, without a parallel in plants or animals, and every effort will be made to secure the results.

"A third line of cytological work on *Drosophila* centers around a study of the maturation processes, especially in the males. Breeding experiments by Morgan, *et al.*, have indicated that (in one species at least) the relation of the chromosomes during synapsis is different in the two sexes—*i. e.*, homologous chromosomes have no effect on one another in the male, while in the female they have an effect, as shown by the phenomena of "crossing over," etc. I propose to determine, if possible, whether this is attributable to an evident difference in the maturation processes of the two sexes. The work has progressed far enough to show that there are most decided cytological differences, but not far enough to single out a particular one as responsible for the genetic differences.

"In addition to cytological work on the genus *Drosophila*, the chromosomes of about 20 species, representing various families of the Diptera, have been studied, with a view to learning more of the characteristics of the order as a whole. When the preparations made during the summer are studied, many more species will be added to the above and extensive material will be available for a comparative study of several families. Some features already appear to be clear. First, the paired association of chromosomes is characteristic of the Diptera as a whole. If any species lack it they are the exceptions. None such has yet been found. Second, several families of flies (Muscidæ, Sarcophagidæ, Syrphidæ, Anthomyidæ, Scatophagidæ, etc.) all appear to have the same number of chromosomes (12) and appear to be fairly uniform in their maturation phenomena. Perhaps it may be said that they have reached a state of equilibrium in these regards. The Drosophilas and their close relatives, on the other hand, exhibit great specific differences, both in chromosome numbers and in maturation processes. As a group they do not seem to have become stable.

"Since the phenomenon of chromosome pairing is so characteristic of the flies, and found nowhere else in anything like such a definite form, I have made a detailed study of it. This study is nearly completed and will appear as No. II in my 'Chromosome Studies in the Diptera.' In this investigation I have studied various species from a number of families, and have found the behavior of the chromosomes, as regards pairing, to be essentially the same in all. I have shown that pairing exists throughout the whole life of the insect, from the embryo to the adult, and in the germ-cells previous to the maturation stages. During each cell generation, somatic or germinal, the two chromosomes constituting a pair become closely associated, in fact almost fused, soon after cell division; then later they separate somewhat and lie side by side until the next cell division. In other words, the maternal and paternal chromosomes of a pair are associated with one another throughout the entire life of the animal, and once during each cell generation they become very closely united. These facts, of course, strongly suggest that the two members of a pair are qualitatively alike and that the members of different pairs are qualitatively unlike.

"The breeding work in which I have been engaged is of several different sorts. Primarily it has centered around the endeavor to cross different species of *Drosophila*, which I have demonstrated to possess different chromosome groups. In preparation for this work it has been necessary, first of all, to perfect methods for rearing the various species, which in itself has taken much time, because the food habits of some are very different from those of others. Nevertheless over 15 species have been bred successfully, and methods have been secured which will probably suffice for almost any species subsequently obtained. With cultural methods perfected another attempt is now being made to secure species hybrids.

"In addition to keeping up stock for hybridization work, four species are being extensively bred for genetic work purely within species. Four species have been selected, each representing a different type of chromosome group, and it is hoped that mutants will be secured, making it possible to test the chromosome hypothesis by breeding from them. If good series of mutations are secured in these 4 species, or in 2 or 3 of them, I will have a crucial test of the chromosome theory from the genetic side, for each species should give a definite result, characteristically different from the others. The work on *D. ampelophila* has shown the presence in that species of 4 groups of linked characters, corresponding to the 4 pairs of chromosomes. I have selected one species having this same group of chromosomes. From it I should get results like

those given by *D. ampelophila*. A second species being bred has four pairs of chromosomes also, but of a different sort (No. 2). In this the minute pair is lacking, and there are two small pairs in place of one large pair of the previous group. The linkage phenomena should be quite different here. A third species resembles the last, but has the minute pair present (No. 3). This is the species which is especially favorable for cytological study in the male, and I am laying particular emphasis on it. Already one character has appeared which seems to be a mutation, although further breeding is necessary to make it certain. The fourth species has 6 pairs of chromosomes (No. 4), all of which are relatively short. This species should give six groups of linked characters as contrasted with 4 or 5 in the others, and the linkage should be very 'close,' since the chromosomes are short. In this species a definite mutation has just arisen, out of many thousand flies examined. Only the F_1 has been secured, but the character appears in this, leaving no doubt about the reality of the 'mutation.' The 4 chromosome groups are shown diagrammatically in figure 6.

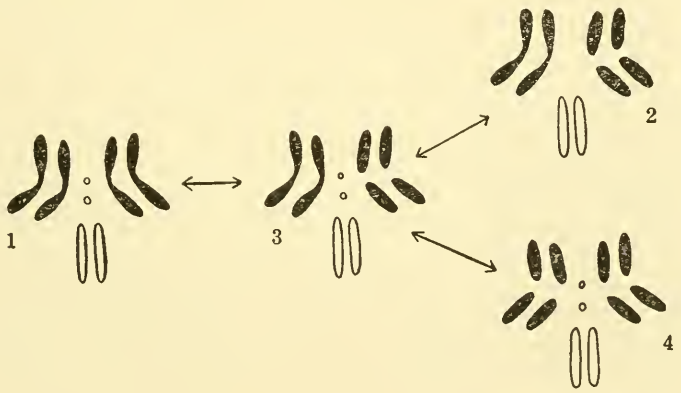

Fig. 6.

"If mutations of similar sorts appear in the different species, as I am confident will be the case, a further and much more detailed analysis can be made, and the relation between homologous chromosomes in different species can be shown.

"While engaged in working out methods for handling Drosophilas I have also experimented with methods for breeding larger flies of various species. This work has resulted in satisfactory methods for rearing 6 or 8 species of the so-called 'higher flies,' and has furnished large amounts of cytological material. It has not seemed advisable to carry these cultures further this year, except for the provision of cytological material.

"As an auxiliary investigation, quite aside from the Diptera work, I am breeding beetles of the genus *Bruchus* (*B. quadrimaculatus*, the cow-pea beetle). The material shows a great range of color patterns and offers excellent opportunity for some phases of breeding. Two generations have been secured thus far (3 months) from an originally mixed stock, and different lines are becoming purified. When this process of selection is completed, the inheritance of the characters will be tested by crossing. Nothing very definite can be said about the results as yet, except that either a large number of factors is involved, or else some very changeable factors are operating. Cytologically the species is good for study, but the number of chromosomes is far too great to allow of such work as is being done with the Drosophilas."

SELECTION AND PURE-LINE WORK.

This field of study deals with problems of the greatest present-day interest. Doctors Harris, Banta, and MacDowell are carrying on this work.

Studies on Selective Mortality, J. A. Harris.

For several years the problem has been investigated whether in a lot of planted seeds of one species there is a selective elimination of any type or whether each occurs strictly at haphazard. Recently Dr. Harris has planted about 46,000 individually weighed seeds of the bean (*Phaseolus vulgaris*), treated them alike, and classified their subsequent history into three groups: (1) seeds that germinated normally; (2) seeds that germinated by producing more or less abnormal seedlings; (3) seeds that failed to germinate. Comparing the weights of the planted beans that had respectively these three fates, it is found that the average weight of all the varieties of beans that germinated normally and of those that failed to germinate was nearly the same, although in two varieties of bean there is a distinct superiority in the mean weight of the survivors, while in one other variety there is a pronounced inferiority in the mean weight of the survivors as compared with those that failed. But, on the other hand, when absolute variabilities of the three sets of progeny are compared, it appears at once that *seeds that germinate vary less around the mean than those that fail to germinate.* When variability is expressed in units of the mean weight it appears still more clearly that the seeds that germinate are a selected lot—selected for their closeness to the mean weight of all the bean seeds of their variety; the seeds of aberrant weight are less apt to germinate. In so far as the weight-aberrancy is an inheritable trait, it is easy to see that the greater mortality among the aberrant seeds will tend to hold the race to the mean or "typical" seed weight. In general, selective mortality operates conservatively, tending to preserve pure the specific characters. These studies have been extended to peas, and in these, also, the seeds that germinate are on the whole less variable than those that fail to germinate. In comparing the weight of the seeds that germinated promptly with those that developed slowly, it became necessary to get the exact time of germination of these 46,000 seeds; and that involved observing at night as well as in the day. As a by-product, the law was established that, in beans, the heavier the seed the more slowly it germinates.

Relationship between the Weight of the Seed Planted and the Characteristics of the Plant Produced, J. A. Harris.

The fact that a certain quality (such as aberrancy of seed weight) is associated with exceptionally great mortality is no evidence that the first quality is the cause of the second. It may be that the first cause

induces a third or a chain of events which are the true causes of the high mortality. Consequently it becomes of importance to know what other characters are correlated with weight of the seed that has been planted. Dr. Harris has shown that in beans there is a sensible relationship between the weight of seed planted and (1) the number of pods on the plant that develops out of that seed; also (2) the number of ovules and the number of seeds in the pod produced by the plant developing from it.

Factors Influencing the Weight of Seeds and their Number in a Pod, J. A. Harris.

In beans, the weight of seeds decreases as the number of seeds per pod increases; also, the seeds are the heavier the farther they are from the attached end of the pod. In fact, the free end of the pod seems more favorable for the fertilization and development of the ovules in the pod. But, remarkably enough, the number of ovules per pod seems not to influence the weight of the seeds eventually developing in the pod in beans. In another legume, *Cercis canadensis*, there is a marked positive correlation between the number of ovules and of ripe seeds in a pod. As a corollary about the same proportion of the ovules are fertilized and develop, whether the number of ovules be small or great; if anything, the pods with the larger number of ovules produce relatively fewer seeds. Dr. Harris has summed up results of his recent work on selection in a paper, "Current Progress in the Study of Natural Selection," published in the Popular Science Monthly.

Selection of Strains of Daphnia with reference to Reaction to Light, A. M. Banta.

The selection in a parthenogenetic species for greatest and least sensitiveness to light has been continued now for 110 generations in some cases and the number of individuals measured approaches 20,000. The results continue to show an effect of selection in some lines, but not in all, and the differences are in most cases statistically significant. The differences produced by selection have become largest in lines of the species (*Simocephalus*) which for a long time seemed the least responsive to selection.

Incidentally to the foregoing investigation, the result has been gained that 100 generations of *Daphnia pulex* have been reared parthenogenetically without sexual forms appearing at any time. There is no evidence of decreased vigor or loss of vitality in the lines. Hence, it appears that there is not a necessary sexual cycle in the reproduction of this daphnid. These observations lend additional evidence to the conclusion that the sexual cycle in *Daphnia* is not an inherent, necessary thing, but that it is determined by external conditions.

Selection of Unstable Determiners vs. Plural Determiners, E. C. MacDowell.

Dr. MacDowell is studying the question of the stability of Mendelian genes or determiners which is a central topic for many investigations, chiefly because of the extensive work of Dr. W. E. Castle. He reports as follows:

"If genes are stable and are passed from generation to generation unmodified by their associations with other genes, the work of selection consists merely of sorting out certain combinations of homozygous factors. After this is done, selection can produce no further changes. If genes are modified by the other genes in contact with which they come, new genes as well as new somatic appearances can be produced by selection. The work of Professor W. E. Castle and Dr. J. C. Phillips on modifying the color patterns of rats by selection, reported in the Year Book for 1913, has been interpreted by these investigators as showing that selection is effective in modifying Mendelian genes and so in producing new kinds of genes. Their interpretation is not the only one applicable. It is possible to suppose that the apparent success of selection was due to the sorting out of multiple genes, which have been assumed by the authors to explain certain phenomena of crossing. Work bearing closely on this subject has been undertaken on the banana fly (*Drosophila ampelophila*). A race of flies has been produced lacking a restrictive gene that limits the number of bristles on the back of the thorax in the normal flies to four. In the absence of this gene the number of bristles is variable, but greater than four. By the closest inbreeding and selection the number of extra bristles was steadily increased for six generations; after this no further increase has been detected. At present the race is in the twenty-first generation. This result, supported by certain other very definite phenomena, has led to the tentative adoption of the hypothesis that there are accessory genes which, in the absence of the main restricting gene, hold down the numbers of extra bristles, and that the success of selection at first is to be accounted for by the dropping out of these accessory genes by using parents with high bristle numbers, which in successive generations lacked more and more of these accessory genes. After the sixth generation a state of equilibrium was produced in which these genes either were all removed or homozygous. This interpretation, involving more than one determiner for a single somatic character, is much like that reported by Shull in the Year Book for 1913, for his work on shepherd's purse. The attempt is being made to test this hypothesis by isolating lines of extra-bristled flies that show constant differences in bristle number, and by crosses between these lines to determine whether or not the differences between the lines are due to accessory restrictors. Before this can be satisfactorily attempted, special studies on the causes of the fluctuations in the bristle-numbers must be undertaken in order to reduce these non-genetic variations. It has already been found that the size of the fly, which varies with the *amount* of food eaten in the larval state, influences strongly the number of extra bristles, as a small fly is apt to have very few extra bristles (1 or 2) and a large fly many (5 to 8). This is a good example of the influence of environment on the development of a Mendelian character, and emphasizes the necessity of careful investigation of the role of environment in all genetic work.

"Besides the plan outlined above, future work will include (1) further selection for increase in the bristle numbers, so that the failure of selection can be absolutely unquestioned, and (2) return selections, *i. e.*, starting with the inbred and selected race, low-grade parents will be selected instead of high-grade. If factors or genes may be modified, a complete return selection should be possible. If the first success of selection was due to the dropping out of ac-

1. Front of New Animal House.

2. Buildings at Station for Experimental Evolution: from left to right, Animal House, Pigeon Houses, Greenhouses and Laboratory in the background. View looking southeast.