SCIENCE

A WEEKLY JOURNAL DEVOTED TO THE ADVANCEMENT OF SCIENCE, PUBLISHING THE OFFICIAL NOTICES AND PROCEEDINGS OF THE AMERICAN ASSOCIATION FOR THE ADVANCEMENT OF SCIENCE

FRIDAY, NOVEMBER 15, 1907

CONTENTS

MSS. intended for publication and books, etc., intended for review should be sent to the Editor of SCIENCE, Garrison-on-Hudson, N. Y.

FACTS LIMITING THE THEORY OF HEREDITY[1]

MY first duty is to acknowledge the honor done me by the suggestion that I should deliver the address in this section. I need not say that I very highly appreciate the distinction thus conferred.

The fact that a heredity section has been constituted is surely a matter for congratulation. It is a sign that the study of zoology is passing into a maturer stage. For the past half century zoologists have been chiefly occupied with the accumulation of morphological facts of structure and development. The perfection of microscopical methods had revealed regions in which knowledge could be readily advanced by simple means. We became, therefore, students of Cœlenterata, insects, Vertebrata, or whatever it might be, according as fancy or opportunity had specially attracted us to one or other of these groups.

Such work was interim work. It was making up arrears. This task is now practically accomplished. Almost all that can be seen by these simple means has been seen. One more phase is over. The division of our subject matter according to the groups of the animal kingdom is no longer adequate.

We are trying for fresh points of attack. Our forces are disposing themselves in new formations, with fresh centers and a new front. In the organization of the present congress the change has been recognized,

[1] Address delivered at the International Zoological Congress, before the Section of Cytology and Heredity, August 23, 1907.

and the creation of this section and of sections for experimental zoology and cytology testifies to the existence of new methods and new hopes.

Limitations of the animal classes do not trouble us. We take facts wherever we can find them. We are botanists to-day, zoologists to-morrow. The widening of interest which the study of heredity is bringing into modern zoology must prove a great benefit to the science.

When morphology was a new idea, everything was sacrificed to its pursuit. Physiology, systematics, all were discarded as useless lumber. Let us not repeat that short-sighted mistake. In the wider survey which we are attempting we shall need all these things. If we are to understand rightly the phenomena of specific difference—to take that problem only—we shall be glad of anything that the systematist can tell us, and of many deductions of pure physiology.

The study of heredity and variation—of genetics, to use our modern term—is itself a purely physiological inquiry, and as such it must range itself among other physiological inquiries; standing next beside, and looking constantly for support to, physiological chemistry.

The accidents of development which dissociated zoology from physiology were, as we are beginning to perceive, a misfortune, though perhaps an inevitable one. The botanists are happy in that their smaller dimensions have prevented such disruption. But let us hope that the dynamics of the zoological system may admit of the retention of that part of physiology which still adheres. Genetics will grow to be a big sphere one day; but may it never break off from the parent body whether as satellite or as sun.

Let us now examine the task which lies before us as students of genetics. Various descriptions of our objects may be made, referring to the phenomena of heredity and variation; their bearing on the theory of evolution, or on the origin and destinies of races. Stripped of all that is superfluous and of all that is special to particular cases, genetics stand out as the study of the process of cell-division. For if we had any real knowledge of the actual nature of the processes by which a cell divides, the rest would be largely application and extension. It is in cell-division that almost all the phenomena of heredity and variation are accomplished. Nothing is more easy than to witness this process. We may behold its minutest visible details when we please and as often as we please, and still no one has even a plausible guess as to the essential nature of the process. Two centers form: the parts collect round each. The two halves withdraw; or, if we may commit ourselves so far, repel each other, and there are then two cells instead of one. The likeness of those two cells we call heredity; their difference we call variation. If the two cells remain constituent parts of one body, we may speak of their likeness as symmetry or repetition; and their points of unlikeness we then call differentiation. But *how* the two centers were formed, not to speak of *why,* and how they came to separate, we have no surmise. Still less can we conjecture what it was that decided the distribution of differences between the two halves. No phenomenon of common life is so obscure.

By suitable means many of the finer details can be watched, but the most meticulous observation has failed to disclose the essential truth which must yet be so near. I am speaking in a country where by the determination of vigorous observers a great school of cytologists has arisen who have greatly added to knowledge of the perceptible features. They will, I think, agree with me that were the powers of the microscope increased many times, it is unlikely that we should be very much wiser than we now are. Evidence of a different sort is needed.

Others by great ingenuity have tried to penetrate a little deeper by making models which in various ways can reproduce something of what is seen to occur, but the features thus represented are those which occur *after* the two centers are formed—the consequences, that is to say, of the division, not the division itself.

That remains a phenomenon unparalleled in the physical world, like consciousness, a distinctive property of living matter. By no confection of chemistry or mechanical contrivance can we yet fit together a system which will dichotomize and grow, dichotomize and grow, repeating the process again and again as long as certain materials are supplied to it.

The point on which I wish here to lay the emphasis is the failure to conceive or to represent the dichotomy. Heredity, as we commonly see it, is much more than that, but the dichotomy is the one feature common to all its manifestations. I have sometimes thought that in our investigations of the later and more special phenomena of inheritance there is a danger of forgetting that this is the essential fact. In the visible rearrangement of the chromosomes, for example, in mitoses, occurrences so tangible and striking are witnessed that the observer can hardly avoid exclaiming, "This is the essential process of heredity," or "Those chromosomes which I can watch and count must be the physical basis of hereditary likeness." Attractive and stimulating as those wonders are to behold, the essential is still beyond. Heredity began in the explosion which impelled the chromosomes on their courses. If it were possible to identify the chromosomes ever so clearly as the physical bearers of hereditary characters, the problem of the division would remain, and I am strongly led to expect that it must be in some new light on the causation of the division that the way to attack the essential problem will be found. In this expectation I am glad to find myself in agreement with Dr. Loeb, whose stimulating address we heard yesterday. The researches which he has so successfully inaugurated have brought the problem of cell division at last within the range of experiment; and if the nature of the explosion remains still inscrutable, Loeb's work has shown how the charge may be fired.

In our deliberations I anticipate that the more immediate question, whether the chromosomes are or are not the bearers of hereditary characters, will be fully debated. Without presuming to a definite opinion on this question, I venture to state what seem to me formidable difficulties in the way of this expectation. If the chromosomes were directly responsible as chief agents in the production of the physical characteristics, surely we should expect to find some degree of correspondence between the differences distinguishing the types, and the visible differences of number or shape distinguishing the chromosomes. So far as I can learn, no indication whatever of such a correspondence has ever been found. Besides this, although no very thorough investigation of the chromosomes of somatic structures has yet been made on an extensive scale, I believe that definite cytological distinctions between the nuclei of the various tissues *of the same body* have not been detected. If chromosomes were the chief governors of structure, surely we should find great differences between the chromosomes of the various epithelia, which differ greatly in their structure and properties. As these cytological differences have not been found consistently there, the prospect of successfully tracing them among the specific types does not look very hopeful.

Again, no correspondence between the chromosome numbers and complexity of structure has ever been asserted to exist. Low forms may have many; highly complex types may have few.

Then, on the contrary, very closely allied types may show great differences in these respects. As you are aware, Rosenberg has shown that one species of *Drosera* has 20, while another has 10.[2] Again, Miss Lutz has found a similar state of things in *Œnothera gigas,* which has 28, while *Œnothera lata* has 14. Obviously this doubling means something definite, but it is not suggestive of the determination of specific difference. In *Aphis* Miss Stevens, on the other hand, has shown how wide a diversity may be presented by the chromosomes of forms so alike as to have passed for one species. These differences prove both too little and too much. I can not but believe that all this evidence points to the conclusion that we are about to find among the chromosomes one more illustration of the paradoxical incidence of specific difference, not the fundamental phenomena on which that difference depends. Among coleopterists punctulation is sometimes a feature of great systematic importance. To dipterists neuration and chætotaxy sometimes give useful critical data. In certain orders of Lepidoptera, the Hesperidæ, for example, the structure of the gonapophyses sharply distinguishes the species where all outward tests fail. But proceeding farther with each of these criteria, we are sure to come upon other groups where for a long series of diverse types the critical feature, so important elsewhere, may show no differences, or, on the contrary, may show hardly any stability. I have digressed outside my province in these remarks. My excuse must be that I have a rare opportunity of speaking to a great school of cytologists, who must, sooner or later, become the colleagues of us breeders in the attack on genetic problems, and I can not resist saying how the facts strike an observer who is highly interested, and I may truly say unprejudiced. I suspect, then, that the specificity of the chromosomes may conform in general to these other phenomena of specificity.

There remains the suggestive fact that all that has been witnessed regarding the behavior of the chromosomes is in fair harmony with the expectations which our Mendelian experience would lead us to form respecting the hypothetical "bearers" of varietal differences. On the other hand, with one striking exception, nobody has been able to connect a cytological difference with a character-difference in any instance. The exception, of course, is the case of the accessory chromosome which Professor Wilson so admirably demonstrated to us yesterday. Of that I shall speak again hereafter.

But though, in regard to these profounder questions, our knowledge is so defective, the results of experimental breeding are beginning to limit the problem in very definite ways. We know first the fact deduced from Mendel's original experiments with peas, that the bodily characters may result from the transmission of distinct unit-factors. According to Mendel's own conception these factors existed in alternative or allelomorphic pairs, of such a nature that only one member of any one pair can be carried by a gamete. Now though we can not quite prove this first account to be wrong, it is nevertheless possible to express all Mendelian phenomena in terms of a simpler system, according to which the allelomorphism may be represented as con-

[2] Important evidence as to these chromosome numbers has been published by R. R. Gates, *Botanical Gazette,* February and July, 1907.

sisting essentially not in the presence of separate factors for the dominant and for the recessive characters, but in the *presence* of something constituting the dominant character which is *absent* from the recessive gametes. So satisfactory, indeed, are the results of this mode of representation that the probabilities are greatly in favor of its truth. Indeed, when the interrelations of a complicated series of varietal types have to be dealt with, the presence-and-absence system, as we may call it, applies so readily that its correctness is scarcely doubtful.

In simple cases, for instance, in that of the rat, we may regard the color gray and black as due to the operations of gray and black determiners acting upon a distinct factor for color. According to the scheme promulgated by Cuénot, the two determiners, gray and black, are regarded as allelomorphic to each other.

Such a system, however, fails when, as in the case of mice, a third color-type (in addition to the albino) viz., chocolate, has to be expressed. If, on the contrary, each determiner is regarded as allelomorphic to its own absence, a workable system is provided, which can deal with almost all the observed facts. The gray—or technically, agouti—mouse, then, contains all the factors. The black is black because it is minus the determiner for agouti, and the chocolate is wanting in the determiners both for agouti and for black. The relations of all the color types to each other are thus clear except in so far as the relation of yellow to the other colors is not quite satisfactorily accounted for on either system.

It is at present beyond my purpose to examine the suggestions made to deal with that particular difficulty, but leaving this special question on one side, we can draw the clear deduction that each of these varieties owes its existence to the absence or removal of some factor, from the gamete of the type.

Conversely in other cases we perceive with equal certainty that the variety is due to the addition of such a factor.

To deal with this series of interactions, the simple conception of dominant and recessive is inadequate. We now need a term to denote the relation between dominant factors belonging to distinct pairs of allelomorphs.

Till lately we spoke of the relations between the gray color of the mouse to the black color in terms of dominance. Those terms, strictly speaking, should only be applied to members of the same allelomorphic pair. We can perhaps best express the relation between the gray and the black by the use of the metaphor "higher and lower," and I therefore suggest the term *epistatic* as applicable to characters which have to be, as it were, lifted off in order to permit the lower or *hypostatic* character to appear. The same method of representation is, of course, applicable to the series of factors for pattern and for intensity of color.

The case of patterns is in a special way instructive. Symbolically we can represent pattern as due to determining factors, like those which cause the tint or the intensity of color.

Though justifiable as a symbolic representation, it is evident that the "factor" for pattern may really be a quantitative difference in the amount of one of the elements, presumably the chromogen. We may imagine that the color appears on special parts, just as color takes on the prepared surface of a lithographer's stone, always remembering that though the distinction between, for example, self-pattern, the Dutch-pattern and the English-pattern rabbit may thus be quantitative, the quantitative stages are fairly well defined.

The point is of interest inasmuch as

when we come to estimate the minimum number of transmitting elements, it is superfluous to postulate additional elements as instruments in effecting these alterations in pattern, seeing that the change may very readily be imagined as due to a series of quantitative subtractions from the qualitative elements. If then we can thus regard the distribution of color as dependent on subtraction-stages of some one element, say the chromogen, we are naturally led to refer the various intensities to another similar but also definite series of subtraction-stages in which the subtraction is spread over the whole field, and so on for the other qualities.

Two fairly distinct classes of difference may thus be presumed to exist, those depending on the qualitative elements and those due to quantitative subtractions from them. The latter may be again subdivided.

It is scarcely necessary at this time to repeat that almost all the subtraction-stages fully studied are fairly definite, and their existence implies no suggestion of general failure of segregation. Interesting experiments have recently been made by Castle and McCurdy, exhibiting positive results of selection inside the limits of one of these stages, viz., the so-called hooded type in the rat. Nevertheless, the maximum result attributable to selection in such cases is a modification within the limits of one particular varietal type.

Such evidence provides no escape from the conclusion that each genetic variety comes into existence by a special addition to or subtraction from the genetic equipment.

Of all the results to which experimental work has led us, that which to me is the most astonishing is the fact that the same systems of transmission should be followed by characters which, by whatever test they are judged, must be supposed to be most diverse in physiological causation. Naturally when we are dealing with changes in color, for instance, or in the reserve materials of a seed, we surmise that the critical factor is a certain ferment, or rather, the power to produce that certain ferment. It is perhaps not too wide a stretch of imagination to regard susceptibility to fungoid disease as caused by some similar body. The diversity of these ferments must anyhow be very great, and it seems very strange that all these multifarious potentialities should exhibit gametic allelomorphism. Let us take an illustration. Color, as we can prove in regard to several plants, and in regard to the plumage of fowls, is due to the meeting of two complementary factors. One is presumably a ferment. Recent research strongly suggests that it is a tyrosinase. The other is referred to as a chromogen. But whatever they are, the two bodies, or rather the factors which produce them, must be of utterly different nature, and yet, genetically, the two potentialities are treated similarly. Each is allelomorphic to the absence of such a power.

How much more astounding is it, that when we pass to qualities such as length of stalk and shape of flower, or of a cock's comb, the quality of the hair in rabbit, we still find the same rules in strict and undeviating operation. Any scheme of heredity on a scale comprehensive enough to deserve the title of theory must deal with this surprising fact.

There is another extraordinary feature in the behavior of allelomorphs which, though known clearly in a few cases only, must certainly play a great part in the fuller elucidation of heredity. This is *partial gametic coupling.*

Mr. Punnett and I have for some time been engaged in studying this phenomenon in the sweet pea (*Lathyrus odoratus*) and we have recognized indications of the same thing elsewhere. The section will perhaps forgive me for taking a botanical illustration. I have no doubt it will not be long before cases in animals are found.

In the sweet pea, then, we know experimentally about eleven distinct allelomorphic pairs. The actual number is, of course, much greater, but eleven have been critically demonstrated.

Of these characters some are concerned with the production of color, others with the determination of form. The composition of the F_2 families shows that several of these allelomorphs are not distributed independently among the gametes, but that certain combinations of characters occur with greater frequency than others. The first of these couplings to be made out was that between the normal or *long* pollen shape and the factor which determines *blue* color. In the absence of the long pollen factor, the pollen is round. In the absence of the factor for blue, the flower color is red. The coupling here is such that the F_2 numbers instead of being 9 blue-long + 3 blue-round + 3 red-long + 1 red-round, are 41 : 7 : 7 : 9, or very nearly so.

This system would be produced by the following gametic series: 7 blue-long + 1 blue-round + 1 red-long + 7 red-round.

It is not possible to decide strictly whether the series is 7, 1, 1, 7, or 8, 1, 1, 8, and, of course, the dichotomies which produce the one or the other of these systems must be entirely different, but the total of the series is either 16 or 16 + 2.

Now the other two instances of partial coupling show that the association is there in groups of either 32 or 32 + 2. In the first case the blue factor and the pollen shape are again concerned, but their proper system of coupling is disturbed by the presence of another element, that which governs the shape of the flower.

The three pairs of characters are then:

Dominant	*Recessive*
1. Blue.	No blue, viz., red.
2. Pollen long.	Pollen round.
3. Standard upright, having central notch.	Standard hooded, without a central notch.

Now, experiment has shown two things. First, that in these families there is a total and complete coupling of *blue* and *hood*. In other words, all gametes destitute of the upright standard factor have the blue factor, while all gametes bearing the upright standard are destitute of the blue factor. Consequently, there are in such families three types of plants, distinguishable by the shape and color of their flowers:

1. Blue—hooded standard.
2. Blue—erect standard.
3. Red—erect standard.

Classes 1 and 3 are homozygous, but 2, which in this curious instance happens to be the wild type of sweet pea, is here always heterozygous, like the blue Andalusian fowl. Consequently we meet the paradoxical result that of the three types produced in such a family the original wild form is the one which does not breed true, but continues to throw off the other two types.

It is only by a stretch of language that we can speak of the blue factor as coupled with the hooded shape; for the hooded shape is recessive, and thus may be regarded as the shape due to the removal of the factor for upright standard. A more strict way of describing the facts would be to speak of erect standard and blue factor as gametically alternative to each other. It is thus possible that we may have eventually to extend the conception of allelomorphism to cases like this where two characters, both dominant, due, that is to say, to the presence of some factor, are alternative to each other in the constitution of the gametes.

To return now to the distribution of the pollen characters in these families: the F_2

numbers prove that the coupling between the blue factor and the long pollen character is altered and becomes far more complete. When the hood standard is segregating from the upright standard at the same time as the blue is segregating from the red (viz., non-blue), and the long pollen from the round pollen, the gametic series is no longer 7 blue; long + 1 blue; round + 1 red; long + 7 red; round, but is evidently 15 + 1 + 1 + 15, unless, as is still possible, the actual numbers are 16 + 1 + 1 + 16.

A second case of this peculiar distribution exists in regard to the two characters, sterility of anthers and absence of colors in the axil; there the association is 15 (or 16) fertile ♂; colored axil + 1 fertile ♂; green axil + 1 sterile ♂; colored axil + 15 (or 16) sterile ♂; green axil.

The F_2 numbers resulting from the recombinations of two pairs of allelomorphs distributed independently, and according to various simple systems of partial gametic coupling may be tabulated as follows. In each pair one of the factors is taken to be dominant over the other.

	AB	*aB*	*Ab*	*ab*	Total
No coupling.	9	3	3	1	16
3 . 1 . 1 . 3	41	7	7	9	64
7 . 1 . 1 . 7	177	15	15	49	256
15 . 1 . 1 . 15	737	31	31	225	1024

and so forth.

Curiously enough, we have as yet no certain case of the coupling in a series of 8, viz., 3 + 1 + 1 + 3, though we can scarcely doubt that the system exists. There are, however, clear indications that couplings of a still closer order exist and we may reasonably expect them to fall into systems corresponding with the series of powers of 2. This evidence will, in all probability, be of great assistance in the attempt to close in on the question of the moment at which the segregation of characters is effected and must be taken into account in any discussion of the nature of the dichotomies themselves. It becomes very difficult to suppose in these cases of close though still incomplete coupling that all the segregations occur at the reduction division—or indeed at any single division—and we await with some interest the result of cytological studies of the antecedent stages in maturation. The difficulty reaches its maximum when we attempt to conceive the process of character distribution among the egg cells of plants. The male cells in plants and animals are so numerous that their numbers supply sufficient scope for the formation even of very long series of couplings. The egg cells, on the contrary, are few, and very often definitely grouped in special organs which again are arranged on a definite geometrical plan relatively to the gross anatomy of the plant. Even if the various accessory cells of the plant ovary are reckoned as belonging to the gametic series, the number seems still insufficient to allow for the development of a coupling which demands a long series for its expression. Is there, then, any organized system of differentiation connecting the several ovaries into a common plan? In maize and peas, where indications of this system might be expected to be found if they existed, the evidence is entirely negative, and that is all which can be positively asserted.

Turning now to another aspect of the problem, we have to look for facts which may help us to limit our search for causes of variation. We may, as I have said, assume that a vast number of variations are due to the addition or removal of definite factors. We begin, therefore, to have some dim conception of the nature of this class of variations, and at all events to appreciate that they must occur as definite and specific events. As to the causation of these events, there is almost no light. A few months ago, I think it would have been scarcely an exaggeration to have said there was none. It is, however, impossible not to recognize that the striking experiments lately published by Tower may be a positive contribution to this part of the inquiry. We can scarcely imagine that changes in temperature or in moisture are the great or chief efficient causes of natural variation; still the fact that in Tower's experiments such artificial changes in conditions appear to have effected a modification in the germ cells of the potato beetle (*Leptinotarsa decem-lineata*) and to have permanently deflected the offspring into a recessive line, must be allowed weight in future discussions of these phenomena. Many points in that fine piece of work still remain to be cleared up, but a very remarkable beginning has been thus made. It is, perhaps, scarcely necessary to add a warning that though the response to change of conditions may have been direct, it must not be hastily concluded that the response is adaptive. The appeal to direct responses so common in evolutionary discussions of thirty years ago, was made to account for the complex adaptations of organism to environment. It is the total want of any evidence supporting that appeal which has driven most of us to disbelieve in the reality of any such claims, and there is nothing in the new evidence, I think, which should shake the attitude of resolute agnosticism which we have thus been led to adopt.

Similar reflections apply to another very curious instance of genetic change induced by more violent means. MacDougal states that by injecting zinc sulphate into the ovary of *Raimannia* he caused the plant to produce seeds which became small and depauperated plants, destitute of the ciliation characteristic of the parent species. These, in their turn, transmitted the new character to their descendants.

The facts which I have referred to as helping to limit our view have been drawn from the behavior of a considerable range of characters and, as I have said, there are strange elements of similarity common to all. Respecting two very important classes of characters we still remain in almost total ignorance. Some years ago in attempting a provisional survey of variations I distinguished a special group of phenomena as *meristic,* that is to say, belonging to those occurrences by which division and repetition are effected in animals and plants. Obvious as the meristic differences are, we know very little as to the system followed in their inheritance. Only one case is clear, I believe. Farabee has shown that the peculiar condition of the human digits in which the fingers and toes have only two phalanges each, behaves as a simple dominant. Dr. Drinkwater has very kindly sent me lately a table which he will shortly publish, showing exactly the same thing in an English family. In his family, as in Farabee's, the affected members were of very short stature. I can not at all readily conceive how any ferment or other transmissible substance can be supposed to be responsible for such a variation as this. It is true that the attacks of gall-flies or of fungi may excite branching, or proliferating cell division in plants, and we may have to suppose that a poison can have this effect. Perhaps we may also imagine that the fine division of the hair follicles in Angora rabbits or Merino sheep may be due to the want of some substance which in the normal type inhibits or checks this excessive subdivision, but if we are to bring the two-phalanged digits into line with the rest of these observations we shall have to make an extreme demand upon the specific powers of chemical substances.

Polydactylism has thus far failed to give clear indications. Sometimes the inheritance is Mendelian, while in other strains or individuals dominance is so irregular that the descent becomes untraceable. Such irregularities of dominance here, as elsewhere, may be referred with some probability to the disturbing influences of other undetected factors. It is much to be hoped that cases of difference in the ground-plan numbers of some radial type will be found amenable to experimental tests. Here the problem may be found in a somewhat simplified form on account of the elimination of serial differentiation.

One most interesting class of characters remains untouched. I refer to right- and left-handedness. I can form no surmise as to the laws which will govern the descent of these characters. From Mayer's observations on *Partula* we learn that parents of either twist may bear young of either twist. The numbers in the uteri were so small that the absolute numbers were insignificant, and it may be an accident that no mixture of types was found in any one uterus. Direction of twist is a fundamental meristic phenomenon, being, as Crampton and Conklin have proved, determined as early as the first cleavage plane; and great light on the problem of cell division might perhaps be obtained if the inheritances of these differences could be determined. The only case we have studied, that of *Medicago,* in which the fruits are right- or left-spirals according to species, proved unworkable, perhaps on account of the minute size of the flower and the roughness of the manipulations.

I must now refer to the one positive case alluded to above, in which a chromosome difference has been proved to be associated with a somatic difference. McClung, studying the accessory chromosome first observed by Henking was the first to insist on its importance. He showed that in certain insects half the sperms have it and half are without it. This fact led him to make the natural suggestion that the structure might be concerned in the differentiation of sex. This suggestion has been shown by Wilson to be correct, but the accessory body proves to be the peculiarity of the sperms which are destined to form *females,* not of those which will form males, as had been previously supposed. It was with no ordinary feelings of pleasure that in the past week many of us in Woods Holl, and again the large audience assembled in this room, beheld the fine series of photographs which so amply demonstrate Wilson's far-reaching discovery.

The definiteness of the facts is evident beyond all question, and whether the accessory body is in these types the "cause" of femaleness or only associated with that cause, we have at last the long-expected proof that sex is determined in the germ cells, so far as these specific cases are concerned. In those cases we may even go farther and declare that the female is homozygous in femaleness, while the male is heterozygous in sex. Such a result accords well, I think, with the general conclusions to which breeding experiments, on the whole, point. For though great disparities between the proportion of the sexes occur in certain matings, these disparities seem to be obliterated in succeeding generations. If the one sex were homozygous and the other heterozygous, such impermanence of the divergences is what we might naturally expect.[3]

[3] In these remarks I have of course in view the case where the actual number of the two sexes show strange departures from equality. The phenomena recorded by Doncaster in *Abraxas grossulariata* and by Standfuss in *Aglia tau,* where the proportions of the sexes belonging to two varietal

Of course, the association of sex-distinction with an accessory chromosome is admittedly a peculiarity of certain types, but science proceeds by the discovery of prerogative instances, of which surely this notable illustration will long be remembered.

While knowledge has of late progressed so rapidly in regard to many genetic phenomena, we still know next to nothing of the facts relating to the incidence of partial sterility among heterozygous forms. Guyer found that the abnormality of which the sterility of hybrid pigeons is the expression, begins in the reduction-division and is apparent as an entanglement of the chromosomes which fail to divide. In many cases sterility is partial; and for example, a proportion of good pollen-grains occurs mixed with the aborted grains. Fuller examination of these cases would probably lead to interesting results.

In selecting facts which tend to limit our outlook on the phenomena of heredity I have naturally chosen to speak rather of features which are positive and mutually consistent than of the many negative and thus far conflicting items of evidence which must perhaps one day be allowed their weight. The real value of these negative and frequent doubtful observations is as yet so uncertain that they must be regarded rather as hints to be followed in the pursuit of facts than as facts already ascertained.

Allelomorphism, as we are becoming more and more disposed to believe, consists in the separation of a positive something from the absence of that something: More correctly, perhaps, we should say that the thing which conveys a certain power segregates, leaving in that cell division no representative of that power behind. This allelomorphism is the one fact of which we have the clearest proof. It may govern, as we have seen, features of the utmost diversity. What then is that allelomorphism? An essential phenomenon of cell division, it is not: for in homozygous organisms the products of division are alike. Any theory of heredity must include and recognize both these two kinds of division in its purview. We seek vainly as yet for a scheme by which these two sorts of division may be represented.

I do not know that analogy is helpful in these cases, but in my own mind I sometimes remember in this connection that the somatic divisions themselves are also of two types. There are segmentations which, as in radial animals or bilateral animals, divide similar parts from each other, and there are also the serial divisions by which series of differentiated segments are produced. It seems to me just possible that the heterogeneity among the differentiated segments may have some point of real resemblance to the heterogeneity of allelomorphs. I suggest this comparison with only a faint hope that it may prove sound.

Lastly, any scheme of heredity must be able to recognize the possibility of gametic coupling between allelomorphs belonging to distinct pairs, and though few such couplings have yet been proved, we have good reason to believe that yet other systems of couplings of much higher complexity exist.

Dr. Loeb encourages us to look to chemistry for the fulfilment of our hopes, and often, as in the case of the sweet peas, of which I have spoken, we come very near indeed to something like simple chemical phenomena. Of chemistry I know little, but I would ask those who are experts in chemistry whether it is in harmony with

types followed peculiar but consistent systems, are evidently to be referred to the effects of coupling, as Doncaster has shown.

chemical conceptions that, in all the range of characters with which we, breeders, have dealt, no phenomenon suggestive of valency between characters has been observed. Everywhere we meet the fact that on an average the number of germ cells in which our allelomorphs are present is the same as the number in which these allelomorphs are absent. Whatever the kind of characters concerned, equality of number is the rule. While, therefore, we see very readily that the operations of the allelomorphs are due to chemical action, allelomorphism itself can not be expected to prove a chemical phenomenon in any simple sense. Allelomorphism is rather to be compared to the separation of substances which will not mix, and it is not impossible then in some of our more complex cases we are concerned with various phenomena of imperfect mixture. The elucidation of this part of the subject must be left to the physicist.

I can not conclude without expressing something of the delight which I feel that biologists are at length devoting themselves in good earnest to genetic problems.

To those whose memories go back even to the International Congress of 1898 in Cambridge the change is indeed amazing. Then we spoke little of genetics—little, that is to say aloud, or in official programs, though under our breath some of us were murmuring of these things. In this congress the voices that we dared not raise in 1898 are rather in danger of hoarseness from too much speaking. But, seriously, we students of genetics may look forward to the future with great confidence and hope. Those who next week will see Professor Davenport's magnificent institution at Cold Spring Harbor will appreciate that a wonderful and most hopeful beginning has been made. The work of Professor Davenport and his staff, of Professor Castle, at Harvard, of Professor Tower, at Chicago, and of others I might name, are all evidences that a great and combined advance has begun. We in Europe will bear our part also, and if we have not any very fine equipment we must console ourselves with the thought that light-armed troops may move the faster for a while. With their base on Cold Spring Harbor, or Woods Hole and the Biologische Versuchsanstalt in Vienna, the allied armies of genetics, cytology and experimental zoology they start for the grand attack; and I think when we meet at the end of another period of ten years, there will be victories to record.

WILLIAM BATESON
CAMBRIDGE UNIVERSITY

SCIENTIFIC BOOKS

Résultats du Voyage du S. Y. Belgica en 1897–9, sous the commandement de A. de Gerlache de Gomery. Rapports Scientifiques. Zoologie. *Insects* par G. SÉVÉRIN (and twenty others), 92 pp., 4°, V. pl., 1906; *Ostracoden* von G. W. MÜLLER, 8 pp., I. pl., 1906; *Holothuries* par E. HÉROUARD, 17 pp., II. pl., 1906; *Medusen* von OTTO MAAS, 32 pp., III. pl., 1906.

A fresh batch of the valuable reports of the Belgian Antarctic Expedition have come to hand, the printing and illustrations of the elegance which has characterized the series.

The number of insects which have been brought back from the Antarctic remains pitiably small, and in marked contrast with the richness of the Arctic regions. Besides the Collembola taken in the Gerlache channel, a *Podurella* and pedicularian obtained by the *Southern Cross,* no insect is known except a Chironomid fly of the new genus *Belgica,* and the larva of perhaps another species of the same family. These minute creatures, whose wings are so reduced that they are incapable of flight, are found in the vicinity of small pools of water where the seabirds roost on the rare bits of bare ground or rock which are exposed along Gerlache Channel.