poration of Harvard is entirely satisfied with the experiment that it has made. It is, in fact, so well satisfied that within a few weeks it has definitely committed the university to the policy of placing the technical work in the university on a graduate basis, and it has closed the Lawrence Scientific School to the further admission of new students.

It is evident, therefore, that Harvard University has made a very great step in advance along the lines which I have suggested for the preparation of the individual for professional studies and fitting him to become a chemical engineer. It seems to me that it will acquire the same reputation from its move in this direction as it has in its law and medical schools.

At Columbia a similar course can be pursued, taking the B.A. in the college or the B.S. in the scientific school after four years' study and then proceeding in two years to the degree of chemical engineer.

Johns Hopkins has a graduate school of applied science, largely devoted to research, while in 1903 the Massachusetts Institute of Technology issued a prospectus for a graduate school of engineering, leading to the degree of doctor of engineering, which has not, as yet, materialized to any great extent, but which we may hope to see encouraged under the direction of the present acting president of the institute, our colleague, Dr. A. A. Noyes.

There are, no doubt, equally satisfactory opportunities in other schools for such a training as I have demanded, if the desire for it is expressed, and I would by no means suggest that continuous study in any one locality is necessary or even desirable.

The instruction in some of our schools is intensive, in others, broad. In one, the student meets an environment which is purely local, in so far as all, or the majority, of the instructors are graduates of the school in which they teach. In another, they have been assembled from a wider field, have brought to the school a broader conception of the science, and a more liberal point of view. The latter is surely the more desirable. It is quite possible, therefore, that it may be as well to move from place to place for the change of atmosphere which may be obtained.

The main thing to be accomplished is the making of the liberal-minded man of broad intelligence who shall possess those qualities which I have cited as being necessary in the chemical engineer and which, in my opinion, are not found in the graduates of our technical schools as they are now thrown on the world.

If time and my confidence in your patience permitted, I might go at length into some other defects in our system of educating the chemical engineer, more especially as to the evils of examinations and of making undue exertions to obtain degrees. But these subjects must be reserved for another time and place. The views of many prominent persons in regard to them are well known to you, and I may add that I am in sympathy with the idea that they are both evils which need very careful consideration.

It is to be hoped that the suggestions which have been made, although in no way novel, may, by reiteration, arouse some attention in so far as they may point out a way of making the chemical engineer of the future a larger, broader and more influential man than he is to-day, and one who will occupy a position in the community of as great importance as the leaders of the other great professions.

CLIFFORD RICHARDSON

THE MECHANISM OF HEREDITY[1]

HEREDITY is to-day the central problem of biology. This problem may be ap-

[1] Address of the vice-president and chairman of Section F, Zoology, American Association for the Advancement of Science, Chicago meeting, 1907–8.

proached from many sides—that of the breeder, the experimenter, the statistician, the physiologist, the embryologist, the cytologist—but the mechanism of heredity can be studied best by the investigation of the germ cells and their development. Although many phenomena of inheritance may be discovered in the absence of any definite knowledge of the mechanism of inheritance, a scientific explanation of these phenomena and practical control over them must wait upon our knowledge of their causes. Only a beginning has been made in this study and it seems probable that it may engage the attention of many future generations of biologists, but, nevertheless, we have come far since that day, only about thirty years ago, when Oscar Hertwig first saw the approach and union of the egg and sperm nuclei. Indeed, so rapid has been the advance of our knowledge within this field that it is hard to realize that this entire period lies well within the lifetime of most of those here present, and that many of the pioneers in this work are still active in research.

In the short time at my disposal I can not present even the briefest summary of the many important discoveries in this field; I can hope only to discuss a few of the most suggestive facts and theories as to the mechanism of heredity.

I

Heredity, which originally meant heirship, or the transmission of property from parents to children, has come to mean "the transmission of qualities or characteristics, mental or physical, from parents to offspring" (Century Dictionary). These qualities are frequently regarded as independent entities or "unit qualities," which are "transmitted" from one generation to the next through the agency of an "inheritance material" or "bearer of heredity." Such terms are not without fault when used merely as figures of speech, but when interpreted literally, as they frequently are, they are altogether misleading; they are the result of reasoning about names rather than facts, of getting far from phenomena and philosophizing about them. The comparison of heredity to the transmission of property from parents to children has produced confusion in the scientific as well as in the popular mind.

It is only necessary to recall the most elementary facts about development to recognize that in a literal sense parental characteristics are never transmitted to children. Every new individual is only a detached portion of an old one, and whether derived as bud, or spore, or egg, it owes its similarity to its parent to the fact that it was once a part of it, and not to something which has been "transmitted" from one generation to the next. Furthermore, from its earliest to its latest stage an individual is one and the same organism; the egg of a frog is a frog in an early stage of development and the characteristics of the adult frog develop out of the egg, but are not transmitted through it by some "bearer of heredity."

Indeed, heredity is not a peculiar or unique principle for it is only similarity of growth and differentiation in successive generations. The fertilized egg cell undergoes a certain form of cleavage and gives rise to cells of particular size and structure, and step by step these are converted into a certain type of blastula, gastrula, larva and adult. In fact, the whole process of development is one of growth and differentiation, and similarity of these in parents and offspring constitutes hereditary likeness. The causes of heredity are thus reduced to the causes of the successive differentiations of development, and the mechanism of heredity is merely the mechanism of differentiation. The peculiarity which distinguishes the differentiation of the egg cell from that of any tissue cell is the fact that the latter gives rise only to a particular type of cell, with the formation of which differentiation comes to an end, whereas the former undergoes a long series of differentiations and gives rise to a complicated organism.

II

The causes of differentiation, and hence of heredity, are in general twofold, intrinsic and extrinsic; the former are represented by the germinal protoplasm, the latter by practically all other conditions. Similarity of differentiation in successive generations, or hereditary likeness depends upon similarity of both the intrinsic and the extrinsic factors. The differentiations of the germ follow a definite sequence because the substance of the germ undergoes definite chemical transformations, which are predetermined by its initial constitution. Similarity of sequence is involved in similarity of germinal substance and of environment.

There are no vital structures or functions which are absolutely independent, self-acting, self-moving, self-differentiating or independently variable. Each part and function exists only in close relationship with other parts and functions and with environmental conditions. Many of the criticisms which have been recently brought against "unit characters," "units of heredity," "organ-forming substances," "individuality of the chromosomes," indeed against heredity and variation as a whole, are applicable only to extreme views, which no one consciously holds. To be sure, an individual, whether a unit quality, a chromosome, a substance or a person, can not exist apart from its environment, but who has ever maintained the contrary?

A study of the phenomena of development, no less than the principle that every effect must have an adequate cause, makes it certain that the characteristics of an organism are in some way predetermined within the protoplasm of the fertilized egg cell. From a frog's egg only a frog will develop, from an echinoderm's egg only an echinoderm, and the course of development is, under constant external conditions, marked out in each case, even down to the minutest details. Since, however, these external conditions may be exactly the same in the case of two eggs, and yet the results of development be very different in the two, we can only conclude that the physical basis of inheritance is to be found in the properties of the germinal protoplasm. To assume that extrinsic causes determine whether there shall hatch from an egg a chicken or an eagle would be the sheerest nonsense. The fact is there is no escape from the conclusion that all really inherited characteristics are predetermined in the structure of the germinal protoplasm. But it should be observed that to say that characteristics are predetermined is a very different thing from saying that they are preformed. The one merely affirms that the causes of the transformations which lead from one step to another in the development are determined by the initial constitution of the fertilized egg; the other affirms that these transformations have already taken place within the egg.

III

It is practically certain that in the last analysis the characteristics of the germ are dependent upon its chemical and physical constitution. Fick has lately maintained that not only the protoplasm of every species, but also that of every individual, must be different from that of every other. At the same time he points out the fact that this apparently stupendous assumption is readily possible within the limits of the composition of protoplasm, since Miescher has shown that a molecule of albumin with forty carbon atoms may have as many as one billion stereoisomers. Reichert and Brown[2] have recently found that many genera and species of vertebrates may be distinguished with certainty by the properties of their hæmoglobin crystals. Here is positive proof that the molecular constitution of at least one important substance differs in different species, and if this be true of hæmoglobin it may be safely assumed to be true of the constituents of the germinal protoplasm.

For the present, however, we must be content to find the distinguishing characteristics of different germ plasms in their morphological and physiological properties rather than in their molecular constitution. And fortunately for the possibilities of research the morphological and physiological characteristics of the germ cells are sufficiently numerous and evident to afford a most fruitful and fascinating field for research.

In practically all theories of heredity it is assumed that there is a specific "inheritance material," distinct from the general protoplasm, whose function is the "transmission" of hereditary properties from generation to generation, and whose characteristics, as compared with the general protoplasm, are greater stability, independence, and continuity. This is the Idioplasm of Nägeli, the Germ-plasm of Weismann. It is further assumed that this germ plasm is itself composed of ultramicroscopical units, which are capable of undergoing transformation during the course of development into the structures of the adult. These are the hypothetical Plastidules, Gemmules, Pangenes, Plasomes, Idioblasts, Ids, Determinants, Biophores of various authors. However necessary such units may be for a complete philosophical explanation of development, it must be confessed that at present they constitute a purely hypothetical system which may or may not correspond to reality. We know that the germ cells are exceedingly complex, that they contain many visible units such as chromosomes, chromomeres and microsomes, and that with every great improvement in the microscope and in microscopical technique other structures are made visible which were invisible before, and whether the hypothetical units just named are present or not seems to be a matter of no great importance, seeing that, so far as the analysis of the microscope is able to go, there are differentiated units which are combined into a system—in short, there is organization.

On the other hand the evidence in favor of an inheritance material, which is distinct from the general protoplasm of the germ and whose function is the reproduction of hereditary characters, is not convincing. All the living substance of the egg cell is converted by growth and differentiation into the mature organism. That there is a species plasm, or an individual plasm, which is continuous from generation to generation, and from which all the qualities of the mature organism are differentiated, is almost a certainty, but there is no satisfactory evidence that this substance is distinct from the general protoplasm of the young germ cells.

IV

Differentiation, and hence heredity, consists in the main in the appearance of unlike substances in protoplasm and their localization in definite regions or cells. Such a definition is as applicable to the latest stages of differentiation, such as the formation of muscle fibers, as it is to the earliest differentiations of the germ cells, and the one is as truly a case of inheritance as is the other. In short, different sub-

[2] By the kindness of the authors I am permitted to refer to this very important research which will soon be published by the Carnegie Institution.

stances appear at an earlier or later stage in the development of all animals, and these substances are then sorted out and localized; this is differentiation. Physiological division of labor involves morphological division of substance; sorting out of functions implies sorting out of the material substratum of functions.

Unfortunately, we do not know many of the steps by which different substances appear within protoplasm. Even the formation of non-living products, such as oil, yolk and secretions, is but imperfectly understood, while the manner of formation of different kinds of protoplasm is almost wholly unknown. No one doubts, however, that different kinds of protoplasm are formed in the course of development, that the substance of a muscle cell, for example, is different from that of a nerve cell, and that both are different from the germinal protoplasm; furthermore, no one doubts that the relatively few substances of the germ cells give rise through many transformations to the relatively numerous substances of the adult.

But although little is known regarding the method of origin of the different substances which appear in the process of differentiation, in all cases which have been carefully studied one significant fact appears, viz., the importance of the interaction of the nucleus and cytoplasm. It is well known that many differentiations first appear in the immediate vicinity of the nucleus; indeed, in many cases various substances have been seen to come out of the nucleus and to mingle with the cytoplasm, while the nucleus in turn absorbs substances from the cytoplasm. It is known that constructive metabolism, differentiation and regeneration never occur in the absence of a nucleus. On the other hand, Verworn has shown that the nucleus alone is incapable of performing these functions, and he maintains that the chief rôle in the life of the cell can not be assigned to either the nucleus or the cytoplasm, but that both are concerned in vital phenomena. Judged merely by the results of observation and experiment, and wholly apart from current theories, it must be admitted that there is good reason to believe that the different substances which appear in the differentiation of a tissue cell arise through the interaction of the nucleus and cytoplasm, and not from either of these alone.

Turning now to the differentiations of the fertilized egg cell, we find that essentially the same conditions obtain as in the differentiation of a tissue cell. Here, also, different substances appear in the egg cell and become localized in different regions of the egg or embryo. In most animals the different kinds of substance in the unsegmented egg are not numerous nor conspicuous, though in all cases so far studied at least three kinds of substance may be separated by means of the centrifuge. Here, as in the case of the tissue cells, it is known that there is an active interchange of nuclear and cytoplasmic substances. In the long growth period of the egg the nucleus grows enormously, evidently at the expense of substances received from the cell body. On the other hand, it is well established that substances issue from the nucleus into the cell body and mingle with the cytoplasm during this stage, and it is generally believed that one of the substances thus formed, the yolk nucleus, is instrumental in the formation of yolk. At the end of the growth period of the egg the nuclear membrane dissolves and a relatively enormous quantity of nuclear material is thus liberated into the cell body, while an insignificant quantity persists in the form of chromosomes and gives rise to future nuclei. During every cleavage of the egg the nucleus grows by absorbing substances from the cell body, only to give back other substances to the cell at every mitosis, thus constituting a sort of systole and diastole of the nucleus, and it may be suggested that this interchange between nucleus and cytoplasm is one of the primary functions of mitosis. Many of the substances which are liberated from the nucleus are visibly different from the other substances of the cell body, and in some cases they may be traced through successive stages of development until they give rise to particular portions of the embryo.

The time at which particular embryonic differentiations appear differs widely in different animals. In some cases the earliest visible differentiations which may be correlated with the later differentiations of the embryo or larva, appear about the time of the formation of the blastula or gastrula, and here the cleavage cells are apparently all alike. In other cases the cleavage cells are not alike; even the first cleavage, as well as the later ones, may be of differential value, thus giving rise to cells which differ in size, symmetry and substance, and these features of the cleavage are inherited as certainly as are the form and character of the larva or adult. In still other cases marked differentiations of the egg are visible before cleavage begins, while in some instances these differentiations are present even while the eggs are still in the ovary.

But whether these differentiations appear early or late, there is reason to believe that the processes by which they arise are essentially the same in all cases, and that there is therefore no fundamental difference between eggs which differentiate early and those which differentiate late. It is quite possible that the time of appearance of differentiations depends less upon the time of formation of different substances in the egg than upon the time of their localization or segregation in specific regions or cells. All eggs hitherto examined show certain differentiations of the cytoplasm even in the earliest stages, though in most cases the different substances are not segregated before the cleavage stages. When such eggs are submitted to a strong centrifugal force the substances of the unsegmented eggs of practically all animals may be separated into at least three zones, which correspond in a striking manner to the three zones which are normally present in the unsegmented eggs of ascidians. This indicates that the real difference between eggs which are highly differentiated and those which show little or no differentiation of the cytoplasm may be in the segregation of unlike substances rather than in the presence or absence of such substances.

Regarding the other factor of differentiation, viz., the segregation or localization of unlike substances, rather more is known than in the case of their origin. Segregation of the different substances of the unsegmented egg and of the cleavage cells is known to take place chiefly by protoplasmic flowing, the direction of the flow being correlated with the initial polarity of the cell, and with the chemotropism of the substances concerned. Segregation thus produced is still further emphasized and rendered permanent by cell division and the formation of partition walls. I have recently found that when different substances of the egg are displaced by strong centrifuging they tend to come back to their normal positions unless prevented by partition walls which have formed in the meantime. In the early cleavage stages of many animals the cell divisions are differential both as regards the size and the substance of the daughter cells, but in such cases the cleavage is not responsible for the differentiation as is plainly shown by the fact that the segregation of the different substances occurs before division, and the inequality of the cleavage may be foreshadowed by lobes of the cytoplasm even before the nucleus begins to divide. Lillie has shown that differentiation may proceed far in the case of *Chætopterus* in the absence of any cleavage. On the whole then, although the lines of cleavage tend to follow the pre-existing lines of differentiation the principal part played by cleavage in the process of differentiation is in rendering permanent the segregation of the different substances.

Finally we may conclude that the nucleus plays a less important rôle in the localization of different substances than in the formation of those substances. Nevertheless, in differentiation, as well as the metabolism, there is every reason to believe that the entire cell is a physiological unit. Neither the nucleus nor the cytoplasm can exist long independently of the other; differentiations are dependent upon the interaction of these two parts of the cell; the entire germ cell, and not merely the nucleus or cytoplasm, is transformed into the embryo or larva; and it therefore seems necessary to conclude that both nucleus and cytoplasm are involved in the mechanism of heredity.

V

It is well known that many biologists believe that the nuclei, and more particularly the chromosomes of the germ cells, are the exclusive seat of the inheritance material. O. Hertwig and Strasburger first formulated this hypothesis as a result of their studies on fertilization. Roux suggested that the chromatin is the most important part of the nucleus, in view of the exact manner in which it is divided in mitosis. Van Beneden and Boveri discovered that the chromosomes come in equal numbers from the egg and the sperm; that the number of chromosomes in each of the germ cells is one half the number characteristic of the species, and that by the union of these cells the characteristic number is reestablished; and finally that the maternal and paternal chromosomes are distributed with exact equality to all the cells of the developing organism. Furthermore, it was shown by Rabl and Boveri that there is a continuity (or persistent individuality) of the chromosomes from one cell cycle to the next. That the nucleus alone is the bearer of the inheritance material was affirmed by Hertwig in 1892, in view of the following facts: (1) The equivalence of the inheritance material in male and female; (2) the equal distribution of the inheritance material to all cells of the organism; (3) the prevention of the summation of the inheritance material, by its reduction before fertilization; (4) the isotropy of the protoplasm.

Since that time many additional evidences that the chromatin is the seat of the inheritance material have been brought to light, only a few of which can be summarized here. Boveri found in the development of *Ascaris* that the germ cells, which preserve all the characteristics of the species, also preserve all the chromatin of their chromosomes, but that in the body cells, which undergo differentiation, the chromosomes undergo diminution. Weismann assumed as a logical necessity that in the maturation of the egg and sperm there must occur a division of a peculiar type, a reduction division, the significance of which is the halving of the germ plasm and its contained hereditary units, in preparation for the union of egg and sperm in fertilization. Such a reduction division of the chromosomes has since been observed by many investigators in a large number of organisms. More recently Montgomery, McClung, Paulmier, Wilson and others have found chromosomes of many different sizes and shapes within the same nucleus, and Boveri has shown, by a masterful analysis, that in echinids the hereditary value of individual chromosomes is different, although here they are all alike in form.

Boveri also discovered that enucleated egg fragments of *Echinus* fertilized by sperm of *Strongylocentrotus* produced larvæ which had purely paternal characteristics. These results have, however, been called in question by Seeliger, Morgan and Driesch; but even accepting Boveri's results, this experiment does not completely demonstrate that the chromosomes are the only "bearers of the inheritance material," as we shall see later. Finally, as a fitting climax to this chapter of remarkable disclosures as to the chromosomes, may be mentioned the epoch-making discovery of McClung, Wilson and Stevens that in certain groups of insects the dimorphism of the sexes is correlated with a chromosomal dimorphism of the spermatozoa.

These are but a few of the many notable discoveries which have been made within recent years regarding the chromosomes, and while they do not demonstrate the truth of the chromosomal inheritance theory, they do prove the very great significance of the chromosomes in the process of heredity. Boveri concludes his last great work on "The Development of Dispermic Sea-urchin Eggs" with these words (p. 260):

> After all has been said, I believe that we may regard the view that specific characteristics are transmitted from the parent to the child through the chromosomes of the egg and the sperm nuclei, as a theory which has a series of facts in its favor and up to the present time not a single one against it.

VI

Against the extreme form of this theory, as held for example by Hertwig, many general and specific objections may be urged. General objections are based upon the consideration that the entire cell, cytoplasm as well as nucleus, is concerned in differentiation and that neither is capable of embryonic development in the absence of the other. Differentiation is indeed the result of the interaction of nucleus and cytoplasm, and how then can it be said that the nucleus is the only seat of the inheritance material? If held rigidly, this theory involves the assumption that the cytoplasm and all other parts of the cell are the products of the chromosomes, and that therefore the chromosome and not the cell is the ultimate independent unit of structure and function—an assumption which is contrary to fact. Furthermore, since heredity includes a series of fundamental vital processes such as assimilation, growth, division and differentiation, there is something primitive and naïve in the view that this most general process can be localized in one specific part of the cell—something which recalls the long-past doctrines that the life was located in the heart or in the blood, or the ancient attempts to find the seat of the soul in the pineal gland or in the ventricles of the brain.

Among specific objections may be mentioned the fact that the cytoplasm is not isotropic, as Hertwig supposed, but rather that many fundamental differentiations are found in the cytoplasm of the egg at the time of fertilization and immediately after. As evidences of such differentiations may be cited, (1) polarity and symmetry, (2) differential cleavages, (3) positions and proportions of important organ bases, (4) various types of egg organization, (5) experiments in hybridization.

1. So far as is known, the animal pole of the egg becomes the aboral pole of the gastrula in all animals, while the cytoplasm in this region gives rise to the ectoderm of the developing animal. This polarity of the egg may be traced back through its ovarian history to its earliest stages, and it is probable that in some cases at least it is directly continuous from generation to generation. Here then is an important character which is inherited through the cytoplasm and not through the nucleus.

2. Similarly, the symmetry of the cyto-

plasm of the egg frequently corresponds to the symmetry of the adult. In many bilateral animals the fertilized egg is bilaterally symmetrical. Such bilaterality is found even in the ovarian eggs of insects and cephalopods, while in other cases, such as ascidians and amphibians, it appears immediately after fertilization. In still other groups there is reason to believe that a bilateral organization may be present in the unsegmented egg, even when it may not be directly visible. Thus in most gasteropods there is no direct evidence of bilaterality in the unsegmented egg, but in *Neritina* Blochmann observed a group of granules on each side of the animal pole, and in later development these were found in the velar cells of the right and left sides. In all gasteropods the velum arises from similar cells of the early cleavage, and yet the bilateral groups of "Urvelargranula" have been found only in *Neritina.* Is it not probable that in other gasteropods similar bilaterally distributed substances are present, although not directly visible?

Gasteropods also show a striking correlation between the distortion of bilateral symmetry in the spirally coiled body of the adult and the symmetry of cleavage. It is well known that in certain gasteropods the body is coiled to the right, in others to the left, and corresponding to this inversion of the symmetry of the adult, Crampton found that there was an inversion of the symmetry of the cleavage. The cleavage of a half-dozen genera of sinistral gasteropods is now known and in every instance it is the reverse of that found in dextral gasteropods. Furthermore, this inversion of symmetry may be traced back to the unsegmented egg. Such a case shows conclusively that not only bilaterality is present in the cytoplasm of the egg, but that even departures from such symmetry are also present.

3. In the cleavage of the eggs of many animals it has been shown that the position, shape, size and substance of the blastomeres; the direction, time and quality of cell-division; the size of the nucleus, centrosomes and chromosomes, are all under cytoplasmic, rather than nuclear control. That the type of cleavage, its rhythm, rate and direction are determined by the cytoplasm of the egg has been shown by myself in the normal development of gasteropods, and by Boveri and Driesch in the case of echinoderm hybrids; that the size of the nucleus, centrosomes and chromosomes is dependent upon the volume of the cytoplasm is clearly shown in Crepidula, where, in the large and small blastomeres, these structures are invariably proportional in size to the volume of the cytoplasm. In the case of echinoderms, on the other hand, Boveri holds that the size of the nucleus is dependent upon the number of chromosomes which it contains, and that the size of the cell is controlled by the size of the nucleus. The latter is certainly not the case in annelids, mollusks or ascidians.

4. Another direct correspondence between the cytoplasm of the egg and the structure of the larva may be found in those animals in which particular substances of the egg become localized in definite regions and finally give rise to specific parts or organs of the embryo or larva. Such cases are known among animals belonging to a large number of phyla. Among ascidians the substances which are to enter into the formation of the ectoderm and endoderm, the muscles, mesenchyme, notochord and nervous system are present in the two-cell stage in relatively similar positions and proportions to the corresponding organs of the larva. If any of these substances is removed from the egg, the embryo which develops from such an egg lacks the corresponding organ; and conversely, if these substances are forced into abnormal positions in the egg, the

characteristic organs to which they give rise appear in these same abnormal positions. There is, therefore, in this case, both negative and positive proof that these materials of the cytoplasm of the egg are actually "organ-forming substances."

5. In different phyla there are marked differences in the localization of the ooplasmic substances, corresponding to differences in the location of the organs in the embryo or larva. Many different phyla may, therefore, be distinguished by the type of ooplasmic localization which they show. In its general features, therefore, the characteristics of the phylum are present in the cytoplasm of the egg cell.

All of these observations on the cytoplasm go to show that it is not isotropic, as Hertwig supposed, but that it is differentiated and that many of the characteristics of animals, especially such as apply to their general type of organization, are represented in the cytoplasm of the egg.

6. Finally as evidence that inheritance may take place through the cytoplasm of the egg, reference must be made to the extremely important work of Loeb and of Godlewski. By concentration of hydroxyl ions Loeb found that it was possible to cause the spermatozoa of starfishes and ophiurans to fertilize the eggs of sea urchins. The embryos and larvæ resulting from such crosses showed only the characteristics of the mother. Later Godlewski, using the same methods, was able to fertilize the eggs of a sea urchin by the sperm of a crinoid, and although such hybrids were raised to the larval stage they showed only maternal characteristics. Still more, enucleated urchin eggs fertilized by crinoid sperm produced gastrulæ of purely urchin type. These results demonstrate, as Boveri admits, that the chromosomes of the sperm do not in this case influence or modify the cytoplasm of the egg cell; while the experiments on the enucleated egg show that the characteristics of the organism, at least as late as the gastrula stage, are derived entirely from the egg cytoplasm.

Boveri long since showed that the early stages of development, perhaps as late as the blastula or gastrula, are uninfluenced by the spermatozoon and are purely maternal in type; in the case of Godlewski's hybrid larvæ he supposes that the sperm chromosomes remain permanently inactive. But however this result is to be explained, it may be considered as definitely settled that the early development of animals is of purely maternal type, and that it is only in stages later than the gastrula, and consequently after the broad outlines of development and the general type of differentiation have been established, that the influence of the spermatozoon begins to make itself felt; and it is equally certain that this type of differentiation is predetermined in the cytoplasm of the mature egg cell, rather than in the egg nucleus.

On the other hand, there is no doubt that the differentiations of the egg cytoplasm have arisen, in the main, during the ovarian history of the egg, and as a result of the interaction of nucleus and cytoplasm; but the fact remains that *at the time of fertilization the hereditary potencies of the two germ cells are not equal, all the early development, including the polarity, symmetry, type of cleavage, and the relative positions and proportions of future organs being predetermined in the cytoplasm of the egg cell, while only the differentiations of later development are influenced by the sperm. In short, the egg cytoplasm fixes the type of development and the sperm and egg nuclei supply only the details.*

This conclusion is not a refutation of the nuclear inheritance theory, but it is a profound modification of it. At once it destroys the argument that since there is equality of inheritance from both parents there must be equivalence of inheritance material in egg and sperm. So far as those characteristics are concerned which appear late in development, it is highly probable that there is equality of inheritance from both parents, but in the early and main features of development, hereditary traits, as well as material substance, are derived chiefly from the mother.

Finally I may call attention briefly to the bearing of these conclusions on the mechanism of evolution. I have elsewhere (SCIENCE, No. 536) discussed the proposition that the evolution of organisms must take place through the evolution of their germ cells, and that relatively slight modifications in the localization of the formative substances of the egg may produce profound modifications in the adult.

One of the principal difficulties in explaining, on evolutionary grounds, the origin of different phyla has been the dissimilar locations of corresponding organs or parts. These difficulties are well illustrated by the theories which attempt to derive the vertebrates from the annelids or from any other invertebrate type. If evolution takes place through the transformation of the egg cell rather than of the adult, it is no more difficult to explain the different locations of corresponding parts in these phyla than their different qualities. Changes in the relative positions of parts which would be absolutely impossible in the adult may be readily accomplished in the unsegmented egg, as is shown by cases of inverse symmetry.

In the light of the conclusion that only the later and more detailed differentiations are influenced by the sperm, it follows that experimental work which aims to modify the fundamental features of an organism must be directed to the ovarian egg rather than to the sperm, or to the developing embryo.

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THE INFLUENCE OF FRICTION IN ECONOMICS[1]

THERE has always prevailed, since the foundation of systematic political economy, a conflict between men of theory and men of action. Men engaged in practical business affairs and even in great financial operations have refused again and again to accept the abstract conclusions drawn from so-called economic laws, and have insisted that the rule of practical common sense, if based upon a careful observation of facts, was a safer guide than economic theory. In the field of tariff legislation this divergence of opinion has perhaps been more marked than in the field of finance. This difference, so far as it exists, tends to support the view which is here laid down—that the economist has erred in a measure in seeking to apply abstract principles too rigidly to actual conditions by failing to take account of friction in the application of these principles.

The economist, working out the theory of the conduct of the economic man according to the principles of enlightened self-interest, finds in them a harmony and a rule of law which in his mind give them something of the beauty and precision of the movement of the spheres. He is impatient of qualifications which detract from the simple and direct operation of the principles derived from these theories. The principles of the flow of capital to the market where the price paid for its use is the highest, of changes in prices according to changes in the quantity of money, of the evolution of production and manufactures in such a manner that each community and each individual shall find his most profitable work under the regime of free competition, are principles so simple to his mind that he can not understand how they can be disputed.

Nor could such principles be long disputed, if the current of trade flowed as freely as the waters of the ocean into a vacuum wherever scarcity indicated a given demand, and if money and capital

[1] Address of the vice-president and chairman of Section I—Economics and Social Science—American Association for the Advancement of Science, Chicago meeting, 1907-8.