

and the mother a mulatto. Some of the children had pronounced negro features with fair complexions, others had dark skins and regular features; the characteristics of the two parental races were not evenly blended in any one of the children. Particulate inheritance is so similar to exclusive inheritance that it is sometimes difficult to determine to which type a given case belongs, as is true for example in regard to the color of the hair of horses and dogs.

Prepotency.—Sometimes the offspring on the average will resemble one parent more than the other, and then the parent with which the correlation is the greater will be said to be prepotent. Breeders find as a rule that pure-bred animals are prepotent over mongrels. The prepotency may affect all offspring alike or it may affect only one sex. Abnormal variations are said to be highly prepotent, and Darwin gives a number of cases of the inheritance of such variations by one sex only.

Inheritance at Corresponding Periods of Life.—Correlations may be observed not only between adult parents and adult offspring, but also between the immature stages of parent and offsprings, and, of course, these correlations come at corresponding periods of life, or there would be no regularity in the course of development. But it has been observed that abnormalities in parent and offspring tend to appear likewise at corresponding periods of life. Of this Darwin gives a number of examples.

Characters that may be Inherited.—In general all congenital characters exhibit the phenomena of heredity, either of one type or another. This includes not only normal variations but also various abnormalities and those constitutional weaknesses that predispose the subject to disease. Pearson has shown that fertility may be inherited and every horticulturalist knows that variability is an inheritable characteristic. As to the inheritance of modifications acquired as the result of external influences upon the cells of the body, we have but few observations of value. The results from Fay's observations on the inheritance of deafness are given in the following table:

TABLE VI.—INHERITANCE OF DEAFNESS.

Condition of parents.	Number of children.	Per cent. deaf.
Both deaf, acquired.....	1,720	2.3
Hearing and deaf, acquired.....	713	2.2
Deaf, congenital and acquired.....	1,820	6.3
Hearing and deaf, congenital.....	528	11.9
Both deaf, congenital.....	779	25.9

The difference of the results between the cases in which congenital deafness appears in the parentage and cases in which it apparently does not is very striking. It is possible that it might be still more so if it were not for the difficulty of distinguishing in every case between congenital and acquired deafness, a difficulty which may perhaps account for the appearance of even the small percentage of deaf children credited to parents that appear to have acquired deafness. (See *Evolution*.)

Reversion.—The discussion of reversion and atavism is reserved for another place. (See article *Reversion*.)

Telegony.—Many breeders of domestic animals are firmly convinced that a previous sire may influence the progeny of a subsequent one. This supposed influence is called telegony and is regarded as a phenomenon of heredity. The subject has been investigated experimentally by Ewart, using horses and zebras, and he found no evidence of such an influence. Pearson has attacked the problem from the statistical point of view and likewise reached negative results.

In plants there is a phenomenon called *venia*. In Indian corn when two varieties are crossed the maternal part of the fruit takes on the characteristics of the male parent, which one would not expect to appear until the formation of the fruit of the next generation. De Vries and Webber have explained this as due to a process of double fertilization first observed by Nawaschin and Guignard (see *Impregnation*).

In concluding our review of the phenomena of heredity it should be noted that little is to be learned by the study of isolated cases. We can acquire ideas of value in regard to heredity only by dealing with large numbers of observations by approved statistical methods. And it has been with the hope of giving some notion of the first principles of that new and important branch of biological science that we have devoted so much space to the subject. We now turn to the theories of heredity.

THEORIES OF HEREDITY.

Importance of the Subject.—We are all interested in the question as to how we have come to be what we are, and we have seen that what we call the principle of heredity has been an important factor in determining the present condition, not only of every human being, but also of every living thing whether animal or plant. We now turn naturally to the study of the mechanism of heredity. But this is a thing which is not open to direct observation, and the best that we can do is to construct a theory of heredity from such facts as we can observe. Such an inquiry is not only of importance to the students of pure science desirous of fully comprehending the origin of organic individuals, but is equally important to the practical breeder of domestic animals and plants wishing to maintain his stock at the highest value and to the practical philanthropist anxious for the perfection of the human species. The medical practitioner is also constantly face to face with questions of heredity, and the value of his advice in such cases will depend on whether or not they are founded upon a sound theory.

We often hear it stated that theory is one thing and practical experience is another. But all experience goes for nothing, if it does not lead to the formation of correct theories. It is the comprehension of theories that makes the difference between the skilled engineer who plans great bridges or powerful machines and the day laborer who mixes the mortar or hammers the iron; and when we realize the immeasurably greater complexity of the simplest organism over the most intricate mechanism of human construction, we can see how much more important a correct theory is in the effort to improve the races of higher animals and plants.

Requirements of a Theory of Heredity.—A theory of heredity is not required to explain the multiplication of organisms, but it must explain the relations of form between parent and offspring. These relations are expressed by the terms heredity and variation. We have seen how intimately connected variation and heredity are with one another, that they are in fact but the opposite phases of the same phenomena. A theory of heredity, therefore, must be also a theory of variation. But heredity and variation are both the result of the process of development and to explain them one must first explain development. The embryologist has explained the development of any structure sufficiently for his purpose when he has shown how this structure is the necessary result of a certain observed order of cell division, growth, and differentiation. For him the cell is the fundamental structure, and unequal growth, fusion, and fission of tissues are fundamental processes. For the student of heredity, however, it is necessary to go deeper and to try to discover the fundamental structure of the cell itself and to investigate the minute processes of cell division to determine, if possible, the causes that result in unequal growth and differentiation and thus control the development of the organism as a whole. A theory of heredity and variation, therefore, must be also a theory of development in the deepest sense. It follows from this that our theory, to be valid, must be capable of explaining all of the phases of development, including direct development, both sexual and asexual, metamorphosis, sexual dimorphism, other forms of polymorphism, regeneration of lost parts, and the alternation of generations. It will readily be seen, moreover, that such a theory necessarily involves some conception as to the essential structure of living matter.

The Fundamental Conceptions in Theories of Heredity.

Theories of heredity are nearly as numerous as the thinkers upon this subject. It would be very interesting to take up the views of each author in their historical order and to study the effects of previous observations and deductions upon them and their influence in turn upon the opinions that have been expressed later. If we should do this, we should find, however, that in spite of multiplicity of distinct theories, there is a comparatively small number of fundamental conceptions, one or more of which form the basis of each of the theories. We should find, also, that as the knowledge of anatomy, physiology, and embryology has advanced with the invention of more precise methods of research, the theories of heredity have come to depend more and more upon observed facts and less upon *a priori* principles. The result, however, has not been, as one might suppose, to simplify the theories, but rather to make them more complex. In fact, the more we know about heredity the more wonderful the phenomena appear and the more difficult becomes their explanation. To discuss all of these theories in their historical relations would unduly extend this article, and we shall have to content ourselves with an examination of the fundamental conceptions underlying them. These conceptions may be enumerated as follows: (1) animism, (2) physiological units, (3) heredity as a form of motion or as memory, (4) pangenesis, (5) idioplasm as distinguished from trophoplasm, (6) germ plasm as distinguished from somatic idioplasm, (7) continuity of germ plasm, (8) evolution, and (9) epigenesis. We shall take these up one by one, judge them in the light of the facts and from such as seem valid try to build up for ourselves a theory of heredity and development.

Animism.—The earliest views as to the causes of the phenomena of heredity may generally be classed under the head of animism. Most of them agree that the character of the material body is controlled by a spiritual body, the soul, or *animus*, which enters the material body at its conception.

Van Helmont and other writers of the middle ages have supposed that there is an actual transfer of spiritual substance not only through the sexual products but also through the milk of the mother or nurse. Indeed, it is said that such is the belief of many persons at the present time.

Others believe that the thoughts of the mother may affect the mental and physical character of the developing child. Birth marks, supposed cases of telegony, and the like, have been explained in this way. When Jacob set up the rods before the cattle he was acting upon this theory.

The animistic theories have the great advantage of simplicity, but they are utterly without scientific basis and, therefore, must be rejected.

Physiological Units.—In direct contrast with the animistic theories of heredity are the materialistic theories,—those that postulate a *physical basis* for heredity. One of the earliest attempts to ascribe a physical basis to heredity is that of Buffon. According to his conception, organic matter is essentially different from inorganic matter and the two are equally indestructible. *Organic molecules* are to be found everywhere and are capable of uniting to form an organism wherever they come together under certain conditions, hence his theory of spontaneous generation.

When Herbert Spencer wrote his "Principles of Biology," it was known that there is no chemical element found in living bodies that is not found also in inorganic substances and that Buffon's idea of organic molecules was without foundation. Spencer, however, made a very decided step forward when he revived the idea in another form.

If living material be separated into its constituent chemical molecules it ceases to be alive. Life is not a property of any ordinary chemical substance. Still you can divide living material, and even particles of a cell will retain for a time at least their vital properties.

Therefore living matter must be made up of units, much smaller than a cell, and much larger and more complex than a chemical molecule. Spencer calls these ultimate particles of living matter *physiological units*. He regards them as possessing the physical basis of life and as being the bearers of the hereditary qualities.

Haeckel accepts Spencer's theory but refuses to believe that the physiological unit, which he calls a *plastidule*, is anything more than a very complex chemical molecule.

Weismann agrees with Spencer regarding protoplasm as made up of units which are of a higher order than a molecule. He calls them *biophors* (the life bearers) and attributes to them somewhat different properties from those that Spencer supposes his physiological units to possess. The biophors carry with them only the elementary qualities of the organism. The true bearers of heredity are higher units, the *determinants*, which are themselves composed of biophors having certain properties and arranged in a definite order.

Nägeli takes a somewhat similar position. According to him, when proteids are formed in a watery solution they are precipitated in minute crystal-like masses that he calls *micellæ*, but they do not form part of the living material until they are united into larger masses which are drawn out into threads. These threads of micellæ are the ultimate particle of living matter and the bearers of the hereditary qualities.

Darwin, who was one of the first to give to the world a definite theory of heredity, made no attempt to discover the ultimate structure of living matter. He believed, however, in a physical basis of heredity, which he thought could be found in minute bud-like bodies, *gemmules*, given off from the various cells of the body. He was followed by Brooks and to a certain extent by Galton, and de Vries attempted to improve his theory by supposing the gemmules, which he named *pangenes*, not to be produced by the cell, but by the nucleus.

In all of these theories the bodies that are supposed to carry the hereditary characteristics are too minute for observation, and therefore it is equally impossible to prove or disprove their existence. In fact, these theories are not intended to be anything more than working hypotheses. The main question with us is, not whether one or the other of these hypotheses is correct, but whether the general principle that underlies them all should be accepted or rejected. It seems to the writer that no one who has carefully studied the phenomena of fertilization and development, and has considered the results of heredity, can fail to believe that it has a physical basis and that this must consist of units that are much less than the cell and much more complex than the molecule.

Heredity as a Form of Motion.—The earliest theory of heredity that is sufficiently well founded to deserve serious consideration is that of Herbert Spencer. But even this theory is conceived to a great extent independently of any facts, and is therefore largely metaphysical and to be understood only in connection with Spencer's philosophical system of cosmic evolution.

He compares the organism to a crystal. The molecules which go to make up a crystal are originally all exactly alike, but in the crystal they do not all have the same relative position nor the same morphological value. One will form part of an angle, another part of a face, etc. In a similar way the organism is made up of physiological units that are all alike but differ in position. The molecules of the crystal on the one hand, and the physiological units of the organism on the other, have a certain *polarity* that causes them to unite whenever possible into aggregates having a certain definite form. If a crystal be mutilated and then placed in a saturated solution of the same salt, deposition of new material will take place in such a way as to restore the crystal to its original shape. Spencer regards the regeneration of lost parts in organisms as an exactly analogous process.

The form alike of the crystal and of the organism is due to interaction of internal and external forces. But the organism differs from the crystal in being much more

sensitive to external conditions; it is due to them that variations occur. When a permanent variation is produced the polarity of the physiological units has been changed. But any force affecting a part affects the whole and, therefore, the polarity of all the physiological units in the body will be altered, including those of the germ cells. Consequently when the physiological units of the germ grow and multiply to form a new organism, they will tend to arrange themselves, not in the form that the parent had originally, but in the form that it acquired as the results of the action of external conditions. In this way all characteristics, whether congenital or acquired, tend to be inherited. According to this view heredity may be regarded as a form of motion or energy that is propagated from all parts of the body to the germ cells.

The famous botanist, Nägeli, spent the latter years of his life in working out a very complete theory of heredity that in many of its essential features closely resembles Spencer's. The threads of micellæ that, according to Nägeli, constitute the active living material are arranged in bundles which are continuous throughout the body and into the germ cells. Each thread is the seat of one of the fundamental characters of the organism, and all of the different kinds of threads necessary to make a complete organism are present in each bundle. From time to time new threads may arise, causing congenital variations in a certain definite direction. External conditions affect the micellar threads, and their reactions lead to adaptive modifications. These morphogenic stimuli set up by external conditions may be transmitted along the threads to the germ cells with the result that the adaptive modifications of the parent may be inherited by the offspring.

If a stone be dropped into the edge of a pond, the surface of the pond at that point is momentarily altered. This disturbance sets up a wave motion in adjacent particles and these set other particles in motion and so on until the wave finally reaches the farthest shore. Spencer and Nägeli think that in the same way anything that affects the physiological units or micellæ in one part of the organism sets up a sort of wave motion that extends throughout the body and into the germ cells affecting their physiological units so that they may give rise to similar modifications in the offspring. Nägeli makes an improvement on Spencer's theory in furnishing a path for heredity along the micellar threads.

Several other authors have attempted to construct similar theories, but none of them presents any advantage over the ones that have been outlined.

Haeckel's theory is intimately connected with the monistic system of philosophy and is almost entirely metaphysical. The cycle of life from egg to egg is, according to Haeckel, a great wave motion. As each individual gives rise to numerous offspring, this wave motion becomes branched with the act of generation. This branched wave motion is called *perigenesis*—and the *plastidules* of which the living material is composed have a similar wave motion, or perigenesis. Heredity is due to the propagation of this wave motion. Haeckel sums up his theory by saying that heredity is the memory of the plastidules; variability, their power of perception.

Orr has made rather an elaborate attempt to show that heredity is a phenomenon akin to habit. The protoplasm of the parent acquires the habit of growing in a certain way, and when a small piece of this protoplasm is separated to form a child it retains its previously acquired habits, with the result that the child grows in the same way that its parent did. Cope also favored a theory following somewhat these same lines.

The only evidence of importance in favor of these theories is the fact that in certain tissues of animals and plants the cells are found to be connected by minute protoplasmic threads. This line of evidence has been gathered together recently (1898) by O. Hertwig, who calls attention also to the interesting experiments of Pfeffer, which show that in one case at least these protoplasmic filaments may transmit a formative impulse. A

vegetable cell deprived of both its nucleus and cellulose wall will not regenerate either, but if the nucleus be present a new cell wall may be formed. Pfeffer prepared cells of the protonema of a moss in such a way that an isolated mass of protoplasm without a nucleus remained connected to its neighboring nucleated cell by the fine protoplasmic filaments traversing the cell wall. In such a case a new cell wall was formed around the protoplasm. But if both cells were deprived of nuclei the cell wall was not regenerated.

On the other hand, there are certainly in the bodies of both animals and plants cells that have no such connections, and a general continuity of protoplasm has not been demonstrated in any organism except in certain algae and in the earliest stages of cleavage in the eggs of some animals. We cannot tell, of course, what future experiments may bring forth, but there is no evidence at present that any formative impulse may pass from one cell through a series of cells to a distant one, as would be required by the dynamic theories of heredity.

The objection to these theories that occurs to one at once is their fanciful character and lack of any really substantial basis of fact. Their real motive is to account for the supposed inheritance of acquired characters. If any one of these theories is true, then the inheritance of acquired characters should be a matter of every-day occurrence. It is impossible to prove that acquired characters are never inherited and it is therefore impossible to disprove any such theory. But the ablest advocates of the doctrine of the inheritance of acquired characters are admitting now that such inheritance is not common, and, therefore, such a theory cannot be a complete explanation of heredity, but must represent at most only a small factor.

We may conclude, then, that the idea that heredity is a form of motion or something akin to memory cannot be accepted until more evidence in its favor is presented, and such evidence does not seem to be forthcoming.

Pangeneses.—Four years after Spencer published his "Principles of Biology," Darwin gave to the world his provisional hypothesis of "Pangeneses," as the concluding chapters in his book on the "Descent of Man."

The fundamental conception in this hypothesis had been expressed about four hundred years before Christ by the Greek philosopher Democritus when he said that the seed of animals is elaborated by contributions from all parts of the body; and Buffon likewise had supposed that the different parts of the offspring are made up of organic molecules derived from corresponding parts of the parents. But the influence that this conception has had on scientific thought is due to the brilliant manner of its presentation by Darwin.

Darwin supposed that the contributions from the various parts of the body are in the form of *gemmules*, little buds given off from each cell in the body. The gemmules circulate in the blood and are finally collected in the sexual products. When the egg develops each gemmule may give rise to cells like the one from which it was derived. Thus by a simple and perfectly intelligible process Darwin explains the inheritance by the child of the various characteristics of the parent, both congenital and acquired. All of the gemmules in the egg are not supposed to develop, but some may be passed on to subsequent generations. This is always the case with the gemmules representing the sexual characters. Individuals of one sex always contain the gemmules of the other in a latent condition. All cases of reversion are supposed to be due to the development of such latent gemmules. Other forms of variation are explained as due to the rearrangement of the gemmules in the egg, or else as due to the direct action of the environment, or the effects of use and disuse upon the cells of the parent which are transmitted by the gemmules given off from them.

The central fact upon which Darwin's theory is based is the supposed inheritance of acquired characters, but it explains equally well the inheritance of congenital variations, reversion, particulate inheritance, alternation of generation, etc. It is therefore a very complete theory of heredity.

As early as 1872, however, Galton was led to doubt Darwin's theory. He urged his objections in the first place on *a priori* grounds. He did not believe that acquired characters are generally inherited. The gemmules, he said, are purely imaginary, and therefore their existence is an unwarranted assumption. But, waiving this last objection, another and more serious one arises. If we suppose that every cell is continually giving off gemmules, the number present in the organism must be enormous; and, if every cell of the offspring is represented by a gemmule in the germ, we see that if a spermatozoon is to contain not only these gemmules, but also a large number of latent ones, in order that so many may lodge in so small a space, they must be excessively minute.

In the second place, Galton tested the question experimentally. He took silver-gray rabbits, which generally breed true, and into eighteen of these he transfused blood from rabbits of other breeds. He reasoned that, if gemmules be given off, as Darwin supposed, the blood must contain a large number, and, if blood of one breed is transfused into the body of another, the offspring of the latter should show some traces of characters of the former. Eighty-six young were reared from the individuals experimented upon, and none of them showed any trace of foreign blood.

He concluded, therefore, that pangeneses pure and simple is an incorrect hypothesis. He was willing to admit, however, that acquired characters might rarely be inherited and that this might be explained by the occasional giving off of germs by cells.

In 1876 Brooks outlined a theory of heredity which was very fully developed in his book on "Heredity," in 1883. This theory is a modification of Darwin's theory of pangeneses changed to meet the objections of Galton and others. According to Brooks, the phenomena of heredity in the strict sense are due to the *continuity of the germ cells*, a principle that will be discussed later, while variability is explained by pangeneses. Brooks supposes the germ cells to contain gemmules representing all parts of the body. Most of these gemmules are derived from more or less remote ancestors, having been passed on in a latent condition from generation to generation. New gemmules are not being given off all the time by cells of the body, but are produced only by cells which for the time being are subjected to unfavorable conditions. The new gemmules may circulate throughout the body, but in the male the sperm cells constitute a special apparatus for the collection and storing of new gemmules. When fecundation takes place the new gemmules unite with the corresponding ones in the egg and hybrid gemmules are produced which *like any other hybrids* are variable. This causes variability in parts of the offspring which correspond to those subjected to unfavorable conditions in the parent, especially in the father. According to this view, the mother is the conservative element, the father the progressive, or variable element in heredity. External conditions affecting the parent cause variability in the offspring, but not in any particular direction. Acquired characters are not inherited. Brooks brings a strong array of facts and much skill in argument to the support of his theory, but, nevertheless, it is far from convincing. The gemmules of Brooks are just as much products of the imagination as Darwin's, and none of the investigations of cell structure or of cell function has revealed any process analogous to the formation of gemmules.

To sum up, the theory of pangeneses presented in various forms by Darwin and Brooks supposes the germ to be made up of material particles derived from all parts of the parents or more remote ancestors and able by developing to form corresponding parts of the offspring. This theory agrees with the dynamic or memory theories in supposing that the characters of the offspring depend on the character of certain physical substances in the germ, and that the germinal characters in turn are influenced directly by the corresponding parts of the parents. The theories differ in the method by which this influence is supposed to be exerted. According to the

dynamic theories homologous parts of the parent and offspring are alike because the germinal rudiments of the parts of the offspring have been subjected to the influence of some sort of formative energy radiating from homologous parts of the parent. According to the theory of pangeneses, homologous parts of the parent and offspring are alike because they are of the same substance (II., Fig. 2607). But these theories are found to be equally unsatisfactory when tested by the light of recent knowledge of the history of the germ cells.

Idioplasm.—The theory of epigenesis is intermediate between the idea of heredity as a form of energy and a third fundamental conception,—*continuity* of the physical basis of heredity. The doctrine of continuity depends upon observations of the structure and history of the germ cells, and involves two other fundamental conceptions in regard to the relations of the parts of the cell. These are the doctrines of *idioplasm* and of *germ plasm*. We owe the first of these ideas to Nägeli. He regards protoplasm as composed of two substances. Both of these consist of proteids in the form of minute rounded micellæ and of water. In one of these substances, the "Nährplasma" or trophoplasm, the micellæ are scattered through the water without any special arrangement. In the other substance, to which he gave the name *idioplasm*, the micellæ, on the contrary, have a very definite arrangement into threads which in turn are united into bundles.

The idioplasm is the true living substance and all of the characters of the organism are due to its activities. The trophoplasm, on the other hand, is not really alive, but is the nutritive material upon which the idioplasm draws in order to grow and to make good its waste. The threads of micellæ have been mentioned before as being, according to Nägeli, the bearers and conductors of hereditary qualities. These threads constitute the idioplasm.

Weismann adopts Nägeli's conception of the idioplasm with some important modifications. He agrees with De Vries in holding that Nägeli's view that the idioplasm forms a connected network throughout the organism is untenable. According to Weismann, the idioplasm is to be looked for only in the nuclei of the cells. It is in the nucleus that new living material is constructed, and it is from the nucleus that it migrates into the cytoplasm where it is used up in the course of its functional activities,—such as secretion, contraction, and the like. The formation of new material takes place in the nucleus, the functional activities of the cell take place in the cytoplasm; or, in other words, the nucleus is the seat of the anabolic processes, while the cytoplasm is the seat of the katabolic processes. According to this view, then, the cytoplasm is actively alive and not merely a mass of nutritive material, but its character is due to the stamp impressed upon it by the idioplasm within the nucleus. There is considerable evidence in favor of the view that such a division of labor between nucleus and cytoplasm really exists, as will be seen later.

Germ Plasm as Distinguished from Somatic Idioplasm.—Weismann goes a step further and divides idioplasm into two kinds,—somatic idioplasm and germinal idioplasm, or *germ plasm*. It follows as a matter of course that the idioplasm of the germ cells must be capable of bearing the heredity qualities of the organism. It is idioplasm of this kind that Weismann calls germ plasm. He thinks that the somatic cells do not contain germ plasm as a rule, but each cell contains only a certain kind of idioplasm which constituted only a small part of the original germ plasm. Thus muscle cells contain only muscle idioplasm, liver cells only liver idioplasm, ganglion cells only nerve idioplasm, etc. It is differentiated idioplasm of this sort that he calls *somatic idioplasm*.

Many critics of Weismann refuse to accept these distinctions. They say that there is no evidence that there is any real difference between germ plasm and somatic idioplasm. We shall be better able to judge of the merits of this controversy later on. In the mean time we may employ germ plasm as a convenient term to desig-

nate the idioplasm of germ cells without implying anything in regard to the somatic idioplasm. Minot goes still further and declares that the whole idea of idioplasm is wrong. That we have no right to say that any part of the cell is more essential to its life than another, that we must regard the life of the cell as the total effect of everything that it contains, whether streaming protoplasm, food particles, products of excretion, or what not, and that the form and functions of the cell depend upon all of these. Minot calls this the theory of panplasm.

In view of these opinions and others that are to follow, it will be interesting at this point to glance at the evidence in favor of the theory that the nucleus is the centre of control for the activities of the cell, and especially of the germ cell.

The Location of the Idioplasm in the Nucleus.—The theory that a part of the protoplasm is differentiated as an idioplasm controlling the destinies of the cell, and that this idioplasm is situated in the nucleus—more especially in the chromatin of the nucleus—rests upon three principal arguments.

In the first place a study of the phenomena of heredity shows that the correlation between parent and offspring is practically equal for both parents (see Table II.). Therefore, if the physical bases of heredity be an idioplasm, it must be contributed to the fertilized ovum in equal proportion by the two parents. Now observations show that the chromatin of the fertilized egg is derived in exactly equal proportions from the two parents, and, moreover, the chromatin is the *only* part that is equally of male and female origin. It was supposed at one time that the centrosomes of the first cleavage spindle (see *Segmentation of the Ovum*) are derived from the centrosomes of both the male and female germ cells. But it has been pretty thoroughly demonstrated in a large number of cases that the centrosome of the ovum disappears at the time of the formation of the female pronucleus (see *Ovum*) and that the centrosomes of the first cleavage spindle are either derived from the spermatozoa only or else arise *de novo*, in the cytoplasm. The centrosome, therefore, cannot be the bearer of the hereditary characteristics. Therefore, if present, the idioplasm must be looked for in the chromatinic element of the nucleus. The evidence upon which this argument is based has been discussed in the article *Chromosome*. (See also *Reduction-division, Ovum, Spermatozoa, and Impregnation*.)

Secondly, it is known that the correlation between homologous parts of parent and offspring is approximately equal for all parts of the body in which the heritage is blended. From this it is evident that physical basis of the hereditary characteristics must be distributed equally from both parents to all parts of the body of the offspring. Now we know that all cells of the body are derived by fission from one single cell, the fertilized ovum. Further, during the first division of the ovum the chromosomes are divided in such a way that the two daughter cells receive chromatin of both male and female origin in exactly the same proportion as found in the fertilized egg; and in each subsequent cell division the chromatin is distributed equally between the daughter cells. Therefore we may infer that under ordinary circumstances the chromatin of every cell in the body is equally of maternal and paternal origin,—provided that it can be shown that the chromosomes maintain their individuality during the so-called resting stage between two cell divisions. It is well known that there is no appearance of such individuality in most resting nuclei. Nevertheless, as the reader may see by reference to the article *Chromosome*, there is a considerable body of evidence to show that this is only an apparent loss of individuality, and that the chromosomes formed preparatory to division are essentially the same as those present at the end of the previous fission, only grown larger.

Historically, then, the chromatin fulfils all the requirements of the supposed idioplasm. It remains now only to examine the third argument, that the chromatin and the nucleus, which contains it, have a controlling effect more

than other parts upon the activities of the cell, especially upon the formation of structures.

As early as 1877 Brandt showed that fragments of a protozoan, if lacking a nucleus, would die quickly, while portions containing nuclear material would heal their wounds and live. These observations have been confirmed and extended by Nussbaum, Gruber, Verworn, Lillie, and others. They find that enucleated fragments of various protozoa may live under favorable conditions for a number of days, or even weeks, and "will perform perfectly normal movements, show the same susceptibility to stimulus, and have the same power of engulfing food as nucleated fragments." "They lack, however, the power of digestion, secretion, and regeneration." In like manner, if a nerve fibre be cut in two the portion connected with the cell containing a nucleus lives and grows, while the distal portion dies and disintegrates. Verworn has found, however, that an isolated nucleus is equally incapable of regeneration, and Lillie has shown that in *Stentor* a fragment containing a nucleus cannot regenerate its lost parts if the cytoplasm is reduced beyond a certain amount—one-twenty-seventh of the original volume in this case. From this it is evident that the life of the cell depends upon the combined activities of the nucleus and the cytoplasm. Perhaps regeneration is impossible because the means of engulfing food has been destroyed. It does not disprove the theory that the nucleus is the nutritive and dynamic centre of the normal cell, a theory that is supported by several other lines of evidence.

The position of the nucleus indicates that it plays an especially important part in the economy of the cell. For example, Haberlandt (1877) showed that in plants the nucleus lies nearest that part of the cell which is undergoing most rapid growth, as in the formation of root hairs, thickening of cell walls, etc.; and Korschelt (1889) has called attention to the fact that in animal cells the nucleus lies on the side nearest the source of food supply. Changes in the form of the nucleus indicate the same thing. In both animals and plants it has been seen that in cells actively forming new material the nucleus becomes enlarged, and sometimes branching. Moreover, an actual transfer of material from the nucleus to the cytoplasm has been observed. Hodge found that the nuclei of ganglion cells shrink during functional activity. In cell division all parts of the nucleus except the chromosomes and sometimes parts of the chromatin disappear in the cytoplasm. They may be lost as products of metabolism, but it is probable that part of them remain as permanent structures in the cytoplasm. Upon the formation of a new nucleus after division the nuclear membrane, linin network, and nucleoli are regenerated from the chromatin.

Finally, we have the interesting experiments of Boveri, which, while unfortunately not perfectly conclusive, tend to show the great importance of the nucleus in heredity. He mixed fragments of eggs of one species of sea urchin with spermatozoa of another and obtained dwarf larvae, presumably by the union of spermatozoa with enucleated egg fragments, and these larvae possessed purely paternal characteristics.

In the cells of higher plants, there are small protoplasmic bodies called *plastids*, and some of these are the chlorophyll bodies and give the color to the plant. Plastids multiply by fission. They are present in the egg cell and are passed on to the daughter cells in cell division. But there are no plastids in the pollen tube so that these structures if they are, as they appear to be, permanent cell organs, are of purely maternal origin. Nevertheless, hybrid plants may exhibit more or less of the color of the male parent, showing that the male component of the nucleus influences the character of these apparently independent plastids.

It is well known that the character of the grain of Indian corn is modified by the kind of pollen that falls upon the stigma. The part affected seems to be of purely maternal origin and this phenomenon, known as *xenia*, was for a long time an unsolved puzzle. Webber has re-

cently suggested that its explanation is to be found in the discoveries of Guignard and Nawaschin, that in the lily and *Fritillaria* there is a double fertilization. While one nucleus from the pollen tube unites with the nucleus of the egg cell, a second one from the same source unites with the nucleus of a cell that by its division is to give rise to the main part of the seed. If the same process can be shown to occur in maize, then *xenia* is explained and the important formative influence of the nucleus is demonstrated, for there is no evidence that any other structure passes from the male plant into the embryo sac.

Continuity.—We are now prepared to consider one of the most important of the fundamental conceptions found in the more recent theories of heredity. The idea is important because it is founded upon the facts of observation which have been outlined in the preceding sections of this article. This is the theory of continuity. Like the theory of pangenesis, it attempts to discover a physical basis for heredity in the germ cells. But it differs from that theory in the view taken as to the history of the bearers of the hereditary qualities, and in regard to the relation of the germ cells to the somatic cells of the parent.

According to the theory of pangenesis, the germ gives rise to an individual like the parent, because the germ is composed of material particles, called gemmules, derived from every part of the parent and capable of reproducing the parts from which they arose (II., Fig. 2607).

In strong contrast with pangenesis is the theory of continuity. According to this theory, the germ gives rise to an individual like the parent, not because any part of the germ is derived from the parent, but because this germ which produces the offspring is a part of the *same* germ that gave rise to the parent (III., Fig. 2607). An egg or a spermatozoon is a cell, and like every other cell is derived from a pre-existing cell by division. If we trace the history of the germ cells in any individual, we find that they have arisen by a succession of cell divisions from the same fertilized eggs that produced the whole body (see I., Fig. 2607). They are the lineal descendants of that egg, and having undergone little or no differentiation they share its qualities. The two germ cells that united to form that egg have had a similar history, and so on back for all generations, and in every case this history is shared by the nucleus and more especially by the chromatin. If we regard the chromatin as the seat of germ plasm, then we have good reason to believe that the germ plasm in every germ cell to-day has been derived by growth and an unbroken series of divisions from germ plasm that existed when germ plasm was first differentiated in organisms living so long ago that even the rocks can tell nothing of their history. According to this view, the successive generations in a family may be compared to a string of pearls in which the cord that holds them can grow at one end and by an annular enlargement and division produce a new pearl one after another. Each pearl would represent the somatic cells (body cells) of an individual and the cord would represent the germ plasm.

Lloyd Morgan has expressed the difference between pangenesis and the continuity of the germ plasm very graphically by saying that by pangenesis the hen produces the egg which in turn gives rise to a new hen, while by continuity of the germ plasm the hen does not produce the egg but the egg produces the hen.

The first to recognize that the germ cells differ from the body cells and are continuous in descent from generation to generation, and that this may serve to explain heredity was Sir Richard Owen, who published this opinion in 1849. Afterward, however, he denied that such an explanation is possible.

The next one to express a similar opinion was Francis Galton, writing in 1872 and 1876. He gave the name "stirp" to the sum total of all hereditary principles, or germs, in the germ cells and, according to his theory, heredity is explained by the multiplication and transmission of this stirp.

Brooks outlined his theory of heredity in 1876 and pub-

lished it in full in 1883. He says: "The ovum is a cell which has gradually acquired a complicated organization and which contains material particles of some kind to correspond to each of the hereditary characteristics of the species. The ovum, like other cells, is able to reproduce its like, and it not only gives rise during its devel-

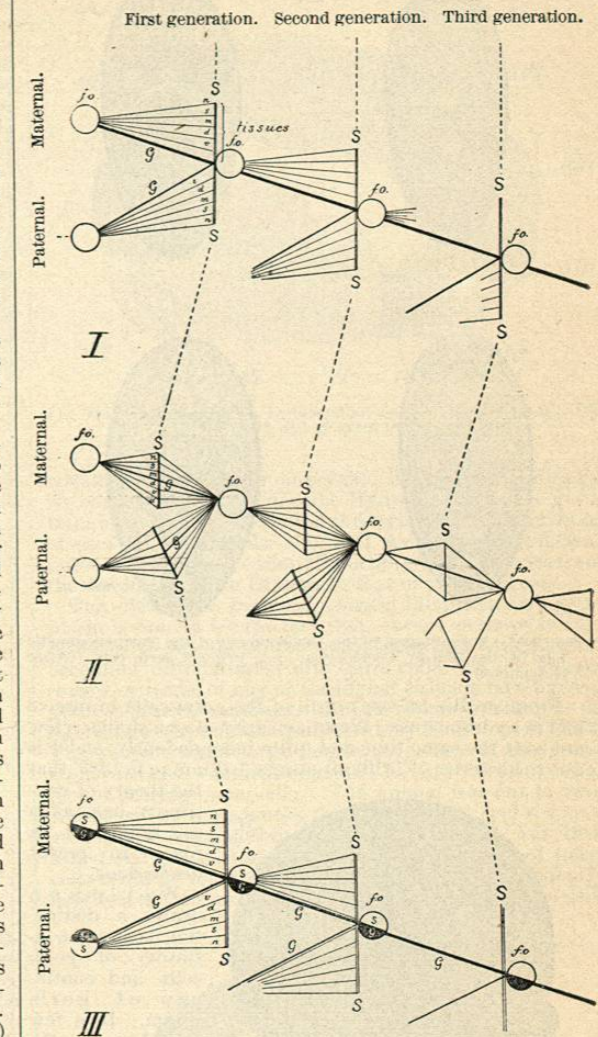


Fig. 2607.—Diagram illustrating, I. Normal Histogenesis; II. Theory of Pangenesis; III. Theory of Continuity of the Germ Plasm. The fertilized ovum (f.o.) by the process of cell division gives rise to the adult body, or soma (S), composed of somatic cells (n, s, m, d, v) constituting the nervous, secretory, muscular, digestive, and other tissues, besides the germ cells (G) of the reproductive organs. I. Histogenesis, showing the successive rise, G, and union (f.o.) of the maternal and paternal germ cells by direct histogenesis. II. Pangenesis, showing the tissues of the body, S, contributory to the germ cells, G, so that each f.o. is composed of elements, gemmules, from both the somatic and germ cells. III. Continuity of the germ-plasm, showing the division of the idioplasm, f.o., of the egg into somatoplasm, S, from which the body cells arise, and germ plasm, G, which passes directly to the germ cells establishing a direct continuity.

opment to the divergent cells of the organism, but also to cells like itself. The ovarian ova of the offspring are these latter cells or their direct unmodified descendants." The child will therefore be like the mother except in so far as it is affected by new gemmules introduced chiefly in the process of fertilization. Here we have the theory of the continuity of the germ cells stated very clearly,