but pangenesis is added to it to explain the origin of congenital variations.

The continuity of germ cells had been recognized by Jäger and Nussbaum in 1879 and 1880, but this did not lead in either case to any important generalizations.

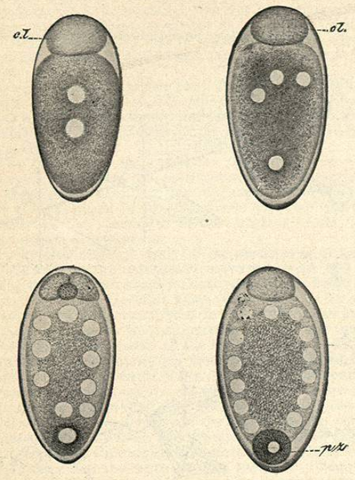

FIG. 2608.—Early Stages in the Development of the Parthenogenetic Egg of the Gall-fly, Cecidomyia. *p.z*, Primary germ cell. (After Metschnikoff.)

From studies on the origin of the germ cells in insects and in hydromedusæ, Weismann arrived at a similar view at about the same time and quite independently, and it is due to his series of brilliant essays, beginning in 1883, that the theory of continuity has taken so important a place in recent discussions.

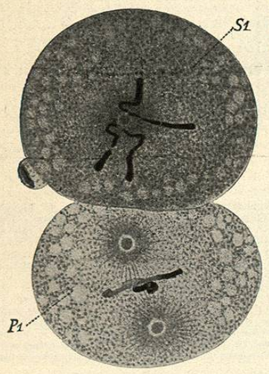

FIG. 2609.—Two-cell Stage of *Ascaris megalocephala* var. *univalens*. *S1*, First somatic cell; *P1*, first cell of the germ tract. Highly magnified. (After Boveri.)

Weismann draws a distinction between continuity of germ cells and continuity of germ plasm. In a few organisms, the germ cells are really continuous. In the Diptera (flies) for example the first cleavage of the egg (Fig. 2608) results in the formation of two nuclei, one of which gives rise to the nuclei of all the germ cells of the embryo and to them only, while the other gives rise to the nuclei of all the somatic cells. A remarkable case of continuity of germ cells has been discovered by Boveri in Ascaris. Figs. 2609 to 2615 represent some of the principal stages illustrated in his beautiful memoir. Fig. 2609 shows the egg in the two-cell stage and both cells, *S1* and *P1*, which are apparently alike, are preparing to divide. In Fig. 2610 the division is farther advanced, and a striking difference is noticeable in the mitotic figures. The chromosomes of the cells *A* and *B*, daughter cells of

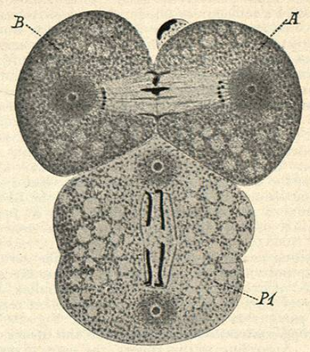

FIG. 2610.—Same. Second Cleavage. *S1* is dividing into *A* and *B*; *P1*, is also in process of division. Note difference in size and number of chromosomes.

S1, are numerous and very small, and in the plane of division there are some dark bodies composed of chromatin, the rejected ends of the chromosomes of *S1*. These will take no further part in the formation of the nucleus and will finally disappear. On the other hand in *P1*, which we may call the first cell of the *germ tract*, using Weismann's terminology, there are only two large chromosomes moving toward each pole to form the daughter nuclei. *A* and *B* are purely somatic cells. Of the daughter cells of *P1*, one is likewise a purely somatic cell, and when it divides the chromosomes undergo the same transformation that has been observed in *S1*. The other daughter cell is *P2*, the second cell of the germ

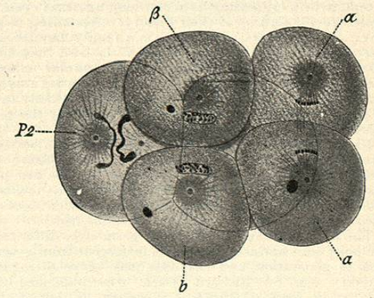

FIG. 2611.—Same. Six-cell Stage. *P2*, Second cell of germ tract. *b*, *β*, Daughter cells of *B*; *a*, *α*, daughter cells of *A*.

tract. This is seen preparing for division in the dorsal view of the six-cell stage, Fig. 2611. The two large chromosomes have been reformed. This cell behaves exactly as *P1* did, giving rise to a somatic cell and to the

third cell of the germ tract, *P3*, Fig. 2612. This cell divides again in the same manner, producing *D* and *P4*, Fig. 2613, and one of the daughter cells of *P4* is *P5*, Fig. 2614, which in turn produces the two priordial germ cells *UGI* and *UGII*, Fig. 2615. Thus the remarkable difference between the nuclei of the germ cells and the somatic cells in this form has enabled Boveri to trace every stage in the genealogy of the germ cells and their nuclei back to the fertilized egg.

In most animals, however, the cells which arise by the cleavage of the ovum appear to be somatic cells, some of which after a greater or less number of divisions give rise to germ cells. In the plants and plant-like animals, such as the Hydroids, we have extreme cases in which there is no trace of recognizable germ cells until we reach the end of a series of several generations of asexually produced individuals. Such being the fact, how are we to explain heredity? There are two possible explanations, according to Weismann. Either the somatic idioplasm in certain cells is reconverted into germ plasm, or else cells in a certain series contain two kinds of idioplasm: their own peculiar somatic idioplasm that controls their activities, and also germ plasm in a latent condition, which is a part of the original germ plasm of the egg. Weissman holds to the latter view. He believes that at the

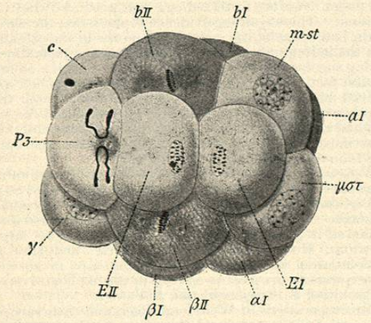

FIG. 2612.—Same. Fifteen-cell Stage. *P3*, Third cell of germ tract.

time of the first cleavage of the egg its germ plasm divides into two similar parts. One of these becomes converted into active somatic idioplasm to form the embryo, the other remains latent and is passed on in this condition to certain cells which become the germ cells for the production of the next generation, as represented schematically at *III.*, in Fig. 2607. In some cases, as in the Hydroids, these germ cells are differentiated, according to Weismann, from ordinary somatic cells. Nevertheless, these cells, like all other cells of the body, have arisen by an unbroken series of cell divisions from the cleavage of the original egg. Therefore, while it is shown that in most cases the germ cells are not really continuous as such, we can suppose that there is perfect continuity of germ plasm. Weismann has invented the name "*germ tract*" to designate the series of cells which forms the line of descent from the egg to the germ cells of the embryo and which may be supposed to contain the germ plasm, for example, *P1* to *P5*, Figs. 2609 to 2615. In the Diptera, Fig. 2608, the germ tract is very short. There is practically none at all, for the primary germ cell is formed at the first cleavage. In Ascaris, as we have seen, it runs through five generations of cells. In the Daphnidæ the germ cells are separated off, likewise, during the early stages of cleavage. In Sagitta this takes place in the gastrula stage. In the Annelids and Molluscs, the germ tract is longer, but may be traced through a relatively small number of very definite cell divisions.

In the vertebrates there is a large number of cell divisions between the cleavage of the egg and the appearance of germ cells in the embryo. Still they appear early,

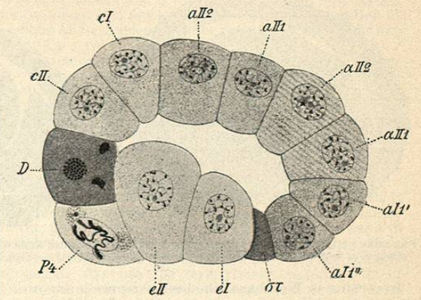

FIG. 2613.—Same. Optical Longitudinal Section of a Blastula. *P4*, Fourth cell of germ tract.

within the first half of embryonic life at most. Finally we come to the plants and the Hydroids where the germ tract is very long, extending through several generations of asexual individuals. Thus if we studied a sufficient number of species we should probably find all grades from the condition of the Diptera to that of the Hydroids.

The distinction between somatic idioplasm and germ plasm is upheld by the fact that, except perhaps in rare cases, cells outside of the germ tracts are incapable of becoming differentiated into germ cells. If the gonads (ovary or testis) of any of the higher animals be removed, germ cells never reappear. In this connection there is an interesting experiment published by F. Braem in 1893. The subject was a large female polychæte of the genus Ophryotrocha with ripe eggs and having thirty-five segments bearing parapodia. The animal was cut in two. At the end of three weeks the anterior part had regenerated seven segments bearing parapodia. It was then killed and cut into serial sections and no trace of germ cells could be found in the regenerated part. Evidently here is a difference between somatic cells and germ cells

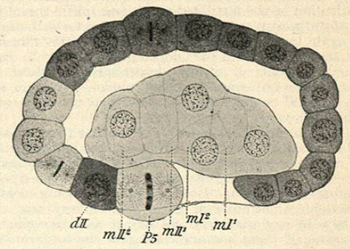

FIG. 2614.—Similar Section of Embryo in the Gastrula Stage. *P5*, Fifth cell of germ tract undergoing division to form the primordial germ cells *UGI* and *UGII*, Fig. 2615. The cell to the left of *dII* is a somatic cell in the same stage of division.

in the powers of regeneration. Of course germ cells might have appeared later, but in the annelids the germ cells are restricted to certain areas of the peritoneum, and it is probable that in this case the wound did not pass

through one of these areas. So it is probable that the germ cells did not receive the same stimulus to growth that affected the other tissues and that therefore no part of the germ tract was included in the regenerated part.

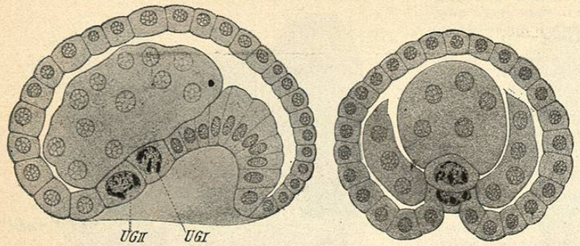

FIG. 2615.—Longitudinal and Transverse Sections of an Older Embryo. *UGI, UGII,* Primordial germ cells beginning to retreat into the interior of the body. (Figs. 2609 to 2615 after Boveri.)

According to Weismann, the best evidence in favor of the existence of distinct germ tracts is afforded by the history of the germ cells of the Hydromedusæ. It is needless to repeat his rather complex argument here, for much better evidence has been furnished recently by Boveri in the history of the germ cells of Ascaris, of which an outline has just been given. The fact of especial importance from Weismann's point of view is the difference between the nuclei of somatic and germ cells; compare, for example, the nuclei of the primordial germ cells, *UGI* and *UGII,* with the nuclei of the somatic cells in Fig. 2615. The origin of this difference may be seen in the two- and four-cell stages, Figs. 2609 and 2610. In the first somatic cell, *S1,* the ends of the large chromosomes are thrown off into the cytoplasm and finally disappear, while the middle part of each chromosome divides transversely into small segments, which behave like ordinary chromosomes in cell division, give rise to small round nuclei, and reappear in subsequent generations of the somatic cells. On the other hand, the large chromosomes of the cells of the germ tract, *P1* to *P5,* behave exactly like the chromosomes of the fertilized egg and give rise to large-lobed nuclei rich in chromatin. "Through this remarkable process," as Wilson remarks, "it comes to pass that in this animal only the germ cells receive the *sum total of the egg chromatin handed down from the parent.* All the *somatic cells contain only a portion of the original germ substance.* The original nuclear constitution of the fertilized egg is transmitted, as if by a law of primogeniture, only to one daughter cell, and by this again to one, and so on; while in the other daughter cells the chromatin in part degenerates, in part is transformed, so that all of the descendants of these side branches receive small reduced nuclei." Wilson adds that it would be difficult to overestimate the importance of this discovery.

All of the evidence goes to show that there is some kind of continuity between the germ cells of one generation and those of the next. The earlier investigators said, "This is a continuity of germ cells." Then came Weismann, who said, "Hold on, you are trying to prove too much. Continuity of germ cells is very rare. Ordinarily the egg gives rise entirely to somatic cells, and then some of these somatic cells give rise to germ cells. But the germ plasm is continuous for it is passed along by the somatic cells of the germ tract until it is finally separated out in the new germ cells. This is proven by the fact that germ cells cannot be produced except by cells of the germ tract." Now come various critics of Weismann and say: "This idea that the cells of the germ tract contain two kinds of idioplasm is a pure assumption that is not warranted by the facts"; and they present a good deal of evidence to show that there is no real difference between somatoplasm and germ plasm. They might add that in the case of the germ tract this distinction is unnecessary, because in every group, not excepting the Hydroids, these cells remain in a more or less undifferentiated embryonic condition. Even if they do form part of the lining of the body cavity or some other organ, the cells which give rise to germ cells have never been highly differentiated as somatic cells. If a muscle cell could by division produce a germ cell, we might be forced to assume that it originally contained two kinds of idioplasm. But there is no reason why the cells which usually produce germ cells should contain anything but germ plasm, for they are not as a rule differentiated in any other direction.

It would seem then that Weismann has been trying to draw too fine distinctions and we must fall back upon the observed facts. These are that the germ cells produced by any individual are derived by growth and fission from the fertilized egg that produced that individual. There is strong evidence to show that the chromatin is the seat of the controlling power in the cell and that the individuality of the chromosomes is maintained during successive mitoses. If this be true, then it is an important fact that the chromosomes in each germ cell are derived by growth and precisely equal fission from the chromosomes of the fertilized egg that produced the individual containing them. I believe that these observations must stand as facts and that they form the only safe foundation for a theory of heredity.

Preformation and Evolution.—The theory of continuity postulates that the child and its parent are alike because both of them have been produced by the same germinal substance. This is a satisfactory explanation of heredity so far as it goes, but it leaves unanswered two large questions, How is variability introduced? and How is differentiation brought about? An attempt to answer these questions involves us at once in the old controversy of Evolution *vs.* Epigenesis (see *Evolution*).

The observations of Wolff, von Baer, and their successors settled this controversy forever so far as the visible phenomena of development are concerned, but the question acquired a new meaning with the advent of scientific speculation on heredity.

Darwin's theory of heredity was the first one in which the theory of preformation was clearly stated. He regarded the egg as made up of gemmules, each one of which is capable of growing and producing one or more cells of a certain definite part of the body. Differentiation is merely the development of the different kinds of gemmules. Congenital variations are due to the transmission from the parent of gemmules having new qualities. Every part of the embryo is represented in the egg by one or more gemmules. The embryo is, therefore, just as much preformed in the egg as it was according to the views of Bonnet a century earlier.

Brooks differs from Darwin in his theory of the origin of the gemmules and of the kind of variability that they produce, but he fully agrees with him as to their function in development. He regards a theory of preformation as the only kind of theory of development that can be defended.

Before Brooks published his theory Wilhelm His, in 1875, presented a theory which has had considerable influence upon subsequent thought. He did not attempt a complete theory of heredity, but aimed to explain only development and differentiation. He rejected the hypothesis of gemmules and relied upon two principles: (1) the principle of differentiation of areas (Princip der organbildenden Keimbezirke) and (2) the principle of unequal growth. He had in mind an egg like that of any of the higher vertebrates, in which the embryo is formed in what is practically a flat blastoderm (see *Area embryonalis*). According to his views the embryo is mapped out at first upon the surface of the egg, each organ and part of organ being represented by a certain area (differentiation of areas). These different areas of the egg differ from one another in density, viscosity, chemical composition, etc., and therefore, when growth begins, it occurs at different times and to different degrees in the different parts. This unequal growth results in the well-known processes of folding, invagination, and the like.

The principle of unequal growth is now universally accepted as one of the fundamental principles of modern embryology. So far as it goes it is undoubtedly a correct theory of development, but we still want to know what causes this inequality. It is due, according to His, to the differentiation of areas; but he does not explain how they arise, and their existence in the unsegmented egg is, to say the least, not self-evident.

Development, according to His, is clearly a process of evolution. In 1888 Roux published the results of some experiments on frogs' eggs that would seem to demonstrate the truth of the principle of differentiation of areas, or germinal localization, as Wilson calls it. By puncturing one blastomere in the two-cell stage he could kill the blastomere operated upon without affecting the other. The result of the operation was that, while the injured blastomere remained inactive, the uninjured one developed into a complete half embryo. Apparently the right and left halves are predetermined in the egg before it divides.

But in the mean time Nägeli had published his idioplasm theory, and various observations upon the functions of the nucleus in fertilization and development had made it seem probable that the idioplasm should be looked for in the chromatin of the nucleus. Roux, therefore, did not look for the predetermination of the two halves of the embryo in the cytoplasm of the egg, as His would have done, but sought for it in the nucleus. In fact, he had five years before these experiments presented the important idea that the chromatin may divide in two ways. It may undergo a *quantitative* division which results in *growth,* by division of the cell into two similar cells, or it may suffer a *qualitative* division, which results in differentiation by the division of the cell into two dissimilar cells. The first cleavage of a frog's egg would be, accordingly, a qualitative division separating the idioplasm of the right side from that of the left.

De Vries in 1889 seemed to help the theory of preformation by supplying a reasonable hypothesis to account for the control of the cell by the nucleus. Although he calls his theory "intracellular pangenesis," it has very little resemblance to Darwin's theory. According to de Vries, the idioplasm has the same composition in all the cells of the body. It is composed of minute particles called *pangenes,* each one of which, like a micellar thread of Nägeli, represents one of the elementary qualities of the organism. The pangenes in the nucleus are in an inactive, or latent, condition and only a few pangenes of each of the many kinds are to be found there. The cytoplasm is made up likewise of pangenes surrounded by a nutritive fluid. But, unlike the nucleus, the cytoplasm contains a great number of pangenes of only a few kinds, and they are all in an active condition. From time to time a pangene in the nucleus will divide. One half remains in the nucleus, the other half migrates into the cytoplasm, where it may undergo repeated divisions. In this way the nucleus controls the cell, while at the same time its idioplasm remains unchanged. Differentiation is brought about by different kinds of pangenes becoming active in different cells.

De Vries argues that various hereditary qualities must be represented by separate material factors, because these qualities may vary independently of one another. It may be supposed that the nucleus controls the cell by liberating some form of energy which acts as a stimulus. But this implies something in the cytoplasm having definite vital properties to receive the stimulus. Or it may be thought that the nucleus secretes a ferment, but this again implies something in the cytoplasm for the ferment to act upon. This something in the cytoplasm requires to be explained, and de Vries concludes that the only tenable hypothesis is that the control of the cell by the nucleus is exercised, not through any power of stimulation nor by means of a ferment, but through the migration of particles of the nucleus into the cytoplasm, of which they then form a part.

We come now to a theory of heredity where the theory of evolution, or preformation, is carried to its ultimate conclusion. This is the theory of Weismann, which has for its basis the hypothesis of the continuity of the germ plasm with the total denial of any inheritance of acquired characters. Superimposed upon this is the idioplasm theory of Nägeli, the theory of qualitative cell-divisions of Roux, and the theory of intracellular migration of pangenes of de Vries.

As has been stated before, heredity pure and simple is explained by Weismann as due solely to the continuity of the germ plasm, some of which is held in reserve in each individual and is passed on to the next generation without receiving any formed material from the somatic idioplasm. We use the term *formed* material, for, of course, the germ plasm receives nutriment just as do all other living parts of the body, and it utilizes this in growth. Weismann rejects entirely both the dynamical and the pangenesis theories of heredity.

According to this view strictly new congenital characters can arise only by the modifying influence of external conditions acting directly upon the germ plasm. External conditions which may affect the germ plasm in this way are food, temperature, and perhaps chemical composition of the surrounding medium. Any change in these factors of the environment may affect the germ plasm within an individual and result in the appearance of a new character in its offspring. The appearance of really new characters, however, is rare. Most variation is brought about by new combinations of old characters, just as any number of new words may be constructed from the twenty-six letters of the alphabet, and innumerable combinations of this kind are produced according to Weismann by sexual reproduction.

The process of fertilization results in the bringing together of two masses of germ plasm having slightly different histories, and, therefore, slightly different qualities. This mingling of two germ plasms is called by Weismann the process of *amphimixis.* In this process the two germ plasms do not fuse, for if they did the child would always have the average character of its parents. As a matter of fact this is a rare occurrence; the individual child is more apt to resemble one parent or a grandparent. We must suppose, therefore, that the germ plasms derived from each parent remain as distinct units in the child, and Weismann calls each one of these units an *id.* If there existed an animal in which sexual reproduction had never taken place its germ plasm would consist of a single *id.* That such units do exist in all organisms now living is shown, according to Weismann, by the presence of a special device for preventing the doubling of the ids that would otherwise occur with each sexual act. This is the reducing division that always precedes fertilization (see *Reduction-division*).

Weismann does not think that the chromosomes are the ids, which of course lie within the nucleus, but he thinks that the small granules of which they are sometimes seen to be composed may be the ids, and therefore he would substitute the word *idant* for chromosome. Each idant of the germ cell he regards as composed of a large number of ancestral germ plasms, or ids, any one of which is capable of directing the entire development of the organism.

Now each id cannot be a homogeneous unit, for we find that a child may resemble one parent in some particular, the other parent in another particular, and perhaps a grandparent in a third, and connected with this there is frequently a lack of correlation so that not only

different parts of the adult but different stages in its ontogeny may be independently variable. As Galton puts it, inheritance is particulate. Each id must therefore contain at least as many smaller units as there are independently variable parts in the organism. Weismann calls these units *determinants*. The id, then, has a certain structure. It is composed of determinants that are arranged in such a definite way in relation to one another that they give rise to an organism of their species. Each determinant may control a single cell or a large number of cells if they all vary together.

But a cell may vary in part and not as a whole. Moreover, the determinant must be supposed to reside in the nucleus and its control over the cell must be accounted for. The determinant must, therefore, be composed of still smaller units which are able to pass out from the nucleus and become a part of the cytoplasm, like the pangenes of de Vries. Weismann points out that we must not regard protoplasm as a chemical substance composed simply of atoms and molecules, for no chemical molecule has the power of assimilation and growth. We have to suppose the living material to be a structural combination of dissimilar molecules. These molecules must be arranged in groups, thus forming units of protoplasm which have the power of assimilation, growth, and multiplication by division, but which if further divided would be separated into their constituent molecules and would then cease to be living matter. These units Weismann calls *biophors*. He insists that their existence is not a mere assumption, but that they must exist. All living material is composed of them, and he asserts that the nucleus exerts its control over the cell body by means of the biophors, which pass through the nuclear membrane and become a part of the cytoplasm, like the pangenes of de Vries. Each determinant, therefore, must be composed of a large number of biophors, and when the part that it controls, its *determinate*, presents a differentiation of parts, it must contain a different kind of biophor for each part.

This, then, is Weismann's conception of the structure of the germ plasm. We can understand now from his point of view how ontogeny would take place. Suppose a species where reproduction had always taken place by means of an unfertilized egg, the simplest possible case, then the germ plasm would consist of a single id containing one determinant for each independently variable quality of the species, and each determinant would contain at least as many biophors as there are distinct parts in its determinate. Now before cleavage begins each determinant divides into two, and one set of determinants forms an id of reserve germ plasm, which is to be handed on to the future offspring; while the other forms the idioplasm for the developing organism. The first stage in development is the rapid growth of one determinant of the active id. This is followed by its division into its constituent biophors, which migrate out of the nucleus into the cytoplasm of the egg and cause it to divide into the first two blastomeres. With the division of the cell, the id and its determinants likewise divide, so that each cell contains an id, but this is no longer an id of germ plasm but an id of somatic idioplasm, for it has been changed by the loss of the determinant that was used up to cause the first division. At least one cell, however, (corresponding to the cell *P1* in Ascaris, Fig. 2609) will contain, besides its own particular id of active idioplasm, also an id of inactive reserve germ plasm. Ontogeny thus proceeds by the orderly division of the determinants and the separation of their biophors. In the course of ontogeny two kinds of cell division will occur. In one the daughter cells will have the same hereditary qualities; in the other they will be unlike. In the first, the division of the id is preceded by the division of each determinant into two; in the second, there is no division of the determinants, but they become separated into two sets, one of which goes to form each new id. Thus at the first cleavage one nucleus may contain all the determinants for the ectoderm and the other all of those for the endoderm, or one may contain all determinants for the right side of the body and the other for the left. When ontogeny is completed the idioplasm of each cell contains but a single determinant, which continues to control the cell by sending fresh biophors into the cytoplasm to replace those that are used up in performing their functions. In addition to this, each cell in the germ tract contains a complete id of reserve germ plasm, which remains inactive or simply grows without influencing the cell which contains it.

Now probably in the history of all living organisms sexual reproduction has occurred during innumerable generations. The germ plasm would therefore consist not of a single id, but of a great many. Each one of these would behave in ontogeny, however, just as we have supposed the single one to act.

Now we can see how sexual reproduction aids variation. When there was but a single id of germ plasm, congenital variations could arise only by the slowly modifying influence of external conditions upon its biophors and determinants; but with sexual reproduction we have brought together a number of ids differing slightly in hereditary qualities and each trying to control the development, the result will bring about variation.

The determinants in the various ids will be related in two ways. Those determinants are homologous that control homologous parts of the body, and homologous determinants may again be either homodynamous or heterodynamous to one another, according as they have the property of impressing the same or a different quality upon the part that they control.

When the homologous determinants of the two parents are homodynamous, the offspring will possess the quality that they control in a greater degree than either parent. When they are heterodynamous there will be a struggle between the determinants and the quality in the offspring will be dependent upon the relative strength or numbers of the two sets. All of the determinants from one parent are not likely to have the same relative strength, and hence it is that the child generally resembles one parent in some peculiarities and the other one in others.

If we accept this theory of the structure of the germ plasm, it is easy to explain all of the phenomena of heredity and development.

Variation in the protozoa is due to the direct effect of the environment and to amphimixis. The metazoa and higher plants inherit their fundamental characters from their protozoan ancestors. New characters have been added to these by direct action of environment upon the germ plasm; but the most usual cause of variation is the formation of new combinations of old characters as a result of amphimixis.

Reversion in hybrids is due to the extrusion of ids of one line of descent in the reducing divisions during the formation of ripe germ cells. In pure races it is due to ids acquiring new strength and thus becoming the more powerful after a latent period.

Sexual dimorphism is due to the doubling of the determinants for the sexual character in each id.

Regeneration of lost parts is produced by special determinants in the germ plasm, and reproduction by fission is due to a higher specialization of the same process.

Budding is explained as the result of a doubling of the ids of germ plasm and the distribution of parts of the reserve germ plasm to the somatic cells from which the buds arise.

Alternation of generations is accounted for by supposing each reproductive cell to contain two kinds of germ plasm, one of which becomes active in each alternate generation.

According to this theory every peculiarity of the organism in every stage of its development is represented by a distinct and definitely located structural element in the germ plasm. Development is an evolution, a becoming visible of pre-existing potentialities.

On its face it is a very satisfactory theory, but we shall find that when tested by experiment it fails in many parts.

Epigenesis.—As was noted at the beginning of the preceding section, if we start with the idea of continuity of idioplasm as the basis for a theory of heredity, we soon find ourselves involved in the question as to whether development and differentiation are due to preformation and a process of evolution or are due to a process of epigenesis. Just as we may take Weismann as the champion of the preformation theory, so may we take Oscar Hertwig as the champion of the more extreme side of the theory of epigenesis. His position is supported to a greater or less degree by de Vries, Driesch, and E. B. Wilson.

Hertwig agrees with Weismann in regarding heredity as being due to a continuity of germinal idioplasm which resides in the nucleus and controls the activities of the cell by migrating out of the nucleus into the cell body and there becoming part of the active cytoplasm. Like Weismann he supposes the idioplasm to be made up of minute structural elements which have the power of assimilation, growth, and reproduction by fission; but he differs from Weismann in regard to their other qualities. He calls these bodies *idioblasts* and they correspond in general to Weismann's biophors, to de Vries's pangenes, and to Nägeli's micellar threads.

According to Weismann, the germ plasm is made up of determinants that represent every part of the body that may vary independently, whether this be made up of one cell or of a group of cells. According to Hertwig, on the other hand, the germ plasm is made up of idioblasts that represent only cell characters. All of the different cellular structures that may occur anywhere in the organism may be represented by separate idioblasts in the germ plasm, but characteristics that depend upon combinations of cells cannot be represented there. The egg and the spermatozoon are cells formed by fission from pre-existing cells, and the fertilized egg is likewise a cell capable by division of giving rise to a colony of cells. An egg may contain elements representing nerve fibre, muscle fibrillæ, and the like, because these structures may occur within a cell; but it cannot contain elements representing a hair or a biceps muscle; for hair and muscle are formed only by the union of many cells, and it is impossible to suppose that characters which can be formed only by the union of many cells may be represented in the structure of a single cell. Nevertheless, Hertwig agrees that the characteristics of the adult depend fundamentally upon the structure of the idioplasm in the fertilized egg from which it springs. He compares the organism to a *state*. If we suppose a community or a state to be composed of the offspring of a single pair, the schools, the markets, the courts of justice, and all departments of the government will be the result of the character of that first man and woman, and yet it would be absurd to suppose that these institutions were present in them in a latent condition. Just as all the characteristics of such a state will be the necessary result of the human nature of the man and woman from which it has descended, so all characteristics of the organism are ultimately due to the cell nature of the fertilized egg from which it has developed. We find Hertwig, therefore, opposing two of Weismann's fundamental conceptions, viz., *preformation* and the *qualitative* division of the idioplasm, and it would be well to make a digression here to test these ideas by the results of experiment.

Let us take up first the facts of normal development. According to Roux's theory of qualitative divisions, which is one of the fundamental conceptions of Weismann's theory, the egg is at first *isotropic*, that is, there is no predelineation of the embryo or of its planes of symmetry in the cytoplasm. But when cleavage begins, the qualitative divisions of the idioplasm have the result that the embryo becomes a mosaic made up of cells having different qualities and capable of giving rise only to certain definite parts of the definitive organism. This is called the mosaic theory of development.

As already pointed out, Roux found evidence for his theory in his experiments on frogs' eggs. Since then other evidence has been produced. Crompton experimenting on the eggs of a marine gasteropod (Ilyanassa) found that isolated blastomeres from embryos in the two-cell or four-cell stage (Fig. 2616), "exhibit a typical partial development; that is, each one develops as if the missing portions of the embryo were present. No regeneration of the missing parts takes place." This bears out what we are led to expect from a study of the normal cleavage of the gasteropods and annelids, two large groups in which the method of cleavage is almost identical. The division of the egg in these groups follows a complex but very definite plan. Wilson found that in Nereis every cell division follows a prescribed order up

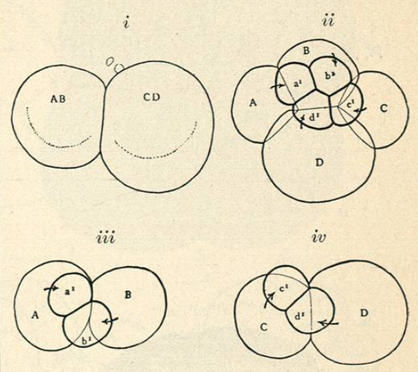

FIG. 2616.—Early Stages in the Development of the Marine Gasteropod, Ilyanassa. *i*, Normal two-cell stage; *ii*., normal eight-cell stage; *iii*., half eight-cell stage developed from the smaller isolated blastomere, *AB*; *iv*., half eight-cell stage developed from the larger isolated blastomere, *CD*. × 112. (After Crampton.)

to the fifty-eight-cell stage. At that stage the chief organs of the body are represented by separate cells. Similar results have been obtained by later investigators working upon the development of other annelids and on molluscs. Conklin has traced the cell lineage in Crepidula to the one hundred and nine-cell stage (Fig. 2617). The cells appear in such definite and similar succession in the various species that each cell has been given a distinctive designation, and the history of each cell division has been traced to the time when the principal organs are outlined. In such a form the embryo is really "a visible mosaic work, not one ideally conceived by a mental projection of the adult characteristics back upon the cleavage stages." There can be no doubt about the truth of these observations, and if they constituted all of the evidence, Roux's theory of qualitative divisions and of the mosaic character of the embryo would be fully verified.

Unfortunately for the theory, however, there is a great mass of evidence to show that these observations must be interpreted differently.

Beginning with the phenomena of normal development, observations of Miss Clapp on toad fish, and of Morgan on other Teleosts and on frogs show that there is no constant relation between the first cleavage plane and any plane of the adult body. Observations of H. V. Wilson on the sea bass, of Jordan on Amphibia, and of E. B. Wilson on Amphioxus show that there may be considerable variation in the process of cleavage and yet normal embryos will result. E. B. Wilson found three types of cleavage in Amphioxus, a radial form, a spiral form, and a bilateral form, with all grades between, and all of these are equally capable of producing normal larvæ.

These cases are enough to prove that the mosaic theory is not universally applicable, and there is experimental evidence that is still more convincing.

Driesch was the first to experiment with segmenting