FERTILIZATION AND HYBRIDIZATION

A Paper

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The essay on "Fertilization and Hybridization" was read in Haarlem in the Dutch language, and appears here in an enlarged form. My conception of the life-processes in the nuclei is chiefly based on the renowned investigations of van Beneden and of Boveri, as well as the most recent researches by Conklin (*Contr. Zool. Lab. Pennsylvania,* XII, 192), Sutton (*Biol. Bull.* IV, Dec., 1902), Eisen, (*Jour. Morphol.* XVII, 1), Errera (*Revue Scientif.* Feb., 1903), and of many others. For the literature I refer to E. B. Wilson, *The Cell in Development and Inheritance,* and V. Häcker, *Praxis und Theorie der Zellen-und Befruchtungslehre.*

My presentation of the processes of fertilization and hybridization is an outcome of the experiments which I have described in the second volume of my *Mutationstheorie* (Leipsic, Veit & Co., 1901-1903. English translation by Open Court Publishing Co., 1909-1910.)

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"Vom Vater hab' ich die Statur,
Des Lebens ernstes Führen,
Vom Mütterchen die Frohnatur
Und Lust zu fabuliren."[1]

In these lines lies the whole problem of heredity and fertilization. What everybody can see, Goethe has voiced clearly and concisely in beautiful, simple words. We have one part from the father, the other from the mother. Or, as it is now usually put, the hereditary characters of the *two parents are combined in the offspring.*

It became the problem of scientific investigation to seek out the cause of this phenomenon. It could not be limited to man. The law mentioned by Goethe[1] must be general, it must be true of the entire plant and animal world, wherever two beings unite for the production of progeny. Furthermore it cannot concern ordinary fertilizations only, but also those abnormal cases in which unlike individuals, belonging to different varieties or species, fertilize each other. The products of such crosses we call hybrids, and for science they possess the great importance that, in them, the manner in which the charactertistics of the parents are combined can be studied more easily and clearly than in the children of a normal union. For the more the parents differ from each other, with the greater certainty must it be possible to determine the share of each *in the characteristics of the offspring.*

[1]Goethe, "Sprüche in Reimen," *Gesammelte Werke,* III, 83, 1871.

Everywhere this law is confirmed, that the child inherits one part of its nature from the father, the other from the mother. The child is, therefore, on the whole, a double being, with twofold qualities, more or less distinctly separated, that may still be traced back to their origin. This *principle of duality,* as we might call it, dominates the entire theory of heredity; it forms the thread that binds together apparently separated cases; it serves as a guidance for the whole investigation.

This investigation occupies two different fields. On the one hand we have experimental research, on the other hand microscopical. Physiology ascertains the relations of the offspring to their parents; it analyzes their characteristics into their individual units, and tries to demonstrate their origin. The history of development discloses to us the corresponding microscopic processes; it looks for the smallest visible bearers of heredity in the cell, and investigates how they are maintained during life, and how, during fertilization, they pass on from father and mother to the offspring.

Few investigators master both provinces; their extent is much too great for that. And especially has the study of hybrids so greatly advanced in recent years, that even here a division of labor will soon be necessary. Both lines of work have therefore developed more or less independently of each other. In both, the main features of the problem begin gradually to arise out of the abundance of individual phenomena. And thereby there is disclosed, one might almost say, beyond all expectation, an agreement in the results of both lines of investigation, which is so great, that almost everywhere the physiological processes are reflected in the microscopically visible changes.

It is true that the final analysis lies yet beyond the limits of our present microscopical vision. Compared with the enormous complexity of the herditary characters of the organisms the anatomical structure of the cells and their nuclei, as it is known to us, is much too simple. The individual traits of father and mother can not yet be found in the cells of the offspring, but the investigations of most recent times indicate clearly that here also the limits of knowledge are being constantly extended.

The double nature of all beings that have sprung into existence through fertilization, is seen in their external appearance, as well as in the finest structure of their nuclei. The principle of duality obtains everywhere, even if, in individual cases, the demonstration of it is yet in its beginnings. But as far as the visible marks can be analyzed and the individual component parts of the nuclei can be traced, so far can the validity of the principle be proven even at present.

Let us consider first the external part, then the internal.

Goethe derived his stature from his father, and not from his mother, and it was not a stature between the two. The sum total of his qualities he had partly from his father, partly from his mother. The illustration explains the rule in a clear manner. In the offspring the characters of the parents are combined. Not always does the child get an even half from each; on the contrary, as everybody knows, it resembles the mother more in some respects, and the father more in others.

It is exactly the same with hybrids. With them a single character is generally derived either from the father or from the mother. The hybrids of white and blue flowers usually bloom blue, those of a hairy or a thorny parent crossed by one without hairs or thorns are usually hairy or thorny. The crossing of a common evening-primrose with a large-flowered species results in a flower of the size of the former. But, if there are two or more points of difference they may be transmitted to the children partly by the one parent and partly by the other, and it is thereby possible in practice to combine the good characters of two varieties into a single race. Thus has Rimpau created a series of hybrid-races of wheat, and Lemoine has produced his large-blooming sword-lilies, able to withstand the winter, and thus have originated, in agriculture and horticulture, the countless hybrids, in which the favorable characteristics of various varieties are combined with more or less diversity. Combined, or as we usually say, mixed; though this is an expression which makes us only too easily lose sight of the independence of the individual factors in the mixture.

This independence is frequently difficult to demonstrate in the mixtures, that is, in the characteristics of the hybrids. Our means of differentiation only too frequently prove insufficient. In the clear cases, however, it appears very distinctly. and the greater the number of hybrids that are studied accurately and thoroughly, the more generally is the validity of the principle established.

If, for example, we find combined in a wheat-hybrid, the loose ear of the mother-plant, with the lack of awns in the father, the share of each appears simple and clear. In the mixture of the characteristics these two are so far apart, that they are always easily recognized. How are such characters *united in the hybrid? Are they fused into* one whole, or do they simply lie loosely side by side?

The splittings, which occur regularly in many hybrids, when propagated by seed, and also, in the case of a few, in vegetative propagation, give us an answer to this question.

Of the last kind the *Cytisus Adami* serves as the most beautiful and striking instance. It is a hybrid between *C. Laburnum and C. purpureus.* Unfortunately its great significance for the main features of the whole problem has been underrated for a long time owing to the fable of its having originated as a graft. As a matter of fact, no hybrids are obtained by grafting, no matter how great the mutual influence of the wild stock and the crown graft. As far as historical evidence goes, the *Cytisus Adami* has always been propagated by grafts since its first appearance, but it did not originally spring into existence in this way.[2]

This tree teaches us how the qualities of the two parents are combined. Ordinarily they occur mixed, the leaves as well as the flowers having some features of the *Laburnum* and others of the *purpureus.* The totality of the characters lies, therefore midway between the two parents. But splittings do occur, and not at all rarely, or rather so commonly, that indeed every specimen of the hybrid, if not too small, will show them. In these splittings the types of father and mother separate sharply and completely. Some twigs will grow that are purely *Laburnum,* while others are only *purpureus.* The former are vigorous and long-lived, the latter remain weak and often die after a few years, which is the reason for their being seen less frequently. But even in this point they resemble exactly the respective parents.

Within the hybrid, the bearers of the parental characters are therefore arranged in such a manner that, so to speak, they can be completely separated, at any moment,

[2]Strasburger (Jahrb. Wiss. Bot. **42**: 69-70. 1905.) finds entire absence of any cytological evidence that *C. Adami* originated as a graft-hybrid. *Tr.*

by a simple cut. And, if not by a simple cut, then at least by a physiological splitting, which passes exactly between the two parental groups and does not leave in one of them any trace of the other.

In this manner we have to picture to ourselves, in a general way, the internal, invisible structure of the hybrids. The bearers of the characters of both parents are intimately connected, and together dominate the visible characteristics. But they are not, by any means, fused into a new indivisible entity. They form twins, but remain separable for life.

In all nature there is probably not another such beautiful instance of splitting as the above-mentioned *Cytisus.* But with lesser differences between the parents, splittings of the parental types occur frequently in the vegetative life of hybrids. Many horticultural plants, and especially the bulbous plants, furnish instances thereof; peas, corn, wood-sorrel, anagallis, oranges, and several others are known instances. The fruits that are half lemon and half orange, belong doubtless to this group. Among the hybrids of the common and the thornless thornapple (*Datura Stramonium*), individuals have been found, although very rarely, that showed a similar splitting, and which even bore on the same fruit armed, as well as thornless cells. In my garden, I cultivated, for many years, a *Veronica longifolia* which was a hybrid from the blue species and the white variety, and correspondingly had blue flowers. But from time to time splittings occurred; either one single spike bloomed white, or a few isolated white flowers appeared on an otherwise blue spike.

During the entire life, up to the time of the formation of the reproductive cells this internal dualism manifests itself in this way. Sometimes proofs of it are even found in the anatomical structure of the tissues, and of the individual cells, where the parental characters are set free and a mosaic-like structure results.

MacFarlane, who has made the most thorough study of the anatomical structure of hybrids, recognizes everywhere the principle of duality, and goes so far as to regard every individual vegetative cell of a hybrid as a hermaphrodite formation. And the renowned French investigator of hybrids, Naudin, also expressed himself about forty years ago in a similar manner. *"L'hybride est une mosaique vivante,"* said he; we do not recognize the individual parts as long as they remain intimately blended, but occasionally they separate and then we are able to distinguish them.

We therefore regard it as established that, in the children, the inheritances from the fathers and mothers are indeed combined, but not fused into a new entity. Acting always conjointly under ordinary circumstances, they yet do not lose the power of separating occasionally.

But now arises the question as to what is anatomically visible of this union. Can the dualistic formation be observed within the cell? Do the parental inheritances, here too, lie side by side as twins?

The hereditary characters are contained in the nuclei, as was first declared by Haeckel, and later demonstrated by O. Hertwig, and, for plants, by Strasburger. This important law forms, for the present, the basis of the whole anatomical theory of heredity, and is recognized as such by all investigators. We may, therefore, expect to find in the nuclei, as well, the dualism of the parental qualities.

Every cell, as a rule, possesses a nucleus. This nucleus dominates the life-activity, and although the current functions can run their course without it, no new ones can be introduced. In certain filamentous algæ (*Spirogyra*) Gerassimow succeeded in producing cells without nuclei; they retained life for several weeks, feeding vigorously, but nevertheless they always perished without any reproduction. In some tissue-cells the nucleus is constantly in motion, and according to Haberlandt's investigations, it stops longest where the work of the cell is most pronounced for the time being, as for instance in unilateral growth, the formation of hair, local accumulation of chlorophyll, etc.

This concentration of hereditary characters is most distinctly seen in the sexual cells. Here the other functions are reduced to a minimum. The nucleus dominates completely. In the male sperms the activity of the protoplasm is limited to moving around and to seeking the female cells. The body is made up almost entirely of the nucleus. In the higher plants the spermatozoids lack even the organs of free motion; they are carried to the egg-cell passively, in the pollen-tubes. The egg-cells are usually immovable and heavy in comparison with the male elements, since they contain the food substance necessary for the incipient growth of the germ, and for the first cell-divisions.

Now fertilization consists in the union of two cells, the male spermatozoid and the female egg-cell. This union is the means of combining the inheritance of the two parents, and therefore the nuclei play the main rôles. The nucleus of the egg-cell lies usually in its center; the male nucleus reaches it by passing straight through the surrounding plasm. Sometimes one sees quite distinctly that it no longer needs its own protoplasm since it strips it off and leaves it at the border of the egg-cell. In the Cycadaceae, in which the spermatozoa are just large enough to be discernible with the naked eye, the cytoplasm with all its cilia remains in the outer layers of the egg-cell, while only the nucleus penetrates more deeply. The beautiful investigations of Webber and Ikeno have brought this process to light.

Finally the two nuclei come into contact and unite into a single body. This is the most important moment of fertilization, the whole physiological process is concluded by this union.

Let us ask now what has been achieved by it. Apparently very little, for the two parental nuclei are only closely appressed to each other. A penetration or fusion of their substance does not take place. They remain separate in spite of the union. With fertilization the life of the new germ begins, and in most cases immediately. Originally a single cell, the germ soon divides into two and then into more cells. But this beginning of the vegetative life takes place everywhere before the two parental nuclei have entered into closer union. Only after the first division does the limit become unrecognizable, the contact of the constituent parts of the male and female halves being now so intimate that there is at least the appearance of a fusion.

It was the Belgian investigator, van Beneden, who discovered this all-controlling fact. He first observed the *independence of the paternal and the maternal nuclei* in the intestinal worm, *Ascaris,* then elsewhere in the animal kingdom, and immediately recognized its significance. Since life could begin without fusion of the two nuclei, he considered that such a thing was not necessary, and assumed that all through life the two nuclei preserve their independence more or less completely.

According to this view the nuclei are double beings, and we thus find, in the material bearers of the hereditary characters, the duality of which Goethe sang in his "Sprüche in Reimen," and which the splittings of hybrids put so clearly before our eyes. Van Beneden chose the name *pronuclei* for the male and the female nuclei that are thus united, and speaks of a *pronucleus mâle* and a *pronucleus femelle.* This designation has been retained since that time, and recommends itself especially for the reason that the union of the two nuclei is usually simply called the nucleus of the cell; and this latter designation will probably not be changed, although the double nature of the nucleus is recognized. Therefore the pronuclei are the entities that concern us; the nuclei are really double nuclei.

If the border line between the two pronuclei remained as distinct through life as before the first cleavage and at the time of it, van Beneden's view would hardly meet with any difficulty. But this is not so. Gradually the line of demarcation becomes blurred, and in most cases nothing more is to be seen of it in later life. But the richness of forms in nature is fortunately so great that the general phenomena in different organisms appear to us with an extremely varied distinctness. And thus it is also here. In one species the border line of the pronunclei is lost sooner, in others later. It is only a case of finding the best illustrations, that is, of selecting a species in which the paternal and the maternal inheritances remain longest visibly separate.

The discovery of such instances is the great merit of Rückert and Häcker. In the one-eyed water-flea of our fresh waters, the well-known *Cyclops vulgaris,* and its nearest allies, they found a group of animals in which the pronuclei remained distinctly separate for a long time. Sometimes during several consecutive cell-divisions, sometimes for a longer period, and, in the best cases, during almost the entire vegetative life, the double nature of the nuclei can here be directly seen. What van Beneden concluded from the incipient stages was here irrefutably proven.

The double nature of the nuclei was also demonstrated more or less distinctly, and during a shorter or longer series of cell-divisions, in other cases, by other investigators. It was observed in *Toxopneustes* by Fol, in *Siredon* by Kölliker, in *Artemia* by Brauer, in *Myzostoma* by Wheeler, in the *Axolotl* by Bellonci. These and numerous other observations now place the law quite beyond doubt. The independence or autonomy of the pronuclei corresponds everywhere with the mode of union of the visible parental characters in the offspring.

In the snail-genus *Crepidula,* Conklin recently discovered a case in which the double nature of the nuclei can be demonstrated perhaps even more clearly and easily than in the Cyclops. If the nuclei remain side by side all through life, the question arises as to how they dominate together the development of the child, the unfolding of its characteristics. Here, too, the results of physiology and of anatomy work beautifully together, and here, too, Goethe's lines serve as a guide. Certain peculiarities are inherited from the father, others from the mother. One individual inherits them in this, another in that mixture. The inheritance therefore consists of separate qualities, which may be united in various combinations in the offspring. We are taught the very same thing by hybrids, especially in their progeny, and the rich floral splendor of our horticultural plants shows us what an endless number of combination-types have already been achieved with comparatively few characteristics.

But we shall not yet leave the subject of the nuclei. The independence of all the hidden potentialities, which in the physiological field is most sharply defined in the theory of pangenesis, we can of course not hope to see reflected in the nuclei. We must, at least for the present, be satisfied to find here any independent parts in the nuclei.

It was well known to the older investigators, and, among botanists, especially to Hofmeister, that the nuclei are not structureless formations, but that they exhibit more or less distinctly certain internal organs. But only about a quarter of a century ago by means of better methods of investigation did Flemming in the zoological field, and Strasburger in the botanical, succeed in getting a deeper insight into this structure, and soon afterwards Roux showed how these achievements are entirely in harmony with the requirements of the theory of heredity. Since then, numerous investigations have confirmed and extended these results, and especially has Boveri brought out the main features in the wide range of phenomena. To him we owe the principle of the independence of the individual visible component parts of the nuclei, a principle, which, in spite of much opposition, is more and more strongly supported, and which has found in the most recent studies of Sutton a brilliant confirmation.

What Boveri's theory offers us is, in the main points, as follows: All the bearers of hereditary characters lie in the protoplasm of the nucleus, in the nuclear sap, as it is usually called, as definite particles, which can be brought out by various methods as distinctly recognizable parts, and which are combined into threads. It is true that one cannot see the individual bearers, because there are too many of them and they are too small. Even a counting of the smallest visible granules succeeds only rarely. In the nuclei of an American salamander, *Batrachoseps,* the members of the nuclear threads are most distinct; at least Gustav Eisen succeeded in making an approximate count of the smallest visible granules. In every pronucleus they form 12 chief parts, the so-called chromosomes. Every chromosome showed as a rule a subdivision into six sections or chromomeres, and every chromomere, in turn, appears again to be built up of six smallest granules, the chromioles. All in all there are here then about 400 distinguishable particles in the individual pronucleus. The number of hereditary characters must certainly be much higher than 400 for such an organism; it would more likely have to be estimated at ten times that value. We must therefore be satisfied, for the present, with the observation of groups of units in the nuclei.[3]

In the end there will surely be found a way of seeing the individual units also. But the resolving power of our microscope will finally reach its limit, and we shall probably never be able to see much smaller granulations than the smallest elements that are visible now. So far, even the causes of many contagious diseases, in plants as well as in animals, are still quite invisible. But the calculations which Errera has lately made on the limits of the smallness of organisms still allow us full play. In *Micrococcus* he finds a structure composed of about 30,000 protein molecules, but many nuclei are much larger. It cannot yet be estimated of how many molecules a whole nuclear thread is composed, but it may be assumed with certainty that not every one of its granules has such a complicated structure that it could hold the factors for all peculiarities of the

[3]Cf. Translator's Preface, p. viii.

whole organism. Their smallness would rather lead us to suppose that every one of them could, at the most, represent only a small group of such units.

To prove this, on the one hand microscopically, on the other hand experimentally, is the task that Boveri set for himself.

The filamentous framework in most nuclei, recognizable by certain staining methods, is now admitted by all investigators as the idioplasm, the bearer of the hereditary qualities. This thread is very delicate, and seems to form a skein. But when the nucleus prepares to divide, the thread contracts, and thereby is seen, what had hitherto been invisible, that it is composed of several separate threads. In the nucleus there are several threads and not one single one. When the contraction of the thread is advanced so far that the individual parts have become quite short and thick, they are called chromosomes. In the nuclei of the body-cells these always occur in an even number, one-half belonging to the paternal, the other to the maternal pronucleus.

In a series of classical investigations Boveri succeeded in showing that the individual chromosomes, on elongating again, when the division is accomplished, retain their independence. They remain the same during their whole life, elongating and shortening alternately throughout their entire development. The purpose of the shortening is to make possible an even division of all parts during cell-division; the threads then split lengthwise, in such a way that every single bearer of heredity first doubles, and then sends the two halves into the daughter-nuclei. This, of course, could hardly be accomplished in a skein. On the other hand elongation has for its object the freeing of the bearers of heredity from that crowded accumulation, their task being to control and to direct the life functions of the cell, and to that end they must be able to enter into as free a contact as possible with the granular plasm. An arrangement in rows, at least of those bearers that are to become active, is the necessary condition thereto, and it is evidently reached by means of the elongation of the threads and the formation of the skein.

In order to make possible an orderly retreat of the individual threads out of the tangle of the skein, every thread is firmly attached by one end to the nuclear wall. It retreats to this point, which is at the same time the point at which its two halves, during cell-division, are pulled apart after the splitting. The whole regularity of the process would be hard to explain without this firm implantation of the individual nuclear threads, as demonstrated by Boveri. Where the nuclei are sinuate and the nuclear threads are attached in the individual curves, the conditions are specially clear.

In the species of locust, *Brachystola magna,* Sutton found the same implantations of the nuclear threads on the curves of the nucleus. But here every thread, of which there are eleven in every pronucleus, forms a skein after the cell-division. These skeins of one and the same nucleus remain separated from each other for a long time, and the independence of the chromosomes can hence be directly demonstrated, even at the stage of the skein. This locust has also proven very instructive in another point of Sutton's studies.

In general, one finds the individual chromosomes to be of unequal length in the most various nuclei. But, in the species of locust mentioned, this length occurs in such a characteristic manner that the chromosomes can be easily recognized in the successive cell-divisions. The pictures taken at the successive stages allow one to follow up, without difficulty, the identity of the short and thick nuclear threads. In doing so one sees that, in the double nuclei, the nuclear threads lie in pairs, that is, that there are two nuclear threads of each individual length. Evidently these belong together in such a manner, that in every pair one thread belongs to the paternal and one to the maternal pronucleus. A border line between them is nowhere to be seen, and yet their independence is very evident. And this harmonizes with the conception, as detailed above, that, according to the species examined, this limit can be observed for a longer or shorter time.

Microscopic examinations teach us, then, to recognize the independence of the two pronuclei, as well as the autonomy of the individual nuclear threads or chromosomes during the development of the entire body. The agreement of this observation with the phenomena of heredity may be considered as fully established.

But it is another question whether the individual chromosomes correspond also to special groups of hereditary characters, or, in other words, whether the bearers of the latter are strictly localized in the nuclear threads. Obviously, this question can be answered only physiologically. It amounts to a decision as to whether, if definite chromosomes, or definite parts in them, as for example, single chromomeres and chromioles, were wanting, definite external characters of the organism would also be lacking. If it were possible to kill a nuclear granule without otherwise injuring the germ, what would be the consequences?

Engelmann has taught us, in his revolutionizing investigation on the activity of the individual chlorophyll grains, how the focal point of a lens can be moved over the field of a microscopic preparation, thereby lighting up quite small portions of a cell, and how these portions can thereby also be heated, and in that way killed. If a part of a nuclear thread could be killed in this way, the externally visible consequences would certainly allow us to draw conclusions on the relations of this part to the hereditary characters. Perhaps an analaysis of heredity can some day be made by this method, but the technique is not yet sufficiently advanced for this purpose.

However, there is another means of removing individual chromosomes, and this again we owe to the classical investigations of Boveri. He found it in abnormal processes of fertilization as they occur at times in eggs of sea-urchins and star-fish, and it can be quite easily produced artificially. It would lead too far from the main question to go into details here. The important point for our purpose is that, by certain interferences, a fertilization of one egg with two spermatozoa can be achieved. This process of dispermia leads in the nucleus of the germ, not to a double, but to a triple number of chromosomes. In the successive divisions the conditions become correspondingly intricate, and almost any imaginable abnormal number of chromosomes occurs. Nevertheless, the germs develop in some cases, and then show deviations from the normal type which allow a recognition of their normal relations to the structure of their nuclei. Without doubt the germs can, in every case, develop only those qualities the representatives of which happened to be preserved in their nuclei.

We shall leave the nuclear threads, at present, and return to the two pronuclei. We saw them intimately combined during the entire development of the body. Now the question arises as to how long this union persists.

And since the double nuclei of the body originated during fertilization, it is evident that the conjugating cells must have single nuclei, and therefore that the separation of the pronuclei must take place at the origination of these cells.

This fact is now so generally established, for animals as well as plants, that it may be regarded as one of the strongest foundations of the whole theory of fertilization. Wherever it is possible to count the chromosomes, we find in the somatic cells twice as many as in the sexual cells. The former contain double nuclei, the latter single nuclei, or pronuclei.

The sexual cells in animals originate directly from the somatic cells, but in plants there is more or less preparation. Correspondingly, the two pronuclei separate in animals at the formation of the egg- and sperm-cells, but in the case of plants before that. In the seed-bearing plants it is the period of the origination of the mother-cells of the pollen and of the embryo-sacs. Therefore all cell-generations which appear after this moment, and up to the final production of the egg-cells in the embryo-sac, and of the sperm-cells in the pollen-grains and their tubes, possess only pronuclei. Such cells are called sexual, and the period of their formation the sexual generation. In ferns the entire life-period of the prothallium lies between the origination of the sexual cells and the appearance of the egg- and sperm-cells. This small plantlet, though built up of hundreds of cells possesses, therefore, as Strasburger has demonstrated, only pronuclei. The alternation of the sexual prothallia and the asexual fern-plant is called the alternation of generations; the two generations are hence distinguished from each other fundamentally by their nuclei, which in the leafy plants are always double nuclei, and in the prothallia always pronuclei. This difference is so constant that one feels almost inclined to call the pronuclei prothallial nuclei.

At the moment when the two prounclei separate, single nuclei appear in place of the double nuclei, and the double number of nuclear threads is thereby reduced to a single one. This process is usually called the numerical reduction of the chromosomes; but this imposing name means nothing but the separation of two nuclei which had so far worked together for a period. It is like the parting of two persons who have walked along together for a while, and will be looking for other companionship presently. And this they achieve by fertilization.

This parting has been minutely studied by numerous investigators. It has the appearance of a nuclear division of a very special nature, and is frequently called the reduction-division, or heterotypic nuclear division. It is necessarily accompanied by a cell-division, since the two separated pronuclei can only part in separate cells, but this cell-division does not always follow immediately, but only after a second essentially normal division of the nuclei. There result, in that case, four sister-cells instead of the usual two.

Shortly before their separation, the chromosomes lie together in pairs, always one in the paternal pronucleus united with the corresponding thread of the maternal pronucleus. They are placed lengthwise side by side. Hence the separation evidently occurs by a longitudinal line, and, in by far the greatest number of cases, this so-called longitudinal splitting of the chromosome-pairs has been observed in the origination of the prouclei. It is true that this does not always succeed at a first glance, and it is right here that the differences of opinion between different investigators have blurred the picture for a long time. But gradually it was discovered that there are a number of secondary details which may obscure the main features, and we owe it chiefly to Strasburger that the latter stand out clearly in the plant-kingdom. In the animal kingdom, however, there is still a series of cases which do not follow this rule, and where the chromosomes of the pronuclei are not placed lengthwise side by side at the moment of separation, but are connected at one end. Hence the separation here takes the form of a transverse division. Some insects and fresh-water crabs, some molluscs and worms offer the best known instances, but according to the most recent studies of de Sinéty, Cannon, and others, the assumption gains ground that here too the microscopic pictures, on closer observation, disclose a better fitting into the otherwise general scheme. It is also possible that, after the longitudinal splitting, the nuclear threads still remain connected for a while by their ends, before they finally separate.

The male and the female sexual cells usually originate in separate organs, frequently on special individuals. This goes to show that, at their origination from the body-cells, the paternal pronuclei do not become sperms and the maternal ones egg-cells. On the contrary, the two pronuclei of a mother-cell in the ovary can become egg-cells, and the two pronuclei of a pollen mother-cell can both give rise, by further splitting, to the formation of spermatozoids. Accordingly, one-half of the forming sperms gets paternal or now grand-paternal pronuclei, and the other half grand-maternal. The same is true of the egg-cells, and this holds good in spite of the circumstance that, in consequence of the crowded condition of the ovaries, the larger part of the female cells has regularly to be sacrificed every time.[2] Therefore fertilization may result in offspring with pronuclei from the grandfather or grandmother only, or from both. This circumstance may not be without significance in considering the resemblance between grandparents and grandchildren among men.

But it is not by any means decisive; daily experience teaches that not only in a part of the progeny, but doubtless in all the offspring, there may be an admixture of the characters of the grand-parents also. This indicates that the separation of the pronuclei is not of as simple a nature as the microscopic pictures might lead one to believe. Another process, which, until now, has defied detection, must take place, probably in the smallest, but to us invisible granules of the nuclear threads. That this is the case we learn especially from the processes in hybrids and their propagation. Here, splittings and new combinations of the characteristics of the grand-parents occur in apparently incalculable numbers, and here it is distinctly seen that the pronuclei do not separate without a lasting reciprocal influence.

We shall first try to get a conception of this influence, for the facts concerning hybridization are rather involved; they can be most clearly explained by means of such a hypothetical conception. We shall accordingly assume a mutual influence as an established fact, and inquire how this can take place.

First of all it is clear that it must be finished before the separation of the pronuclei. Once they are apart all intimate relation between them ceases. They go their separate ways, each living for itself. Only in the double

[2]The reference is to the resorption of the sister-cells (when such occur) of the embryo-sac mother-cell. *Tr.*

nuclei do the paternal and the maternal pronuclei lie so close together that their individual parts can exercise an influence on each other.

We have further seen that, during the life of a double nucleus, throughout the successive cell-divisions, from the origination of the germ to the complete formation of the offspring, the contact of the pronuclei becomes gradually more intimate. Before the first cell division they are, as a rule, still visibly separated; soon afterwards the border-line begins to look more indistinct, and, shortly before the formation of the sexual cells, the double nature is disclosed with certainty only in the rarest cases by special structural relations. It is, therefore, clear that their opportunity for mutual influence gradually increases during somatic life. Perhaps it first occurs only at the end, possibly even, only at the moment immediately preceding their separation. A decision on this point has not yet been reached.[4] But the above-mentioned vegetative splittings of hybrids indicate that the process is deferred as long as possible. It also seems simpler to assume that it occurs only in those cells which actually lead to the formation of sexual cells, because in the leaves, bark, and other vegetative parts of the body, it would evidently be without significance.

We therefore imagine the mutual influence to be exercised towards the end, or even at the very last moment before the separation of the pronuclei. In the first case

[4]More recent investigations indicate that the fusion of the male and female chromatin elements is completed during the stage known as *"synapsis,"* which immediately precedes the reduction-division, or heterotypic nuclear division, referred to above. During synapsis the chromatin is aggregated into a compact mass within the nuclear cavity. *Tr.*

it could extend over a long time; in the latter it must take place suddenly. In the first case the individual parts of the nuclear threads could be mated one by one; in the latter this would have to take place everywhere simultaneously.

How this process comes about is self-evident when we assume special units, special granules in the nuclear threads, for the visible characters of the organisms. There must be as many units in the nucleus, as a plant or animal possesses individual characters. And this, of course, is the rule for both pronuclei. In the condition of the short and thick chromosomes these units lie crowded together. This is a definite stage in cell-division; the units, at least those of the interior of the group, remain in a condition of enforced rest. But as soon as cell-division is completed, the nuclear threads stretch; they become quite long and thin, and indeed so long that a large part, perhaps most of them, possibly all of them, come to the surface. At least stretched out in a row in this way, the granules must then be arranged one after another, perhaps in the threads themselves, perhaps in their finest ramifications. Now they become active, and if, at this time, nuclear threads of the paternal and the maternal pronuclei lie together in pairs, every granule can enter into communion with its corresponding unit in the other pronucleus.

There is no reason to assume that the exceedingly fine structure of the nuclei, which is so strikingly to the purpose and yet so simple, should be limited to what is visible to us at present. On the contrary everything points to the probability that, in the internal structure also of the nuclear threads this same serviceable rule must prevail. The whole complicated process of nuclear division has for its object the division of the two pronuclei in such a way, that their daughter-nuclei will share alike in the hereditary characters that are present. The lengthening of the nuclear threads at the close of division, their so frequent ramification, and the seemingly irregular intertwining of their parts, evidently indicates the possibility of a domination of the cell-life by the bearers of the inheritable qualities. These must impress their character on the surrounding protoplasm either dynamically or, as I have assumed in my *Intracellulare Pangenesis,* through a giving out of material particles to the surrounding protoplasm, and thus promote growth and development, in the prescribed direction, into the specific form of the species to which the organism belongs.

This secretion of material chromatin particles from the nuclei was recently demonstrated by Conklin in *Crepidula.*[5] In this way considerable quantities of chromatin, and therefore probably of pangens also, are transferred into the somatic protoplasm.

Thus we consider that the structure of the nuclear threads is such that it not only makes possible, but regulates and dominates the relations of the two pronuclei. In an ordinary animal, or in a plant which is not a hybrid, both pronuclei possess the same units, only with a somewhat unlike degree of development. We assume; therefore, that the cooperation comes about in such a way that the individual units in the stretched threads lie in the same numerical order. Then, when the threads are closely appressed lengthwise, in pairs, we can imagine that all the like units of the two pronuclei lie opposite each other. And this is obviously the simplest assumption for a mutual influence.

[5]Strasburger failed to find any direct evidence of such a transfer of particles in plants. Cf. the Translator's Preface, p. viii. *Tr.*

If every unit, that is, every inner character or every material bearer of an external peculiarity, forms an entity in each pronucleus, and if the two like units lie opposite each other at any given moment, we may assume a simple exchange of them. Not of all (for that would only make the paternal pronucleus into a maternal one), but of a larger, or even only a smaller part. How many and which, may then simply be left to chance. In this way all kinds of new combinations of paternal and maternal units may occur in the two pronuclei, and when these separate at the formation of the sexual cells, each of them will harbor in part paternal, in part maternal units. These combinations must be governed by the laws of probability, and from these, calculations may be derived, which may lead to the explanation of the relations of affinity between the children and their parents, the grandchildren and their grand-parents. On the other hand a comparison of the results of this calculation and of direct observation will form the best, and for the time being, the only possible means for a decision as to the correctness of our supposition.

The mutual influence of the two pronuclei shortly before their separation is therefore brought about, according to our view, by an exchange of units. Every unit can be exchanged only for a like one, which means for one which, in the other pronucleus, represents the same hereditary character. This rule appears to me to be unavoidable and really self-evident. For the children must inherit all specific characters from their parents, and they must also transmit all of them to their own progeny. This exchange must hence be accomplished in such a way that every pronucleus retains the entire series of units of all the specific characters, and this result can evidently be obtained only when the interchange is limited to like units.

We distinguish here specific characteristics from individual features. The units in the hereditary substance of the nuclear thread compose the former. Every species has an often exceedingly large and yet definite and invariable number of them. The sum total of these units forms that which distinguishes any given species from all others, even from its nearest allies. A complete diagnosis of a species would have to embrace all of these characteristics, and therewith all the material bearers underlying them.

The individual features, that is, the differences between the individuals within the species, and not only of the systematic but of the so-called elementary species, are of quite another nature. It is true that they are, in a way, hereditary, but with that they are subject to constant changes. The average stature of man remains the same in the course of centuries, for the same race (elementary species), but the individual stature changes constantly from one individual to another. In the somatic cells of man the bearers of the stature of the father lie opposite those of the mother. At the moment of exchange these are mutually transferred, and the sexual cells receive partly one, partly the other stature, but this in the most various combinations with the other characters. Thus one might continue. Every visible quality, every trait of character is to be found in all individuals, only in some they are strongly developed and prominent, in others weak and recessive. Ordinary observation takes more interest in differences than in similarities, and for this reason the former are designated by contrasting expressions, as large and small, strong and weak, forward and modest. But these are, in each instance, only degrees of the same hereditary characteristic, or the same trait of character. And such more or less differing stages of development of the same inner units we represent to ourselves as the entities which are exchanged by the nuclear threads.

Individual differences are thus not included in the type of the species. They form deviations from this type, and are conditioned by causes which were formerly generally described as conditions of nutrition, but now more frequently as environment. Under these influences every character can develop more or less strongly than the average type. And the environment, provided it remains constant during the entire period of development, must affect all the unfolding characters in the same way. If it is favorable it furthers all parts of the body and all mental gifts, if it is unfavorable it has the opposite effect on all of them. Not, by any means, to the same degree upon all of them: that does not depend upon the environment but upon the units themselves; this, however, can not lead to essential differences between separate individuals. But our supposition of such a uniform environment would probably be met with only in the rarest of cases. And, as soon as it changed, it would influence one individual differently from the others. Moreover the characters do not unfold simultaneously, but successively, the higher ones for the most part later than the lower ones, mental characters later than those of the body, the reason later than the memory. And all those wheels work into each other so that small deviations will rather tend to become greater than to be equalized. Though children of the same parents but of different age might, during their entire youth, live under the same circumstances, they will yet react differently to them. This also holds true for plants where, in the same bed, a delay of only one day in germinating will, according to the weather, lead either to equal or to quite surprising differences in size and qualities.

If favorable and unfavorable conditions of life alternate during the individual development, and if they strike a group of individuals sprung from like seeds at different periods of their growth, quite a considerable degree of individual differences must thereby result.

These differences play in nature the same rôle as in human society. One is adapted for this kind of task, the other for that. With men it is the duty of every one to develop his own talents to the best of his ability, and to render as favorable as possible the circumstances for the most perfect development of his children. The highest efficiency of society in general demands of each the strongest effort in the direction of his most favorable talents. To ascertain this direction ought to be one of the chief aims of education and instruction. In animals and plants this highest efficiency can obviously not be achieved in the same way. And especially are the conditions different for plants, which are tied for life to the place where they germinated. Here, as is well known, nature is assisted by the astonishingly great number of seeds; she sows so many in every individual spot that only the best, that is, the individuals best adapted for the given locality, need retain life. But, by sacrificing countless seeds, she also accomplishes here that adaptation of the individual specimens which is the condition for the complete unfolding of their abilities and advantages.

Very great weight is therefore given to individual differences in the life of the entire species. The greater they are, the greater the power of adaptation, the greater the chance of victory.

And in this I see the significance of sexual reproduction. It mixes the potentialities that have developed in the single individuals in the most complete manner imaginable; it achieves, at one stroke, all possible combinations. It cancels, as Johannsen expresses it, the previous correlations. Asexual propagation confers a certain degree of variability, and this may be quite sufficient in many cases, especially in the case of a low organization or of quite special adaptation, as in many parasitic and saprophytic organisms. Under such conditions the variability remains, in a certain sense limited, more or less one-sided, because every individual is the result of the varying, but, on the whole, one-sided environment in which his progenitors existed. Only an exchange of qualities can help to overcome this one-sidedness; only this can cause all the combinations to arise which are demanded by the varying environments. If we assume that *the bearers of the individual characters are, as a rule, independent of each other during their exchange,* and also that the latter is ruled by chance, two pairs of characteristics would directly result in four, three in eight, four in sixteen combinations. The sum total of the points of difference of two parents must therefore give rise to such an incredible number of possibilities that no struggle for existence, no annual rejection of hundreds and thousands of germs could demand a richer material.

Hence sexual reproduction brings individual variability to its highest point. It produces a material that corresponds to almost any environment. It is the principal condition for the greatest efficiency of cooperation, be it by a selection as free as possible of the line of development for the single individuals, or by a sacrifice of all the individuals that do not quite meet all the requirements.

This service of sexual reproduction is evidently not limited to a single generation. It exercises its influence throughout successive generations, and it is probably indifferent whether the effect follows directly, or whether it manifests itself in the course of time. Even without that, the complete utilization of all given possibilities requires, as a rule, more individual beings than are born in a single generation. And with this, the otherwise strange fact is explained, that the exchange of the units does not immediately follow fertilization, but only takes place a short time before the succeeding period of fertilization. But obviously an exchange, ruled by laws of chance, could not benefit a given isolated individual or, more correctly speaking, it would most likely, just as frequently be harmful as useful. It can only be of use in connection with an increase in the number of individuals, for it is its task to bring about as great a variety as possible, and with that, the highest possible prospect for the required quantity of superior specimens. At the moment when the production of the sexual cells begins, in such enormous numbers, it also finds the best opportunity for fulfilling its task.

Thus, sexual reproduction has only a subordinate significance for the children, while for the grandchildren it is of the utmost importance, because only for them does the urn mix up all its lots.

The same laws that govern normal fertilization, are, of course, valid for hybrids also. There cannot be special biological laws for them, because they are only derived phenomena, deviations from the normal. Now the question is, to which results, departing from the rule, will the common laws lead in these special cases. And with this it is clear that the phenomena must keep nearer to the normal the less the deviation is from the type.

This type is conditioned by the fact that the two organisms that fertilize each other belong to the same small or elementary species. They have then, on the whole, the same characters, even if these are, according to their environment in various degrees of development. There are no differences among them independent of this, at least if we consider the cumulative effect of uniform influences in the course of several generations.

As soon as such independent differences occur, and as soon therefore as there are present constant contrasts, which are retained in the sequence of generations and cannot be blended by environment, we call the sexual union of two individuals a crossing or a hybridization. If the contrasts are slight, we call the two races varieties, if they are greater, they assume the rank of species. The crossing of varieties keeps quite near to normal fertilization; that of the species deviates the more the slighter the relationship between them. The crossing of varieties forms a type complete in itself, that of the species forms a series which descends from almost normal processes, by gradual progress, to a complete reciprocal sterility. The variety-hybrids are fertile like their parents, but in the species-hybrids the diminished fertility indicates abnormal phenomena either in fertilization or in the exchange of the units.

We must therefore discuss these two groups separately, and we shall begin with the varieties.

In daily life and in horticulture, any thing that deviates from the normal is called a variety. Even the new forms obtained by crossing are quite commonly counted among the varities. In science, therefore, the word would really be useless. Nevertheless it has been retained and its meaning has been gradually limited. Especially in describing horticultural plants the conception is sufficiently restricted by excluding on the one hand the hybrids, on the other hand the improved races obtained by selection, and finally the so-called elementary species that, taken together, form our ordinary species.

Upon reviewing the cases that are left, two types can be plainly distinguished, the constant and the inconstant varieties. The former are not inferior to true species in point of constancy. Their characters vary, in the single individuals, around a mean, but in the main not more so than the corresponding characteristic of the species. From this they are separated by a decided chasm. In pure fertilization they never bridge this chasm, or at least, extremely rarely, but in crossing they revert very easily to the species. It is this very reversion that stamps them varieties, and when the crossing is not artificial but natural, brought about by insects, it escapes observation, and only the fact of the reversion strikes the gardener.

These constant varieties are, as a rule, distinguished from the species to which they belong, by lacking some striking quality that adorns the latter. Most frequently it is the coloring of the flower or, in the case of flowers with combined colors, as in the yellow and red tulips, one of the individual colors, that is wanting. Often they lack hairs or thorns, very frequently the development of the blade is arrested, and split leaves originate. In all of these cases there is no ground for the opinion that the failure of the visible character means also the loss of the respective unit. Rather does everything point to the fact that the unit has simply become inactive, that it is in a state of rest, or as it is usually expressed, that it has become latent. Especially the reversions, which in individual specimens of such varieties are, at times, quite common phenomena, betray this latent presence.

Inconstant varieties are distinguished by a strikingly high variability, by an exceedingly great range of departure from the norm. But here we encounter the double meaning of the designation inconstancy. On the one hand the word means a certain relatively great richness of individual forms, on the other hand it relates to differences between the parents and the progeny. In choosing from an inconstant variety a single individual, and sowing its seed, after pure fertilization, the whole play of forms of the variety can be found again in the children,—hence a palpable proof of the inconstancy. But, on choosing several individuals, and on sowing their seeds separately, each of them will produce almost the same series of forms. The whole group is transmitted from year to year, and does not change. The variety has a definite circle of forms in which the descendants of every specimen choose freely their place, but they do not go outside the circle. The limits are constant, and remain so in the course of generations; within the limits, however, a motley variety prevails.

Such is the concept of plants with variegated leaves, of double and striped flowers, and many other most highly variable garden-plants. The new character is not based here on the loss or the latency of some characteristic of the species. Indeed, on the contrary, it is usually a peculiarity which is already present in the species itself, or at least in one of its races, in a latent state. Especially do variegated leaves occur, not so very infrequently, on otherwise green plants, and the same is true of stamens with petal-like broadenings. The relation of the inconstant varieties to the species from which they are derived, is therefore quite different from that of the constant varieties.

Nevertheless, the two crossings behave in the same manner in regard to their mother-species. From the latter they are distinguished, for the most part, only in one point, though sometimes in several. But we have always to deal with the distinction between active as contrasted with latent, be it that the given character is active in the variety and latent in the mother-species, or latent in the former and active in the species itself.

If to this we apply the conception of the arrangement of the units in rows on the nuclear threads, as explained above, it is quite evident that everything will follow exactly the same course as in normal fertilization. Every unit in the paternal pronucleus corresponds to the representative of the same peculiarity in the maternal one. The nuclear threads fit as nicely into each other as in a pure species, and all the units which do not directly bring about the point of difference behave quite normally. Cooperation in vegetative life, and exchange during the formation of the sexual cells need not be disturbed. We may confine our whole consideration to the point of difference, and we shall select, for the purpose, as simple an illustration as possible, one in which there is only one difference between the species and the variety, for example, the color of the flower.

The material bearer of the color-characteristic is situated in the mother-species so that it can display its full activity while in the variety it is unable to do so. If the paternal and maternal nuclear threads of the hybrid come into contact for the purpose of exchange, and with the same sequence of units in both, the active unit of coloring matter naturally gets the equivalent inactive unit as an antagonist. With this it must therefore be exchanged. We assume that in this the latent condition is without significance, that hence the exchange comes about in the same manner as in normal fertilization.

Over this, however, the crossings of varieties have the great advantage that there the origin of the characteristic in question can always be clearly and positively recognized. Both units of a pair of antagonists are otherwise distinguished only by a more or less of development, here by a sharp contrast. And for this reason it is experimentally much easier to discover the laws with varieties than with purely individual differences.

In doing this, two points have to be distinguished; the consequences of fertilization and the consequences of the exchange of the units. The former we see in the hybrid itself, the latter in its descendants.[6] And since fertilization and exchange are two such fundamentally different things, we must not wonder that there exist such decided differences between a hybrid and its descendants. These differences show themselves essentially by the fact that the hybrids of a mother-species with a variety of the same are alike, even if they are obtained in great numbers, while their descendants always display a certain variety.

Let us first consider the first generation of variety-hybrids. How do the two pronuclei, notwithstanding

[6]In the fertilized egg, resulting from the crossing, the chromatin from the male and female parents is not completely fused. As pointed out in a preceding footnote (p. 240), this fusion, called synapsis, occurs as almost the last step preceding the nuclear and cell-divisions that give rise to the reproductive cells. The characters of the first hybrid generation are a result of fertilization. Following synapsis, the pure bred offspring of this generation differ from their parents and also among themselves. *Tr.*

their inequality, cooperate in order to regulate the evolution? This question amounts to the same as asking, what is the sum of the influence of an active and a latent unit? At first glance one would expect that this influence would correspond to half the value of a pair composed of two active units. Previously this opinion was rather generally accepted, and there was an inclination to regard plants with intermediate characters as hybrids. Especially many plants with pale red or pale blue flowers were regarded as such. But the experience of later years has decided differently.

Variety-hybrids generally bear the characteristic of the species, sometimes fully developed, sometimes more or less weakened, but this for the most part only so little that superficial observation sees no difference. An active and a latent unit are not essentially different in their cooperation from two active ones; a fact which may probably be best explained by the assumption that two cannot accomplish more than one already does. This conception finds a very strong support in the results of the most recent investigations by Boveri on dispermia, which we have already partly discussed. By fertilizing one egg with two spermatozoa the composition of the structure of the nuclear threads can be altered in different ways, for instance, in such a manner that in one nucleus there lie not two, but three pieces of any one of its chromosomes. It might then be expected that the given characters would be very strongly developed, to about one and one-half of their intensity. But, as far as can be judged from Boveri's experiments, this is not the case, and the influence of the three equivalent units is not noticeably greater than that of two.

We come now to the progeny of hybrids, and we, of course, presuppose self-fertilization. At the formation of the sexual cells the two pronuclei separate; this happens at the origination of the egg-cells as well as of the sperms. Through exchange, the active units of our differing pair combine partly with new units of the other pairs, and thereby new combinations originate as in ordinary fertilization. But if we consider only the differing pair, exactly one-half of the egg-cells must obviously have the paternal, and the other half the maternal character. Or, in other words, in one-half of the egg-cells the given character occurs in the active, in the other in the latent state. Exactly the same is true of the male sexual cells, the sperms, in animals as well as in plants, and independently from the circumstance that in the higher plants the sperm-cells are conducted to the egg-cells in the pollen-tube.

The male sexual products of a hybrid are therefore unlike each other, and the same holds true of the female. In the simplest case selected both groups consist of two types, in the more complicated cases this number will obviously become greater. The paternal and maternal factors of the hybrid become, in its progeny, grandpaternal and grandmaternal. Hence, in regard to the point of difference, one-half of its egg-cells and one-half of its sperm-cells have grandpaternal factors, while the other halves possess grandmaternal ones.

By means of this principle the composition of the progeny in the simple as well as in the complex cases, and for constant as well as for inconstant varieties can be calculated. Thus we obtain the formulæ which are now universally known as Mendel's law.

They indicate, for any given number of points of difference between two parents, how many children correspond to every individual combination of the respective character. And, on the whole, experience has so far proven the reliabilty of these formulæ for animals as well as for plants.

It would be too great a digression to consider here the formulæ themselves. We shall therefore leave the field of the variety-hybrids, and turn to the hybrids between different species, especially between allied elementary species.

In order to understand these we must get a clear idea of the nature of the points of difference in this case, or in other words, what is meant by relationship. Species originate from each other in a progressive way. The number of the units in lower organisms is evidently only small, and must gradually increase with progressing organization. Every newly arising species contains at least one more than the form from which it has arisen. Only in this way can one imagine the progress of the entire plant and animal world.[7]

It is indeed questionable whether the acquisition of a single new unit, the increasing by one unit of the entire stock, amounting to hundreds and thousands, would be sufficient to make the impression of progress on us. The

[7] A quite different hypothesis is thinkable, as, for example, that suggested by G. H. Shull, "The Significance of Latent Characters," *Science* N. S., **25**: 792. 1907.

"All the visible variations of the present plant and animal world were once involved in some generalized form or forms, and the process of differentiation pictures itself to us as a true process of evolution brought about by the change of individual character-determining units from a dominant to a recessive state. This conception results in an interesting paradox, namely the production of a new character by the loss of an old unit."

This hypothesis, however, as de Vries has pointed out, seems too much like a revival of the old evolution theory as opposed to epigenesis. *Tr.*

difference will in most cases be too slight. Only when two or three or more units have been added successively to those already present, will we recognize an increase in the degree of organization.

The progress of every individual species can apparently take different directions. In some genera there are species so typical that they may be regarded as the common origin of the others. Where these are lacking it is manifest that the systematic relations are still too incompletely known to us, or that the given forms have died out. Every species can therefore be compared with its own ancestors or with other descendants of the same ancestors.

This consideration leads us to the recognition of two different types of relationship, and therewith also of two groups of crossings between allied species, which have to be kept absolutely apart. One of them we shall call the avunculary, the other the collateral. In the first case we cross a form with an "avunculus" or ancestor in the direct line, in the latter case with one of its lateral relatives. *Obviously the first relation is very simple* while the latter is more complicated.

Every character and every unit corresponding to it, which in a crossing is present in one species and lacking in the older one, forms a special point of difference. Hence the simplest case is the one in which there is only one such difference between the two parents of a cross. But generally several of them exist.

Now in such a cross, the differing factors evidently do not find any antagonists in the sexual cells of the other parent. When, during fertilization, the pronuclei unite into a double nucleus, all the other units are present in pairs. Not so the differing ones; they lie unpaired in the hybrid.

If we apply this reasoning to our conception of the arrangement of the units in rows on the nuclear threads, the immediate result would be that their cooperation must be disturbed. The threads no longer fit, neither during fertilization and in vegetative life, nor later when the units are exchanged before the formation of the sexual cells.

If we imagine two corresponding chromosomes of the two pronuclei placed exactly side by side, and in such a way that every unit of the one has the corresponding unit of the other for a neighbor, this will occur in a species-cross only as far as the point of difference. Here one nuclear thread has one unit more than the other. The latter has, so to say, a gap.

The greater the number of points of difference, the more numerous are these gaps, and the more will the cooperation of the two nuclei be interferred with. And this must diminish the vitality of the germ or at least the normal development of all characters.

If the differences between the two parents are too numerous, a crossing, as is well known, remains quite without effect. Crossings between species belonging to different genera succeed in very rare cases only, indeed within by far the most genera even the ordinary systematic species are not fertile when united. Genera such as *Nicotiana, Dianthus, Salix,* and others, which are rich in hybrids, are, as a rule the very ones in which the species are exceedingly closely related to each other.

Even if the agreement of two species is great enough for mutual fertilization, the life of the hybrid is by no means assured thereby. Some of them die as seeds within the unripe fruit, as has been specially described by Strasburger for the hybrid seeds of *Orchis Morio* after fertilization with *O. fusca.*

Others become young plantlets, but are too weak to develop any further, and perish during the first weeks after germination, as I have frequently seen, for example after crossings of *Oenothera Lamarckiana* and *O. muricata.* Or only the most vigorous individuals continue to grow, while the weaker ones perish, and this, in diocious plants, sometimes results in the male seedlings perishing while some of the more vigorous female ones develop flowers, as Wichura observed in several willows. Finally there might originate hybrids that grow vigorously, but do not flower at all or only incompletely, or begin too late to do so. There is a whole series of cases between the unsuccessful crossings and the development of hybrids into adult plants. And on the whole this series runs parallel with the increasing systematic relationship.

If the hybrid has succeeded in reaching the period of flowering, that is, the period of the formation of the sexual cells, a new difficulty arises at the moment of the exchange of the units. Whereas, up to that time, the cooperation of the two pronuclei was more or less disturbed, now the gaps become very important. Hence the quite common phenomenon that the production of egg- and sperm-cells fails more or less completely, that the hybrids either produce no ovules that are capable of being fertilized, or no good pollen, or neither. They are more or less or even completely sterile. They either form no seed at all, or only an insufficient quantity. Only where the differences between the parents are quite small, does one succeed in harvesting any seed, and even here frequently only a little.

How the unpaired characters behave during the exchange, when they are not numerous enough to make a failure of the entire process, is at present unknown. Experience teaches, however, that in these cases the descendants of the hybrids do not display that multifariousness of type, nor those splittings that are characteristic of variety-hybrids. They usually all resemble each other and their parents, the original hybrids, and this constancy persists through the course of generations. Accordingly there originate races of hybrids which, apart from their possibly diminished fertility, can hardly be distinguished from true species. Sometimes they are found wild, as for example a hybrid race between two Alpine roses and other races of the kind in the genera *Anemone, Salvia, Nymphaea,* etc. Sometimes they have been obtained artificially or have accidentally originated in the gardens. The genus *Oenothera* is exceptionally rich in such hybrid races, especially in the sub-genus of the common evening-primroses, *Onagra.* Very frequently such hybrids are simply described as species, on the one hand because they can be reproduced, without deviation, from seeds, and on the other hand because systematic works frequently do not sufficiently consider the elementary species. The distinguishing of the latter from hybrid races is frequently by no means easy.

The purpose of my explanations compels me to restrict myself to simple and clear cases. In nature these occur relatively rarely, and the individual elements of the phenomena are usually commingled in most motley variety. By far the greater number of crossings take place between parents whose mutual relations do not wholly fit either the one or the other concept, but where the characteristics of the different types of hybrids are intermingled. I cannot consider these cases here; they are of too complicated a nature for an address.

Only one point I wish to touch upon. In the preceding pages I have always taken for granted that the species and varieties are in their ordinary and unchanging state. But this is by no means always the case. The origination of new species and varieties demands that their immutability should not be absolute, or at least should be suspended from time to time. Experience confirms this by showing that there are periods in the life of species, during which they are, so to speak, especially inclined to produce new types. At that time they produce the new varieties and species, not only once but repeatedly, and not only a single one, but frequently a considerable number. Genera rich in species, such as the pansies and the rock-roses,[7] are the remains of such periods of variability, and everywhere in nature we meet with similar ones. In garden-plants we see, from time to time, periods during which certain varieties occur by preference, as the double dahlia of about the middle of the last century, the forms of tomatoes in recent decades, and numerous other instances teach us. On its first appearance the gardeners call the new form a conquest, the later appearances are only repetitions, and are therefore of only very secondary practical value.

The power of reproducing one or more new species indicates a condition of unstable equilibrium of the given internal units. In the nuclei the new characteristic is already invisibly present, but inactive. Certain causes, unknown to us, can transform this into a permanent condition. This state of unstable equilibrium may be maintained in the great majority of individuals, through a series of generations, as is the case with my *Oenotheras*. But from time to time, sometimes in individual cases every year, there is a shock, and the equilibrium becomes

[7]*Sonnenröschen (Helianthemum). Tr.*

stable. The given individuals overstep their bounds, abandon the earlier type, and form a new species.

It is evident that in crossings such unstable units will behave differently from normal, stable ones. Their chance of becoming stable is evidently considerable, owing to the phenomena of fertilization and the exchange of units. In this way constant races originate, at least in the genus *Oenothera,* and this, on the one hand, with the respective characteristic in an unstable condition, or in other words, in a state of mutability; and on the other hand with stable equilibrium corresponding to a new species. But researches in this field are only in their beginning, and do not yet permit of a detailed analysis. Besides they represent, for the present, a case in themselves.

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In conclusion, on reviewing the course of our deductions, we see that hybrids follow normal fertilization quite closely, the more completely the less numerous and the less pronounced the points of difference between the parents of the crossing. If these are of such a kind that the number of units in one parent is different from that in the other, disturbances take place which, if of lesser influence, diminish the fertility of the hybrids, and if of greater significance, affect their own power of development, or even make the crossing a failure. If these units are present in equal numbers on both sides, and if the differences are limited to latency in one parent and activity in the other, the normal process is not at all disturbed, but striking phenomena occur, which find their explanation in the peculiar manner in which the parental inheritances co-operate in the hybrid and in the formation of its sexual cells.

This co-operation is reflected in the life of the nuclei.

In fertilization the nuclei of father and mother simply touch each other. In the course of development the contact becomes gradually closer, bringing their equivalent elements as near to each other as possible, in such a way that the latter finally all lie side by side in pairs. But the pronuclei by no means lose their independence thereby, and for the purpose of every nuclear division they separate their component parts more or less distinctly. Shortly before their separation, their leave-taking, they are still *the same as before. But now they exchange their individual units*, and thus cause the creation of those countless combinations of characters, of which nature is in need in order to make species as plastic as possible, and to empower them to adapt themselves in the highest degree to their ever changing environment.

This increase of variability and of the power of individual adaptation is the essential purpose of sexual reproduction. It can be attained only by a mutual combination in all conceivable forms of the peculiarities developed in different individuals in different directions and degrees. To this end the pronuclei mutually exchange their units from time to time, and by assuming, on the ground of experiments with hybrids, that this takes place, on the whole, according to the laws of chance, that is, according to the theory of probability, we have gained a basis which allows us to probe to its very bottom this most significant and mysterious process.