CHAPTER IX

ONTOGENY RESULTING FROM THE UNION OF THE GERM-PLASM OF TWO PARENTS

1. The Nature of the Offspring Determined by the Process of Fertilisation

The first question which presents itself in the consideration of 'amphigonic heredity' is concerned with the relative share taken by the germ-plasm of each parent in the control of ontogeny: — whether the paternal and maternal ids always co-operate simultaneously, and the forces contained within them together form a single resultant, or whether one group only is active while the other remains passive. This question cannot at present be decided from the results of observations on the nuclear substances themselves; the phenomena of heredity, together with what we know concerning the composition of the idioplasm resulting from amphimixis, can alone help to elucidate this problem. These phenomena must therefore be analysed as accurately and minutely as possible.

We must base our analysis on the fact which we have already proved, that the germ-cells of an individual differ from one another as regards the hereditary substance they contain, and that the proportion of paternal and maternal ids in a germ-cell varies between wide limits, the degree of variability being greatly increased by the union of the germ-cells of two individuals in the process of amphimixis. This fact is sufficient to account for the difference existing in the human race between children of the *same* parents. The fundamental law of amphigonic heredity enunciated by Victor Hensen follows directly from this fact: — '*the individual is determined at the time of fertilisation*;' or, in other words, *the individuality of an organism results from the fact that the germ-plasm is composed of the paternal and maternal ids which are brought together in the egg-cell.*

This law is not self-evident, for we might have believed, *a priori*, that the development and mingling of parental characters in the offspring is due entirely, or at any rate to a great extent, to external influences of nutrition, &c., to which the germ is subject after fertilisation. The existence of 'identical' human twins, however, proves the contrary. Some twins do not resemble one another more closely than do children of the same parents which are born consecutively; and, in fact, this is apparently true of the greater number of twins, in which the *dissimilarity may even be very considerable. We have every* reason to suppose that such 'dissimilar' twins are usually derived from *two* ova, which must of course have been fertilised by *two* different spermatozoa. On the other hand, in the case of those twins which I speak of as 'identical,' the resemblance, although not perfect, is much closer than has ever been observed in children born successively. There is every reason to suppose that such identical twins are derived from a single ovum and spermatozoon. If this is actually the case, it furnishes a proof of the above statement that heredity is potentially decided at the time of fertilisation, or, expressed in terms of the idioplasm, that *the nature of the combination of the parental ids which takes place during fertilisation predetermines the whole subsequent ontogeny.* The slight differences which exist between identical twins would therefore probably indicate to what extent the course of development may be affected by external influences. These differences are generally so slight that it is difficult to observe them at all, unless they are specially sought for; as a rule such twins can only be individually recognised by the parents or brothers and sisters, and cannot be distinguished from one another by strangers.

These slight differences might, however, be due to an imperfect predetermination of the influence which is exerted at every ontogenetic stage by the idioplasm of each of the parents. We can hardly decide between these views from the consideration of identical twins only. Mr. Otto Ammon, of Karlsruhe, has kindly furnished me with two photographs of identical twins taken in consecutive years at the ages of seventeen and eighteen, as well as with exact measurements of all parts of their bodies. In spite of a striking resemblance, not only in face but in all parts of their bodies, certain differences are nevertheless recognisable between them. For instance, the height of the one marked No. 507 on Mr. Ammon's list, measured, when lying down, 172 cm., and that of No. 508 only 170 cm.; and again, although the length of the hand and of the left arm is the same in both, —

the latter measuring 74 cm., — the right arm of No. 507 is only 71 cm. long, while that of No. 508 reaches 74 cm. The relative lengths of the upper arm and fore-arm are also different, that of the left upper arm of No. 507 being 27 cm., while in No. 508 it is 27.5 cm.; and consequently the length of the fore-arm in No. 507 is also 27 cm., while in No. 508 it is only 26 cm. Even if we possessed the measurements of the parents at the same age, we should probably be unable to draw any definite conclusions as to whether these slight differences in size are due to a corresponding difference in the combination of the germ-plasm, such as might arise from a slightly inexact division of the nucleus of the fertilised ovum in the process of doubling or at a later stage, or whether they simply owe their origin to slight general or local differences of nutrition taking effect during ontogeny.

Other facts are, however, known, which prove that although the nature of the combination of the parental idioplasms during ontogeny is in general, as a matter of fact, determined at the time of fertilisation, it is nevertheless liable to slight individual fluctuations. Instances of this kind are furnished by the *hybrids of certain species of plants*, many parts of which exhibit a considerable degree of variability, and fluctuate between the specific characters of the two parents. The blossoms of the hybrid plants obtained by crossing *Digitalis lutea* and *D. purpurea*, for instance, 'vary in colour; in some instances they are pale, with a slight pink tinge, which latter, again, may be entirely absent; and in others they have a more or less bright purple colour.'* These observations appear to me to be particularly important, owing to the fact that we may assume with certainty in this case, in which two distinct and sharply defined species were crossed, that both parents possessed the specific characters in the same degree of purity and strength, and that consequently the relative proportion of the parental idioplasms does not remain quite constant during ontogeny, owing either to slight irregularities in the nuclear division, or — and this is less probable — to inequalities in nutrition and in the growth of the idants derived from the two parents. Owing to the kindness of Professor Hildebrandt of Freiburg i. Br., I have had an opportunity, in the case of hybrids of two species of *Oxalis*, of observing how extremely detailed the process of predetermination is. The flowers of

* Focke, 'Die Pflanzen-Mischlinge,' Berlin, 1881, p. 316.

one of the parent-species were large, and of a pale lilac colour, while those of the other were smaller, and their colour was red, with a dark crimson ground. The flowers of the different hybrids were by no means quite similar, but three principal forms could be distinguished according to the combination of colours in the flowers, which I shall not describe in detail: *the flowers of the same hybrid, however, resembled each other in their most minute details.* One plant, for instance, had violet petals of a rather pinker tint than those of one of the parent-species, and all the petals were strongly tinged with red on one and the same lateral margin. As far as I could observe, *all* the flowers were similarly coloured on this stock. On another stock, all the sepals had brown rims, and on a third there was a narrow dark orange-coloured band in the centre of each flower. *In these cases, therefore, the combination of the colours of the parents which appeared in the petals of the hybrids must have been decided at the time of fertilisation.* It will be shown later on how this combination may vary somewhat in different plants.

Even although the slight differences in identical human twins, which can be proved to exist, are certainly due in part to minute differences in the idioplasm itself, some of them must nevertheless with equal certainty be attributed to the effect of various external influences. My photographs of the above-mentioned identical twins show that No. 507 has particularly white hands, while those of No. 508 are much browner. No one would attribute this fact to dissimilarity in the respective germ-plasms, or to an alteration in the proportion of paternal and maternal idioplasm which occurred during ontogeny: it must be due to the fact that the hands of No. 508 had been more exposed to the sun than those of No. 507; and, as it happens, the former of the two had been more employed in the open air than the latter before the photograph was taken. Several differences in the proportional sizes of parts of the body may possibly have been brought about in a similar way.

2. The Share taken by the Ancestors in the Composition of the Germ-plasm

If, then, it is certain that the characters of the developing offspring are essentially decided by the mingling of parental idioplasms which takes place in the process of fertilisation, we must next try to ascertain whether *the entire parental idioplasm,* *with all its constituent determinants, or only a portion of it*, is passed into the germ-cell which will give rise to a new individual; and also *what proportion of it is constituted by the germ-plasm of the grandparents, great-grandparents, and more remote ancestors.* The fact that the reducing division, which takes place both in the male and female germ-cells before fertilisation, removes half of the idants from each, leads us to conclude that *only half the normal number of ids can be contained in each germ-cell;* and this could only be the case if two of each kind of parental idant were present in the germ-plasm, and if the reduction resulted in each individual germ-cell containing a similar group of idants. But this cannot be so, for the germ-plasm must consist of a number of entirely different idants, unless, in consequence of interbreeding, two of the same kind are present in certain of the groups. *The whole of the idants of both parents evidently cannot possibly be contained in any one germ-cell,* because the total number would be twice as great as that which actually occurs in a ripe germ-cell. If in Man, for example, there were thirty-two idants in the fertilised ovum, sixteen of them would be derived from each parent. Of this latter number, sixteen at most could be derived from *one* grandparent, and this could only occur if no idants at all from the other grandparent had passed into the germ-cell in question. It is evidently more than inaccurate to fix the limit of the hereditary power — as is done by animal-breeders — of a parent at $\frac{1}{2}$, of a grandparent at $\frac{1}{4}$, of a great-grandparent at $\frac{1}{8}$, and so on.* These numbers do not even represent the maximum or minimum share in heredity which may be taken by the respective ancestor in the constitution of the fertilised egg. The

* Galton has also emphasised this fact in the concluding chapter of his book on 'Natural Inheritance' (p. 187 et seq.). According to his view, the 'personal heritage' of each parent = $\frac{1}{4}$, and the heritage of 'latent elements' of the parent likewise = $\frac{1}{4}$, the two together thus making up $\frac{1}{2}$. Naturally I cannot agree with this calculation, for in my opinion the latency of the characters of a parent does not result from the 'primary constituents' of these qualities, but from the struggle between the primary constituents of both parents; and I do not in the least suppose that the primary constituents which practically give rise to the individual become separated from those which form the latent germ for the germ-cells of the next generation. But I fully agree with Galton that all the 'characters' of the ancestor — the grandparent, for instance — are never present in every germ-cell from which a grandchild may arise.

parent is certainly always represented by one-half, but the share varies even in the case of the grandparent; in the instance just given it would vary between 0 and 16. For the reducing division may, for instance, cause the sixteen paternal idants resulting from the reduction of the thirty-two originally present in the sperm-cell, to contain idants derived from the grandfather *only, and none from the grandmother; or, again, there might* be fifteen from the grandfather, and one from the grandmother, or fourteen *pp* and two *mm*, or thirteen *pp* and three *mm*, and so on.* This would be so, at least, if any kind of combination of the idants may result from the reducing division. It may perhaps not be the case absolutely, but the capriciousness with which reversion to a grandparent may occur nevertheless indicates that a considerable latitude exists with regard to this combination.

In passing back to the third, fourth, and fifth generations, we cannot in the least determine, *a priori*, to what extent an individual ancestor of the animal in question is still represented in the germ-plasm of a germ-cell; we can only state the maximum which *might* be possible in the most favourable case. In the above-mentioned instance, an ancestor of the third generation *might* still be represented by sixteen idants, for the sixteen idants which this ancestor furnished for the purposes of amphimixis in the second generation might, all in fact, possibly have passed into *one* germ-cell in the process of reducing division in this generation, and the same, again, might have occurred in the first generation. Such a case can only be of rare occurrence, but it apparently accounts for the instances of reversion in Man to ancestors more remote than grandparents, which, though rare, certainly occur occasionally. The more remote the generation, *the greater are the chances against the entire half of* the total number of idants remaining together through several generations in individual germ-cells, and the probability of such an occurrence will very soon be reduced to zero.

We may suppose that, as a general rule, the number of ancestral idants contained in a fertilised egg-cell becomes less in pro-

* I shall now denote the paternal ids or idants by the letter *p*, the maternal ones by *m*, and those derived from the grandfather by *pp* or *pm*, and from the grandmother by *mp* or *mm*, &c. The first letter in each case signifies the parent, the second grandparent, the third the great-grandparent, and so on.

portion as the ascendancy of the ancestor concerned decreases. Any more exact calculation of the share taken by a certain remote ancestor in the composition of the germ-plasm of its descendant would be erroneous. Hitherto the customary method of making such a calculation has been to assume that the following shares are taken by the various ancestors in the predisposition of the offspring:—parents, $2 \times \frac{1}{2}$; grandparents, $4 \times \frac{1}{4}$, and so on; that of the sixth generation of ancestors being $32 \times \frac{1}{32}$. Thus, in the last-mentioned generation, *one* idant out of the thirty-two assumed to be present in Man would, according to the theory of the germ-plasm, still remain. This does not by any means imply that each of the thirty-two ancestors of the sixth generation is still represented by one idant in the germ-plasm of the descendant; it is quite as probable that thirty or even twenty of these ancestors take part in its constitution, and the number may possibly, though improbably, be still less than this. In treating of the phenomena of reversion, I shall have occasion to refer to this subject again.

It is at any rate certain that *in no case can more than the half of the idants of one parent be present in the germ-plasm of the fertilised egg-cell.*

This statement is, however, apparently contradicted by certain facts.

Plant-hybrids frequently keep to the mean between the two ancestral species; that is to say, they contain *all* the characters of these two species in equal proportions. Thus all the primary constituents of each parent would be contained in the fertilised egg-cell, although, according to our theory, only half of the parental idants are concerned in its constitution. This contradiction is easily accounted for, if it be borne in mind that we are here concerned with the mingling of the characters of two *species*, and not of those of two *individuals* of the same species. The *characters of the species must be contained in the majority of ids in each idant*, if not in every id, *and half the idants may in this case produce the same effect as would result if all the idants were present:* that is to say, they contain *every* specific character. In cross-breeding, specific characters are opposed to specific characters, and in comparison with the greater differences between these, the lesser individual ones disappear.

The reverse is true in the case of reproduction in Man, especially within one and the same race. The specific characters are probably contained in all the ids of the father as well as of the mother, and the differences between the parents refer to individual characters only. Our theoretical conception of the idants as a collection of ids seems incompatible with the above-mentioned statement that the child can only closely resemble *one* parent, for only half of the idants of this parent take part in the construction of the child. We shall, however, be able to explain this apparent contradiction later on.

The facts of the case may be stated in general terms as follows. Half the number of parental idants always reach the germ-cells of the offspring, but this half may consist of all possible combinations of the parental idants: that is to say, either of idants derived from the grandfather or grandmother only, or of a combination derived from both, in which one or the other may predominate. Nothing will be gained by taking the ancestors of the third or fourth generation into consideration until we come to consider the phenomena of reversion.

3. The Struggle of the Ids in Ontogeny

a. Plant-Hybrids

The structure of the offspring results from the struggle of all the ids contained in the germ-plasm.

That this statement must be in general correct is to some extent indicated by the fact that all parts of hybrid plants, produced by crossing two species or varieties, usually possess the characters of both parents. The details concerning hybrids are of far greater value for theoretical purposes than are those relating to the normal offspring of any particular species, as we know for certain that the characters which compete with one another or combine, so as to result in the production of a hybrid, must be contained *in every idant* of one or other of the parents; for these characters are those of the *species*.

The difference as regards the idioplasm between *individual* and *specific* characters, seems to me to be due to the determinants of the latter being present in an overwhelming majority in all the ids of every idant of the germ-plasm, while the determinants controlling the structure of individual characteristics are only contained in a portion of the idants of which the germ-plasm consists: *at most* they can only be present in all the idants of one of the parents,— that is, in half the entire number of idants. The extent to which the determinants of any individual character are represented — whether they are contained in all the ids, or only in a small portion of them — could only be ascertained from the phenomena of heredity if we knew the cause of the predominance of any particular 'successful' character. This, however, can only be inferred from crosses between species, the great constancy of the specific characters in which leads us to presuppose that their determinants predominate in all the idants of the parental germ-cell.

In plant-hybrids, paternal and maternal idants come together in the process of amphimixis, and each group of them may be assumed to consist of *similar* idants. The effect this arrangement will produce on the phenomena of heredity must now be considered, and conclusions drawn from these considerations.

From a very large number of observations on hybrid-plants, we find that, in the first place, parental characters may be variously intermingled. From a comparison of all the cases observed up to the year 1881, Focke * concludes that these combinations of characters may be divided into three principal groups, viz.: — (1) *a mean between both parents is maintained in all parts of the plant*; (2) *the characteristics of the father or mother predominate*; and (3) *certain parts of the hybrid exhibit the maternal, and others the paternal, characters.*

The first-mentioned case is by far the most frequent: we may take as an example the hybrid obtained by Köllreutter from two species of the tobacco plant, — *Nicotiana rustica* ♀ and *N. paniculata* ♂. Köllreutter † himself stated that this plant was exactly intermediate between its parents, while it was considered by Gärtner to bear a slightly greater resemblance to *N. paniculata*, and by Focke to *N. rustica*. Köllreutter's opinion is probably therefore a fairly accurate one, for in any case the point can only be estimated, and cannot be decided with mathematical precision. According to Focke, the corolla-tube of *N. rustica* is 14 mm. long, that of *N. paniculata* 26 mm., and that of the hybrid 19 mm. The exact mathematical mean between these is 20 mm.; and hence in this character the hybrid approaches *N. paniculata*. As regards the diameter of the widest part of the

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* 'Die Pflanzen-Mischlingen,' Berlin, 1881.

† Joseph Gottlieb Köllreutter, 'Vorläufige Nachricht von einigen das Geschlecht der Pflanzen betreffenden Versuchen u. Beobachtungen,' 1716.

corolla-tube, on the other hand, the hybrid inclines more to *N. rustica*, while in the narrowest part it exhibits the exact mathematical mean. This case is instructive, for we cannot recognise the true *physiological* mean, because the length, as well as the diameter, of the corolla-tube is determined by the same cells. Any estimation of the mean between the colours must be still less precise, for the different shades depend on entirely different morphological constituents. If the yellow and red of two different species were blended in the flower of a hybrid, the intensity of both these colours might conceivably be as great as in the parent plant, and yet one of them might predominate because it happened to cover the other. For the yellow is due to special pigment-granules, while the red occurs only in the cell-sap, which might possibly be nearly hidden by a superficial layer of chromatophores.

In any inquiry with regard to the factors which control the struggle of the parental characters, it must, above all, be borne in mind that *the cells are always the determining agents.* The determinants of the father and mother come together in the cell, and in the cell only; and all characters, whether relating to a large part of the organism, or merely to a single cell, can only be determined by processes taking place within the substance of one or of many cells.

This does not mean that the *visible* differentiation of every individual cell always constitutes a 'character' of the organism. The nature of the histological differentiation of the cells — that is to say, whether muscle- or nerve-substance, or chlorophyll granules, for instance, are produced in the cell-body or not — only comes into consideration in connection with the *number* of cells in the *definitive* cell-aggregate constituting the organism. Very many characteristic qualities cannot be due to this fact, but must chiefly depend on the number and arrangement of the cells in an organ, which again must be due to qualities of the embryonic cell which are invisible to us — principally those which relate to its *method of division*, and its *vigour and rate of multiplication*.

We must suppose that these factors are wholly determined by the idioplasm of the cells quite as much as is the visible differentiation of the latter. The division of a cell certainly originates in its apparatus for division, and primarily in the 'sphere of attraction' and its contained centrosome; but we should have to give up the whole idea of the controlling influence of the nuclear substance were we to suppose that this apparatus actually *directs* the process of division. The entire process of development of the animal from the ovum depends so essentially on the rate of division of the cells, that the nuclear substance could no longer be considered to correspond to the hereditary substance if it merely caused the visible differentiation of the cell. But in the Introduction I have already stated the reasons which prove beyond a doubt that the nuclear matter actually contains the primary hereditary constituents, and it follows from this fact that there can be no question of a self-determination of the apparatus for division. We must, in fact, suppose that the ultimate structure of the cell-body, which is invisible to our eyes, controls its entire growth as well as its method and rate of division, this structure itself being controlled by the nuclear substance or idioplasm. Ultimately, therefore, everything depends on the determinant of the cell; and in the case of sexual reproduction, the co-operation of the paternal and maternal determinants determines the character of the cell, whether this character is visible or invisible. As every cell in the entire ontogeny is, according to our view, controlled by *one kind* of determinant only, irrespective of the fact whether it also contains other determinants in a latent condition or not, the co-operation of maternal and paternal determinants always determines the character of the cell, and controls the development of the individual as far as the influence of this cell extends. In spite of its greater histological differentiation, a slighter influence is therefore obviously exerted by one of the final cells in ontogeny, — that is, one of the tissue-cells, — than by one of the first four segmentation-cells, or by the primary cell of the entire germinal layer, or, again, by any cell from which many and various kinds of cells may subsequently arise. On the other hand, we must not forget that each embryonic cell only determines its *own* method of division, and not necessarily that of its daughter-cells, and that consequently in these a new counter-balance or co-operation of the paternal and maternal determinants again takes place.

The determinants which control the daughter-cells are, however, derived from the *latent* ids of the mother-cell, and it therefore essentially depends on the methods of division and on the architecture of these ids as to which determinants are to control the daughter-cells. *That portion of the ids of the mother-cell, therefore, which is for the time latent, exerts a definite influence on the determination of the subsequent development*; on it alone, indeed, depends the number and order of succession of the determinants which will subsequently become active, and all those characters which result from the number and grouping of the cells, as well as from the histological nature of the individual cell, are also determined in the first instance by their ids.

We can thus explain why cross-breeding is only successful in the case of nearly-related species, and not in that of members of entirely different families. If it were possible, for instance, for the ovum of a sea-urchin to be fertilised by the spermatozoon of a worm, such as *Rhabditis nigrovenosa*, the disintegration of the ids of germ-plasm derived from the father and mother respectively would take place in an entirely different manner even in the first stage of segmentation; the maternal ids might become disintegrated into the groups of determinants for the right and left halves of the body, while the paternal ids became separated into the groups for the external and internal germinal layers. But dissimilar groups of determinants of this kind could not co-operate and give rise to intermediate structures; and even if the ontogeny advanced a few more stages, embryonic structures could never be produced which would work together harmoniously.

The term *homologous* determinants and ids may be applied to those which control homologous cells and groups of cells. It may therefore be stated that *structures which are intermediate between those of the two parents may arise whenever homologous determinants and ids come together*. If a small spot is present on a certain region of the wing in two allied species of butterflies, for instance, and this is represented in the germ-plasm by a *single* determinant, the homologous determinants of the two cells in which this spot was first contained will be brought together when these two species are crossed, and will eventually be able to share in the control of the cell in question. They need not, however, necessarily be exactly alike; the spot may be brown in species A, and red in species B. In this case the determinants would be homologous but not *homodynamous*, and might possibly combine to form a reddish-brown spot. The essential point in amphigonic heredity is, that *the idioplasm in each cell in the entire ontogeny contains ids which are individually* *different from one another, and does not consist of a number of identical ids; and that the cell may take on an intermediate character in consequence of their co-operation.* In normal reproduction the active ids of the idioplasm are all *homologous*, — that is to say, their function is to control the same part of the body, — but they differ among themselves, *i.e.*, are *heterodynamous*, or, in other words, they tend to impress a somewhat different character on the same part of the body. In the crosses between different species, the idioplasm of a cell in many stages will be composed of homologous as well as of *heterologous* ids, and, as has just been shown, it then remains to be decided whether a common control of the cell is possible at all, and if so, over how many generations of cells it can extend.

The scales of butterflies are cells belonging to the final stage of ontogeny, and their ids are made up of determinants of one kind only. The further back we pass towards the beginning of ontogeny, the more numerous are the determinants composing the ids; only one of them, however, breaks up into biophors and controls the cell. If the determinant which actually controls the cell is homologous in both parents, an intermediate form of cell may result; but as soon as the rest of the determinants in the id no longer correspond to one another, the further development gradually becomes checked, and will ultimately be brought to a stand-still. The processes which must be supposed to take place from the beginning of ontogeny onwards in the case of the supposed cross between a sea-urchin and a worm may very possibly be only *partial, i.e., they may refer merely to special parts.* Let us suppose that a certain species of insect, which is normal in other respects, possesses limbs on the dorsal side instead of wings, and that this is crossed with another insect possessing normal wings, development of the fertilised egg taking place up to the stage in which the wings arise. The idioplasm of the primary cell of the wings and 'dorsal limbs' respectively would then contain two perfectly *heterologous* ids, one derived from the father and the other from the mother, and none of the determinants in these two ids would be respectively homologous. In the first stage of the development of the wings or 'dorsal limbs,' as the case may be, antagonistic determinants would be opposed to one another in each cell-generation, and would prevent a common determination of the cell.

Such extreme cases do not actually occur, as very different species do not interbreed; but the principles which may be deduced from these imaginary cases may be applied to the production of hybrids. *Homologous* determinants and ids co-operate, while *heterologous* ones do not; and the larger the number of heterologous determinants present in the homologous ids of the parents, the more do the hereditary tendencies of the latter tend to nullify one another.

We must now attempt to give a theoretical explanation of the *first of the three kinds of combination of parental characters in the offspring mentioned above*, viz., that in which '*a mean between both parents is maintained in all parts of the plant.*'

If we assume that the two parental species are so closely allied that each determinant in the one corresponds to a homologous determinant in the other, a form exactly intermediate between the two species must result, supposing that the number of ids in either parent is the same, and that a similar controlling force acts on the homologous determinants.

If the idioplasm of one parent is represented by a larger number of ids, its controlling force must obviously be greater; and as regards the controlling force of the individual determinants, we may state as follows:—the control of the cells is in our opinion effected by the disintegration of the determinant into biophors, which, like the pangenes of de Vries, migrate into the cell-body, multiply at its expense, and give rise to definite cell-structures. This multiplication must take place with a certain amount of energy, the degree of which varies in the different kinds of biophors. Thus, whenever such controlling biophors, possessing the energy of growth in different degrees, migrate into the same cell-body, *a struggle of the parts* (Roux) must ensue, in which the stronger part will be successful, and the weaker will be more or less, or even completely, suppressed.

The formation of structures which are strictly intermediate between those of the two parents, implies that the homologous determinants possess a similar controlling force. All the determinants of any two species are, however, never homologous: this follows from the fact that the *number* of cells in homologous parts is often very different. The characters of the species do not by any means depend only on the histological nature of the individual cells, but, as already stated, are due in almost a greater degree to the number and arrangement of the cells, to the repetition and position of certain organs, and so on. Thus the flower of *Nicotiana paniculata* is decidedly longer than that of *N. rustica*, and the former species is more extensively branched and possesses a larger number of glands than the latter. The above assumption that the individual determinants correspond to one another in the two species cannot therefore be quite an accurate one; the germ-plasm of *N. paniculata* must, on the contrary, contain a larger number of determinants than that of *N. rustica*, and the process of disintegration of the two species must differ in many ways.

If an equal number of ids from each of these species occurs in the hybrid, the two kinds of ids will only be able to co-operate in ontogeny as long as their determinants still correspond to one another. As soon as a point is reached in which the ids of *N. rustica* begin to decline in number, and their last determinants have become disintegrated, the ids of *N. paniculata* will alone be able to produce series of cells; but as only half the normal number of these ids are present, the structures arising from them cannot be as complete as they are in the pure ancestral form: and, apart from this, the ids of *N. rustica* may possibly not have disappeared entirely, but the succession of the determinants, which are, properly speaking, the final ones, may persist beyond the normal period, and may in this way interfere with the development of the pure characters of *N. paniculata*. This would, at any rate, render the fact comprehensible in principle that intermediate forms may also arise in cases in which the struggle of the parental ids does not extend into the final cells of ontogeny, and the characters of the species come into contact at an earlier stage, as in the case of the greater or less degree of ramification in plants. The following considerations will make this more evident.

In the *second kind of combination*, either the paternal or the maternal characters predominate in all parts of the hybrid, so that the latter bears a closer resemblance to one parent than to the other: in this case, therefore, *the transmission is apparently monogonic*.

Several cases of this kind have been recorded, in some of which the paternal, and in others the maternal characters predominate. Instances of both kinds occur in the genus *Nicotiana*. 'The hybrid *Nicotiana paniculata* ♀ × *vincæflora* ♂ bears so close a resemblance to the last-named species that the character of *N. paniculata* can hardly be recognised at all.'* In this case, therefore, the paternal plant predominates, while the cross between *N. suaveolens* ♀ and *N. langsdorffii* ♂ 'bears little resemblance' to the latter species. Here, then, the maternal characters predominate, and the hybrid plants are 'extremely similar' to *N. suaveolens*, and are only to be distinguished from it by a partial separation of the stamens from the corolla-tube, a slight difference in the colour and size of the flowers, the violet or bluish coloration of the anthers, and by complete sterility.'

On p. 474 of his book, Focke gives further instances. 'In many cases the resemblance of the hybrid to one of the ancestral forms is so close, that it might easily be taken for a minor variety of this form.' Thus in the following instances the hybrid resembles much more closely the parent form mentioned after each: — *Dianthus armeria* × *deltoides*, *D. deltoides*; *Dianthus caryophyllus* × *chinensis*, *D. caryophyllus*; *Melandryum rubrum* × *noctiflorum*, *M. rubrum*; *Verbascum blattaria* × *nigrum*, *V. nigrum*; *Digitalis purpurea* × *lutea*, *D. lutea*.

These cases seem to me to be of special importance on account of the conclusions which can be drawn from them respecting perfectly similar cases of *individual* transmission in Man. This '*pseudo-monogonic* transmission,' as I shall call it, must be explained in terms of the idioplasm somewhat as follows.

The predominance of one parent — *e.g.*, the mother — might be due to the presence of a *larger number of idants and ids* of the species in question. If, for instance, *Digitalis lutea* possessed thirty-two idants and *D. purpurea sixteen only*, the idants in both cases consisting of the same number of ids, and if the controlling force of the ids were the same in both species, the ids of *D. lutea* would then predominate over the others in every cell during the entire ontogeny; that is to say, the character of *D. lutea* would be impressed more strongly than that of *D. purpurea* on the cell. The objection might be raised that the cell which is thus produced must possess an intermediate character, and cannot be a pure cell of *D. lutea*, even though it resembles the latter most closely. As yet, however, we are unable to determine to what extent intermediate forms of individual cells may occur in individual cases; and the expression 'resultant,' in connection with the unknown forces of the

* Focke, *loc. cit.* p. 289.

biophors, does not indicate anything beyond a mere abstract idea, which is in any case totally insufficient as an explanation of the phenomena. We must be satisfied with the statement that, *when the controlling forces of the two determinants acting together in the cell* are very unequal, the effect of the weaker will be extremely small under certain circumstances. *A 'struggle between the biophors'* takes place, in which we may suppose that the stronger assimilates, grows, and multiplies more quickly, and thus deprives the weaker of room and nourishment, prevents its multiplication, entirely destroys it, and even makes use of it as nourishment. Without a very considerable multiplication, the crowd of biophors which migrate from the nucleus into the cell-body cannot, indeed, exert any determining influence on the latter. It therefore seems to me to be conceivable that an apparent pseudo-monogonic transmission—*i.e.*, a complete suppression of the elements of one parent — may take place even when exactly the same number of ids are derived from both parents.

This is still more likely to be the case if the number of ids derived from one parent is greater than that from the other. We know that the number of idants may vary considerably, even in allied species, and it is therefore not improbable that 'pseudo-monogonic' heredity is sometimes due to this fact. In many plant-hybrids this assumption can be tested directly by ascertaining the number of idants present.

The *third* of the above-mentioned kinds of combination of parental characters seems to me to be theoretically almost the most important of all, for it is most intimately concerned with the ultimate processes which take place in the idioplasm. *In this case the parts of the hybrid plant most nearly resemble those either of the paternal or the maternal form.*

Such cases are apparently not often very pronounced, but fluctuations from the paternal to the maternal side occur to a slight extent in almost all those hybrids which are usually described as intermediate forms. The hybrid between *N. paniculata* ♂ and *N. rustica* ♀, which Köllreutter considered to be a pure intermediate form, bears, as mentioned above, a somewhat closer resemblance to the former species as regards the length, and to the latter as regards the diameter, of the corolla-tube. Such slight fluctuations to one side or the other from the pure intermediate form seem to be of frequent occurrence. Cases are, however, also known in which these fluctuations are so considerable as to become conspicuous. Sometimes, for instance, the hybrid resembles one species as regards its leaves, and the other with regard to its blossoms. Brandza* has recently examined the general, as well as the microscopic structure of certain hybrids, in order to ascertain the parental characteristics exhibited by them, and has succeeded in proving that a fluctuation of this kind exists. *Marrubium vaillantii*, a cross between *Leonurus cardiaca* and *Marrubium vulgare*, for instance, exhibited the winged leaf-stalk characteristic of *M. vulgare*, while the arrangement of the vascular bundles of the petiole resembled that existing in *Leonurus*. The upper surface of the petiole bore branched hairs like those of *Leonurus*, while on the lower surface the hairs resembled those of *Marrubium*.

I shall speak of this fluctuation in the resemblance of the *organs* to those of the parents as '*the shifting of the hereditary resultants in ontogeny*.'

We might imagine, *a priori*, that such a shifting cannot possibly occur. If, as has been proved, transmission is virtually completed at the time of fertilisation, and if therefore the relative proportion of the two parental idioplasms is also fixed *for all the subsequent ontogenetic stages* when they have once been combined, we might expect a *similar combination* of the characters of the parents to appear in all parts of the young plant, so that these would either be exactly intermediate between those of the two parents, or else that the paternal or maternal characters would everywhere predominate in a similar manner. The fact that this may not be, and in fact is usually not the case, may be accounted for in several ways.

In the first place, we must bear in mind the statement made above, that a combination of two characters in equal proportions need not always give rise to one which is apparently intermediate, and that it is impossible to give an exact definition of what is meant by such a character, because we only observe the final effect of forces acting within the cell, and not the actual processes by which this effect is produced. This, however, would not be a true shifting of the hereditary resultants, but only an *apparent* one.

Genuine cases of such a shifting, however, undoubtedly occur;

* Brandza, 'Compt. rend.' 1890, T. III, p. 317.

and I believe that they are principally due to the fact that the *number of homodynamous determinants in the idioplasm of a cell may vary in the course of ontogeny, and that, in fact, it must always do so.* In one stage or in one organ the paternal, and in another the maternal ids will contain the majority of homodynamous determinants, and the fluctuations in the predominance of the maternal or paternal characters, *which is definitely determined in advance,* must depend on this fact.

To make this clear, I must intrench somewhat upon the chapter on *Variation.*

b. Intercalary Remarks on Variation

Hitherto we have assumed that the germ-plasm of a species is composed of ids, each of which contains *all* the characters of the species. A brief consideration, however, shows that this cannot be the case. Not only is it conceivable, but it is even necessary to assume that the development of the characters of the species, as well as those of the individual, is only the expression of the forces to which these processes are due, the ids in which the forces are situated being by no means perfectly similar to one another. A great majority of the ids certainly contain all the determinants of the species, — that is, they are capable of giving rise to all the specific characters; but in a minority of the determinants, to which, indeed, the origin and development of this species was due, will not yet have begun to undergo a phyletic transformation. All the determinants in this minority need not necessarily be similar to one another; one id, for instance, may contain unmodified determinants of the ancestral species; while another, although still retaining some of the old determinants, may exhibit a greater resemblance to the pure ids of the existing species, and so on. Such a *gradual transformation of the ids* affecting the majority of their determinants must constitute, indeed, the process of the formation of the species; and it will be quite in accordance with the principle of variation to assume that modifications must take place in the invisible vital units of a lower order, viz., the ids and biophors, in exactly the same way as they occur in different degrees and directions in different individuals in the visible vital units, — the unicellular organisms and persons of stocks.

Thus the provisional hypothesis put forward above, that the germ-plasm of a species — as far as it concerns the specific char-

acters — consists of a number of identical ids, cannot be a strictly correct one: the germ-plasm must, on the contrary, contain a majority of completely modified ids provided with new determinants of the species, and of a minority of ids of the ancestral species which are only slightly or not at all modified. The number of the latter will diminish in the course of time in consequence of selection of the individuals, and the new specific characters will gradually lose their original variability. Owing to natural selection, the germ-plasm will gradually be relieved of those of its ids which have become only slightly or not at all modified in the new direction, for those individuals in which it still contains a large number of unmodified ids are as well adapted as the others for the conditions of existence. As these individuals are gradually eliminated in the struggle for existence, the number of unmodified ids in the subsequent generations must gradually become reduced; and *this process of selection in the germ-plasm will only reach a limit when the number of unmodified or incompletely modified ids has become so small that their influence on the development of the essential characters of the species is inappreciable.*

This process of transformation of the ids of the germ-plasm will, however, reach a limit, as do all processes of selection, when its continuance is no longer of any advantage. All adaptations in an animal remain stationary and are not further perfected, directly further improvement becomes useless; and in the same way the process of modification and elimination of the ids, which forms the basis of other adaptations, will cease as soon as the completely modified ids are present in such a majority that the others can only exert an inappreciable influence on the nature of the offspring. The useful and adaptable characters will always undergo complete development in the normal process of reproduction, — that is to say, in the intermingling of individuals of the species, — even though some unmodified ids may be present in the germ-plasm. Let us take as an example the well-known case of the butterfly *Kallima parallecta*, which resembles a leaf. The resemblance is very marked, although not a complete one. The form of a leaf, with its midrib and veins, — some regions appearing more or less faded, and some dry or wet, and even of the appearance of a dewdrop, — is indicated on the folded wings, but *only certain of the secondary veins on the right and left of the middle line are represented.*

This is quite sufficient to deceive the birds which pursue the butterfly, and a more accurate copy of the markings on a leaf would not increase the deception; for it only needs to be effective at a certain distance, and therefore has not increased in perfection, but has reached its limit at this stage. A precisely similar occurrence must take place as regards the modification of the ids of the germ-plasm if a new adaptation of the species is concerned. In such a case, again, only a *relative* and not an *absolute* perfection will be attained. The majority, but not *all*, of the ids may become modified by selection, while a minority must accompany these through long periods and generations in an unmodified or slightly modified condition.

I have had to make this digression on the transformation of species in its relation to the germ-plasm, in order that my explanation of '*the ontogenetic shifting of the hereditary resultant*' may be comprehensible. It follows from the process of the gradual transformation of the ids of germ-plasm and the transference of unmodified ids from one cell-generation to another, *that the germ-plasm of every species must consist of a combination of ids of a somewhat different nature.* For although specific characters must have appeared simultaneously, and many others must have arisen successively, in the course of many generations, all the characters of the species will not be represented by determinants in the same number of ids. The oldest character, in fact, will be contained in almost all the ids; those which are somewhat younger, in a considerable majority; and still younger ones, perhaps also in a slight majority; while those which have only just begun to be of use to the species will only be present in a minority of the ids of each individual.

This circumstance is evidently connected with the degree of variability of characters, which may, in fact, be a very different one as regards the different characters of a species. Characters on which selection is only beginning to act, can only be represented by a majority of ids in a minority of individuals, and the less variable characters are those which have been selected for a greater number of generations, and are therefore present in a large number of ids of numerous individuals; and again, those characters which have long become definitely fixed in all or almost all the individuals of a species, must be also represented in the majority of the ids in almost all these individuals. *Conversely, those characters which are beginning to become useless to the species must be contained only in a gradually increasing minority of the ids*; the number of the latter must gradually decrease, until it finally becomes so small that it can no longer give rise to the character in question in consequence of an overwhelming majority of the other ids.

The above conception of the germ-plasm enables us to understand why the force of heredity may vary *in the course of ontogeny* in the case of crosses between two species, and why the paternal tendency may dominate in one character and the maternal in another. For, quite apart from the possible degree in which the force of heredity may be present in the individual determinants, and assuming it to be equal in the two species, the *number* of ids which contain homodynamous determinants will nevertheless vary *according to the age of the character in question*. A greater number of ids containing homodynamous determinants will indicate a greater force of heredity. If the form of the flower in a species A was acquired long ago, while that of the leaf is a new acquisition, and if the reverse is true in the case of a species B, the hybrid which would be obtained by crossing these two species would resemble species A in the form of its flowers and species B in that of its leaves. A larger number of homodynamous determinants of species A, for the rudiments of the flowers, will be opposed to a smaller number of homodynamous determinants of the species B, which, on the other hand, will contain a larger number of homodynamous determinants for the rudiments of the leaves. The importance of the whole principle will be made still more evident in the following section.

c. The Struggle of Individual Characters

The question of *individual* characters in the two parents has not been taken into account in our previous investigations: in crosses between different species they may be looked upon as insignificant when compared with the specific characters. We must now consider those cases in which the two parents differ in respect of slight individual characters only, confining ourselves to the human race, the individual characters of which we can recognise most clearly.

What strikes us most forcibly in connection with the process of reproduction and transmission in man, when compared with that of the formation of hybrids in the vegetable kingdom, is *the dissimilarity between children born of the same parents.* In the case of plant-hybrids, a striking constancy is observable in the offspring of a cross, and this is true not only of the offspring of the same parents, but also of all the hybrids produced by crossing any individuals of the two species in question, if the latter also are constant.

The dissimilarity between the children of the same parents has been already mentioned, and was explained as resulting from the halving of the germ-plasm in the process of 'reducing division,' which takes place in a different manner each time, and, when a larger number of idants are present, gives rise to a surprising number of combinations. As the idants are very different with regard to the *individual* primary constituents they contain, new combinations of the latter are thus continually being formed without affecting the characters of the species.

Three principal kinds of combination have to be considered in any attempt to explain the blending of parental characters in the child, — that is to say, to refer it to processes which take place in the idioplasm: these are (1) *the characters of the child are intermediate between those of the parents*; (2) *the child exclusively or principally resembles one parent*; and (3) *the child resembles the father as regards some characters and the mother in respect of others.*

The first case, if it ever *strictly* occurs, must be attributed to the presence of a precisely similar controlling force in all the determinants.

The number of idants derived from each parent must be the same in this case, as the parents belong to the same species, and there will certainly also be very little difference as regards the number of ids; the number of determinants, moreover, will be the same, or almost the same, in the germ-plasm of the two parental germ-cells. Theoretically, an exactly intermediate form would therefore result if each determinant of the father and mother were homologous to one another, and if the homologous determinants were controlled by precisely similar forces, — *i.e.*, if they contained the same number of biophors, and the homologous biophors of either side possessed the power of assimilation and reproduction to the same extent. These conditions which we have presupposed will, however, hardly exist all together, but they may concur approximately with regard to a certain number of characters.

It can hardly be doubted that the *second kind of combination* occurs, and that in some cases the *offspring take after one or other of the parents only*, — not only in respect of those characteristics with regard to which the term 'resemblance' is generally applied, such as those which concern the form and expression of the face, but equally as regards stature, form of the body, proportions of the limbs, nature of the skin and hair, character, and temperament.

We are met with a two-fold difficulty in attempting to explain these facts: in the first place, how is it possible for all the primary constituents of one parent — *e.g.*, the father — to be present in one of the germ-cells of this parent, as the germ-plasm was halved by means of the reducing division before these germ-cells become ripe? — and secondly, how can it happen that the maternal germ-plasm exerts no influence on the formation of the child?

Let us first consider the former of these two difficulties: how is it possible for all the characters of the father to be contained in one paternal germ-cell in spite of the reducing division? If the latter process resulted in a quantitative halving of the germ-plasm, no further explanation would be necessary, for the quality of half the mass might be exactly similar to that of the whole. But a reduction of the units of the germ-plasm to half their number occurs in this process; the number of ids is reduced by one half, and the structure of the offspring results from the combination in the germ-plasm of the ids of both parents, as was shown in the case of plant-hybrids; it is difficult, therefore, to understand why half the number of ids can nevertheless give rise to all the characters of the parent. Strictly speaking, it is immaterial whether we concern ourselves with *all* the characters, or with only a *single* one; for many characters, in fact, depend on the co-operation of all the ids of the ontogenetic stages in question.

There is only one way out of this difficulty, — we must accept the assumption, which has been confirmed by fact, *that the controlling power of the ids of one of the parents may become nullified at every ontogenetic stage.* Observations on plant-hybrids are invaluable in this connection, for in them we know for certain that the ids of another species are present, even although they may not produce a perceptible effect. We may conclude from the phenomena of 'pseudo-monogonic' heredity exhibited by these hybrids, that the ids of one parent may, as has already been explained, prevent those of the other from taking part in the control of the cell, group of cells, or part of the body.

We may therefore assume that if by means of the reducing division, all the idants *which controlled or dominated the ontogeny of the mother*, for instance, reach one of the germ-cells produced by this parent, this germ-cell will be capable under certain circumstances of reproducing the maternal 'type'* in the child. But in order that this may happen, it is necessary for this cell to unite with a sperm-cell, the germ-plasm of which possesses on the whole a weaker controlling power than its own, so that the germ-plasm of the father is dominated by that of the mother.

As in the case of crosses between species, the controlling power of the idioplasm will not always be dependent on the same cause.

We cannot enter more deeply into those cases in which a more marked force of heredity of individual characters occurs. Darwin mentions, for instance, that the 'white' colour, in flowers as well as in animals, is very commonly transmitted to the offspring when white individuals are crossed with dark-coloured ones, the majority of the descendants inheriting the white colour. We can in this case only assume that those biophors which dominate the cell, and give rise to the white colour, must be 'stronger' than those which cause the formation of pigment, and this 'strength' must, in fact, be attributed to the possession of a greater power of assimilation.

The case is different in many other instances in which the greater hereditary power is attributable to *quantitative* differences in the constitution of the paternal and maternal groups of idants.

The number of ids contained in each idant is certainly constant, or nearly so, in all individuals of the human spe-

* I shall make use of the term 'type' ('Bild'), to express the whole aggregate of essential characteristics which together constitute the individuality of a human being.

cies;* but a predominance of paternal or maternal ids may nevertheless exist, so that there may be *a greater number of homodynamous determinants* in one line of ancestors than in the other, as has already been shown to be the case in hybrids.

By the term *homologous* determinants, we understand those elements of the idioplasm which are capable of so controlling homologous parts of the body or determinates; *homodynamous* determinants, on the other hand, are those of the homologous determinants which have the special function of impressing *a like character* on any part of the body, and which, taking an example we have already made use of, serve to produce a *particular form and colour* in a certain region of a butterfly's wing. That parent in which the ids contain numerous homodynamous determinants, or at any rate a larger number than are contained in the ids of the other parent, must undoubtedly exert the greater controlling power. The power of homodynamous determinants is simply cumulative, whereas dissimilar or heterodynamous determinants may, in the most favourable cases, co-operate to form a single resultant, but may, under certain circumstances, counteract or even neutralise one another. The larger the number of homodynamous determinants which the entire aggregate of ids of a parent contains at any ontogenetic stage, the greater will be the likelihood that these will predominate in the struggle of the parts which takes place in the cell, and will therefore stamp the latter more or less distinctly.

The colour of the eyes may be taken as an example. Let us take a case in which those of the mother are blue, and those of the father brown. The number of ids in the idioplasm of the pigment cells of the iris will be the same in both parents, but in the case of the father nine-tenths of them, let us say, are composed of 'brown'† determinants, and only one-tenth of deter-

* It is conceivable that individual fluctuations in the number of ids may occur, although the number of idants always, indeed, remains the same — if one can judge by its constancy in many animals and plants. Unfortunately we do not yet know the number of idants in the case of man; I have, at least, been unable to obtain any information on this point.

† 'Brown' and 'blue' determinants are spoken of in this and subsequent passages simply for the sake of brevity. I am not ignorant of the fact that the blue colour of the iris is not due to blue pigment. The above terms merely indicate that the determinant produces a structure in the iris which causes it to appear blue or brown, as the case may be, quite apart from the histological details on which this depends.

minants of other colours; two-thirds of the ids of the mother on the other hand consist of blue, and one-third of brown determinants. The iris of the child will therefore most probably be brown, for in its formation nine-tenths of the determinants of the father will co-operate with one-third of the determinants of the mother, which are homodynamous with these. The predominance of the brown determinants would also, however, still be assured if the maternal ids contain no determinants at all of this colour, but only red or green ones,—supposing that red or green pigment cells occurred in the human iris. For in this case nine-tenths of the paternal determinants would be opposed to various small groups of heterodynamous determinants of the mother. The latter might possibly modify the brown colour which would be produced by groups of paternal determinants *alone*, for they also control part of the cell-body; but it is quite as conceivable that they might be completely overcome by the paternal determinants, and thus excluded from the control of the cell. We cannot, as already stated, at present judge as to the result of the struggle of the parts in individual cases, but there is no doubt that, provided the controlling power of the determinants is similar, the *number* of the latter is of the first importance.

Since, therefore, the nature of the combination in the germ-plasm is different in every individual in consequence of sexual reproduction, the number of homodynamous determinants of any particular characteristic must also be different in every case. It will be shown in the chapter on variation that processes of selection may even bring about an increase or decrease in the number of the homodynamous ids of individual characters, although these are never of sufficient biological importance to give rise to specific characters.

The same competition of forces must take place in the case of individual as in that of specific characters. A child may inherit the colour of the eyes from its father, and the shape of the mouth from its mother, just as in a plant-hybrid the form of the leaf may resemble that in the paternal, and the flower that in the maternal plant. In both instances the character is inherited from that parent in which the group of idants contains a *preponderating majority of homodynamous determinants* of this character. When this is the case, this majority preponderates over the scattered minority derived from the other parent.

In neither instance, however, does the preponderance of the father, as regards a *single* character, necessitate that *all the other* characteristics will be controlled to the same degree by this parent. The germ-plasm consists of an equal number of paternal and maternal idants and ids, which remains constant throughout ontogeny. We suppose that every id of the germ-plasm contains all the determinants of the species, *e.g.*, the determinant a for the character A, the determinant b for the character B, and so on. But all ids of the germ-plasm need not contain a number of homodynamous determinants only; for if id i, for instance, contains the determinant a^1, id ii may perhaps contain the determinant a^2 for the homologous character, and id iii the determinant a^3, id iv the determinant a^4, and so on. There is no reason why id i, in which the determinant a^1 represents the character A, should not contain the determinant b^2 instead of b for the character homologous to B. If we denote the determinants of corresponding characters — *i.e.*, those which may become substituted for one another — by the same letters, a certain id of the germ-plasm — *e.g.*, id i — might contain the determinants $a^1, b^2, c^4, d^3, e^1, f^5, g^6, h^8, i^5$, &c. If in the germ-plasm of the father id i, id ii, id iii, id iv, and so on to the last, which I will call id xx, all contain the determinant a^1 for the character A, and none of the variants a^2, a^3, &c., are present in them, this determinant a^1 will be more powerful than any other variant of a derived from the mother, which may exist in the idioplasm of the cell in question, provided that the total number of each of these variants is less than twenty. Hence the character A^1 will be impressed on that particular cell, or group of cells, and not A^2 or A^3. The case may be entirely different as regards the character B; the determinant b^3 or b^4, for instance, may be the dominant one in most of the ids and idants: and in this case, one of the other variants of B, such as B^3 or B^4, will be produced.

If we may compare the groups of paternal and maternal idants to two centres of force each of which attempts to obtain control over the cell, each of these two forces will be determined by the individual forces of the idants in which they are contained, while the force in each idant will be controlled by the individual forces of the ids of which it is composed. If, for instance, there are two idants derived from each parent, each consisting of ten ids, the following considerations would enable us to ascertain which variant of the character must actually be produced. The paternal idants P^1 and P^2 might each consist of ten ids, the same determinant a^5 being contained in six ids in P^1, and in eight ids in P^2. These two idants would then combine in the attempt to give rise to the character A^5, with a controlling force of $6 + 8 = 14$ ids. Each of the maternal idants M^1 and M^2 might also contain ten ids, M^1 being composed of two determinants a^1, four a^3, three a^7, and one a^{10}; this idant will therefore tend to produce the character A^3 with a power of four ids only. If now, the other maternal idant M^2, with all its contained ids, tended to give rise to the character A^6, with a power, that is, of ten ids, the group of paternal idants would nevertheless predominate over that derived from the mother, as fourteen paternal are opposed to ten maternal homodynamous determinants. In this case both parental groups might possibly control the character of the child together, but the paternal group would be the stronger of the two. If, however, eighteen homodynamous ids of the father were opposed to four homodynamous ids of the mother, the influence of the latter would be entirely suppressed as regards the character A. We must at any rate conclude from the facts of the case, that the characters of one parent may be strictly inherited without any apparent intermingling of the corresponding characters of the other parent. As already mentioned, this very point in the theory seems to me to be the most reliable one, and known facts concerning plant-hybrids compel us to accept this assumption. The controlling force of the groups of paternal or maternal idants may be entirely different in respect of individual characters and groups of characters, according to the number of homodynamous determinants by which these are respectively represented. Moreover, this depends not only on the fact as to whether the individual character is derived from the father or the mother, or is a mixed one, but also on the entire number of homodynamous determinants present from each parent.

Although I have all along spoken of idants, I do not wish to imply that every idant behaves as an *independent whole.* Neither do I suppose that the resultant of the forces of the whole aggregate of paternal, is opposed to that of the maternal ids. It is quite conceivable that the same homodynamous determinants occur in the ids of both parents, and that their forces are cumulative, just as they would be if present in *one* or *the other* parent only. Homodynamous ids *must*, indeed, frequently occur in both parents in cases of close interbreeding, as well as in species which exist in comparatively small numbers in small isolated districts.

It is obvious that this struggle of the parental ids takes place at every stage in ontogeny, and that its result is different according to the state in which the forces exist at this stage. This accounts for the frequent changes as regards the resemblance to one or other of the parents, and for the combination of parental characters which occurs in different parts of the body.

The facts, so far as they are known to me, apparently agree very satisfactorily with the above explanation. I have attempted to collect fresh evidence bearing upon this question, which till now has not been closely kept in view. This, however, has unfortunately not been so easy a matter as might have been expected, but I will mention some of the facts relating to this point.

In some cases a child resembles its father in most respects, and takes after its mother as regards a few minor parts. This would be inexplicable if the whole part were not controlled by the resultant of a determinant other than that for the individual portions of this part. The single determinant and its immediate successors, which control the primary cell of the whole part, determine, in the first place, the rate of the cell-division and the primary form of the entire organ; but in each subsequent stage, one of the succeeding determinants takes on a controlling function, and as its influence is always the resultant of the homologous determinants of all the ids of the cell, the successors of this cell may at any time differ from one another with regard to their resemblance to those of the father or mother.

A person of my acquaintance resembles his father very closely in respect of that portion of the skin which is derived from the external germinal layer. In both the father and son the epidermis is thick and inclined to be horny. The nails of the hands are much thickened, and the skin on the soles of the feet is especially hard. In this case, therefore, the force-resultant of the paternal determinants must continually have been stronger than that of the maternal ones from the primary ectoderm onwards, through a long series of cells. On the other hand, the resultant of the maternal determinants seems to have predominated at the formation of the brain, which likewise arises from the external germinal layer, for the person in question resembles his mother as regards most of the mental qualities, such as intelligence, talents, and strength of will. This can only be accounted for on the supposition that the determinants of the subsequent descendants of the primary ectoderm-cell were unable to exert any influence *upon this cell itself*; in it they were still latent, and in this condition were merely passed on to succeeding cells. If the ids of subsequent generations of these primary ectoderm-cells which formed the rudiments of the brain, contained more maternal than paternal homodynamous determinants, a resemblance to the mother instead of to the father would arise at this point.

In the above case, the *entire* brain does not seem to have taken after that of the mother, for marked paternal traits also exist in it. According to our theory, it may well be conceived that even such a repeated alternation of hereditary tendencies as has occurred in this instance is predetermined in the germ, for the power of the paternal, and naturally also of the maternal ids, varies throughout ontogeny at every further stage in the division of the ids, and the relation between the controlling forces of the father and mother may be transposed. In general we might even expect that one or other group would predominate in most cases, and that the child is consequently composed of a combination of parental characters which varies in different parts. The parts or organs which resemble those of the same parent may also vary very considerably as regards size: this is possibly true of a single cell, as well as of a whole organ or an entire germinal layer, or even of the entire organism.

This theoretical deduction is in general supported by facts, for a child is rarely or never an exact repetition of either parent. It is by no means easy, indeed, to form a correct estimate with regard to the resemblance between parent and child, for in order to do so, an exact knowledge of both at the same ages would be necessary, and a detailed comparison is only possible between father and son, or mother and daughter. It would therefore be essential to compare photographs of the father and son, *at the same ages*; and this, as far as my knowledge of the observations which have been made on heredity extend, has never yet been done. It would, moreover, be necessary to photograph the whole body, and not merely the face.

As far as we can at present gather from the facts, even in those cases in which the resemblance is a close one, the child always differs from the parent either as regards individual characters, or, as is more frequently the case, in undefinable slightly characteristic details, such as the length of the limbs, colour of the hair or eyes, or the quantity of hair. These parts cannot be said to resemble those of the other parent, but they give the impression that the main direction in which heredity has tended has been slightly changed in an undefinable way. A daughter may resemble her mother, for instance, so closely that she is universally said to be an exact image of her mother; and yet a close comparison will show that the likeness is by no means an exact one, and although the child may not display a single paternal character, there are nevertheless a number of parts which respectively differ from those of the mother. In the case of identical twins, there can be no doubt that many of the minor differences existing between them are due to differences in the germ-plasm, and not to the diversity of external influences. The germ-plasm of both parents, that is to say, has taken part in determining the different parts of the child, although in the case of one parent this determination is slight and little marked, and has caused a slight deviation from the maternal characters rather than the development of specifically paternal ones.

If this view is correct, and the germ-plasm of *one* of the parents alone never determines the formation of the child, it becomes more obvious than ever that even when heredity tends to follow in the direction of one of the parents in the greatest possible degree, the mother and daughter can never resemble one another so closely as do identical twins. Owing to the slight influence of the germ-plasm of the father, the type of the daughter deviates somewhat from that which would have been produced from the maternal germ-plasm *alone*; and similarly, if the mother owes her nature to the predominance of the germ-plasm of one parent, a slight deviation must have occurred owing to the weaker influence of the other parent. But the whole of the germ-plasm of *both* grandparents cannot possibly have been contained in the maternal germ-cell from which the daughter arose, for the reducing division causes the removal of half the germ-plasm from the egg-cell before fertilisation takes place. Even if the idants which materially determine the type of the mother remained in the ovum from which the daughter was developed, the group of idants of the other grandparent, which would modify this type somewhat, must necessarily be absent; the types of the mother and daughter consequently cannot exactly correspond, for the double reason that the influence of one grandparent was wanting at the development of the daughter, while that of the father was present in addition.

The following examples may serve to show *in how many different ways the hereditary tendencies of the parents may*, in accordance with our theory, *be interchanged in the course of ontogeny*. In the bilaterally symmetrical human being, all those parts which are not situated in the median line are paired, and the corresponding organs generally behave nearly, if not quite, similarly as regards heredity. If one hand bears a decided resemblance to that of the mother, the same will, as a rule, be true of the other also; and if the left leg is intermediate between the character of both parents, the right one will also be so in exactly the same degree. Even such a subtle characteristic as the colour of the eyes usually corresponds in both organs; and even in those cases in which it is intermediate between that of the two parents, the colour only varies slightly in shade in the two eyes. One might be disposed to conclude from this fact that paired organs are represented by a single primary constituent in the germ-plasm. This, however, would be an erroneous conclusion; for, apart from the facts already mentioned which contradict such a view, there are *exceptions to the rule that paired organs are similar to one another*. One brown and one blue eye sometimes occur in dogs, especially in boar-hounds, and I know of a similar instance in the human subject: the father, a brewer in a small Suabian town, has blue eyes, and the mother brown ones, while a daughter of twelve years of age has one blue and one brown eye.

In addition to these cases, the frequent *inheritance of birth-marks* and other minor characters on one side of the body only, necessitates *the assumption of double determinants for the corresponding parts of each half of the body*. We must therefore imagine that each id of the germ-plasm of bilateral organisms is primarily bilateral, and that all the determinants, indeed, of the whole body are double, even of course including those for the organs which are apparently situated in the median plane, but which actually consist of corresponding halves. In a large number of animals the two first segmentation-cells of the egg, or blastomeres, correspond to the future right and left halves of the body. The first division of the nucleus of the fertilised ovum must therefore separate the determinants for the right and left halves of the body; and the occurrence of this process is rendered all the more probable from the fact that a longitudinal division of the idants actually occurs, and results in each of the spherical ids being halved.

The explanation of the striking correspondence of the homologous parts of *antimerous* or paired organs must be referred to the history of the transformation of species. The permanence of this resemblance during the continued crossing of individuals, is naturally due to this approximate similarity of the corresponding determinants for the right and left sides in both parents. It is evident, according to our conception of the structure of the idioplasm, that the resemblance of the corresponding parts of the child originates in the antimerous determinants of both parents, for the latter determine the comparative number of homodynamous ids on the paternal and maternal sides, together with the relative 'controlling power' of the idioplasm of the father and mother in the organ in question. And since this must be the same on both the right and left sides, the organ itself must display the same combination of paternal and maternal characters on either side: that is to say, its two sides must be alike.

I do not think that these facts can be understood by the aid of any other theoretical assumption with regard to the structure of the hereditary substance. The assumption of the existence of pangenes, for example, might certainly explain the circumstance that a combination of the paternal and maternal characteristics does indeed occur in the organ in question, — in the external ear, for instance, — but it cannot account for the fact that this combination is similar in the right and left ears.

These very facts seem to me to furnish a further welcome proof of the correctness of the view arrived at by other methods, that the hereditary combination in each part is predetermined from the germ onwards. The right and left ears could not possibly resemble each other, if the relative strength of the hereditary tendencies on both sides were not predetermined for all parts of the child by the nature of the paternal and maternal idants.

There are, however, exceptions to this rule. As already stated, the homologous parts of the two antimeres may differ from one another; and such a difference is even frequent in certain animals, though it only affects characters which are of minor biological importance. Little attention has hitherto been paid to the fact that many of our *domestic animals have lost the original symmetry of the marking of their coats*. Piebald cats, dogs, horses, cows, and guinea-pigs are not uncommon, and show that the symmetry of the markings may become completely lost by domestication. This must be owing to the fact that these originally symmetrical patches of colour are, in consequence of domestication, no longer of biological importance. If the determinants for these characters varied in different ways on the right and left sides, and the animal in question thus became spotted, no disadvantage would thereby result, and the animal would nevertheless be able to exist and produce offspring. If two individuals with different piebald markings then paired, the asymmetry in the coloration and markings would be increased; and as a matter of fact in many of our races of cattle no parts of any two animals are alike in this respect, and the same is true with regard to many dogs and guinea-pigs. We know how important these markings and coloured patterns may be for the preservation of individuals and species *in the natural condition*, and are therefore justified in attributing the retention of the symmetry to natural selection, and its loss to panmixia.

Certain facts with regard to the *metameres*, or successive parts of which the body of a segmented animal is composed, show that the maternal or paternal characters may preponderate in different segments. This naturally cannot be proved in the case of Man, as the metameric segmentation only affects the bones, muscles, and nerves, which are not externally visible. But I think I have observed that consecutive parts, even when they are homologous, may occasionally exhibit different hereditary types. A child may closely resemble its mother as regards the arms and hands, and nevertheless may take after its father in respect of the legs and feet. I have endeavoured to ascertain whether any definite rules are followed with regard to certain organs which are closely related to one another in ontogeny, according to which these organs would exhibit a similar combination of parental characters; but the only rule I could discover is that which relates to the symmetry of the two halves of the body. Apparently all possible combinations may actually occur. The form of the skull may resemble that of the father, and the face that of the mother; or the form of the entire head and face may be like the mother's, while the eyes may be similar to the father's in every detail. The son may, like his father, possess a dimple on the chin, although he takes much more closely after his mother as regards the shape of the face and nose. That the combination of parental characteristics may even extend into far greater details, is shown especially by the remarkable amalgamation of the mental qualities of the parents which often occurs. The intellect and practical talent may be inherited from the mother, and strength of will and unselfishness from the father; and all these qualities may be contained in one skull, the form of which essentially resembles that of *one* of the parents only. These combinations of mental characteristics of the parents cannot, however, always be definitely analysed, owing in the first instance to the fact that they are not always sharply contrasted in the parents, but more frequently are only different in degree. We may, however, at any rate consider it certain that *the brain rarely resembles that of one parent only in all its parts and as regards the most minute details of its structure;* it usually, on the contrary, exhibits a combination or alternation between that of the two parents, and this combination is of the most varied kind.

In connection with this statement it may be mentioned that no part of the human body is so important as the brain in the struggle for existence, and its importance extends even to the minutest details; its parts must therefore be subjected to incessant processes of selection. In other words, the number of homodynamous determinants in the various parts of the brain must be extremely different in the individual, and must vary extremely in different individuals.

These statements with regard to the struggle of the individual characters may perhaps be objected to on the ground that they contradict the suppositions with which we started. It may be contended that an alternation of paternal and maternal hereditary parts is rendered possible on the basis of my theory, because the transmission of a paternal character implies that the whole dominant group of idants of the father passed into the germ-plasm of the child at the reducing division, and the transmission of a maternal character necessitates the presence of the whole of the dominant group of the mother. It might be considered improbable that both of these groups should come together in one germ-cell, or that this can occur as often as must be the case in reality, considering the frequency with which a combination of the two parental characters exists.

In reply to this it may be stated that the meeting of two germ-cells in the process of fertilisation, one of which contains the dominant group of idants of the mother and the other that of the father, must take place from time to time, for every possible combination will occur at one time or another. It must, moreover, not be forgotten that it is extremely difficult to distinguish between the pure individual characters of a parent and those of one of the immediate ancestors of this parent; but the production of these characters in the latter does not necessitate the presence of the whole of the dominant group of parental idants, for a portion of them will undoubtedly suffice if the character in question is represented by a majority of homodynamous determinants. The characters which alternate are very often not the specifically paternal or maternal ones, but those which in general characterise the mother's or the father's family. These, however, must be represented in most of the ids of the dominant group of idants, and may therefore become apparent even when the reducing division only causes a certain number of idants, instead of the entire dominant parental group, to pass into the germ-cell of the child.

On the other hand, the frequency with which a child bears a closer resemblance either to its father or mother — and this in many families is actually the rule — can also be easily explained by our theory. In such cases, not only can the whole number of dominant idants produce the type of the parent in question with approximate accuracy, but even a majority of them will be sufficient to do so, provided that a large number of ids with homodynamous determinants are contained in them. Many germ-cells will, therefore, contain a sufficient number of the dominant idants of the parent, while others, although perhaps containing an equally large number of these idants, will consist of various combinations of ids enclosing relatively few homodynamous determinants. If, then, an idant of the former kind, derived from the father, should, in the process of amphimixis, meet with one of the latter kind, derived from the mother, the type of the father would predominate in the child, and *vice versa*. If two germ-cells of the first kind, derived from the father and mother respectively, came together, a mixture of the characters of the two parents would result; and if two of the latter kind came into connection, none of the special characteristics either of the father or mother, would be recognisable in the child, which would only possess such characters as are common to the two families.

4. The Force of Heredity

We have now seen that 'pseudo-monogonic' heredity is to be explained in terms of the idioplasm as follows: — the dominating group of idants from one parent — the mother, let us say — passes over completely into the germ-cell of the offspring, and there meets with a weaker group of idants from the father in the process of amphimixis. Although not all, but only a large number of the determinants in the maternal group of idants predominate, a marked resemblance between the mother and child will result.

The fact that such cases as this occur at all, was taken above as a proof that the combination of ids in the idants persists during ontogeny, — *i.e.*, from germ-cell to germ-cell, — and that the idants often, or even generally, remain unchanged in the reducing division. It naturally does not follow, however, that precisely that combination of idants which predominated in the ontogeny of the parent must remain unaltered in the germ-cell of the offspring: it *may* do so, and such cases will frequently occur amongst the thousands of ova or still more numerous sperm-cells which are produced by a single individual in the course of its life.

In some families it certainly appears as if the perfect type ('Habitus') of an ancestor had been transmitted with great constancy to the children through a great number of generations, and we must therefore assume that the dominant group of idants in the ancestor reappears very frequently in the germ-cells of the offspring. Thus the high forehead, widely-separated eyes, and small mouth of the imperial family of the Cæsars, the large and peculiarly hooked nose of the Bourbons, and the projecting lower lip of the Hapsburgs, can all be traced through several generations. It is, however, difficult to say whether such similarities are not accidental, or whether our recognition of them is merely due to an incomplete knowledge of the facts, only those descendants being taken into consideration in whom these family characters were prominent; but similar observations with regard to animals lead to the conclusion that they are not *all* due to chance.

The phenomenon which breeders describe as '*individual prepotency*' comes under this category. It seems that a marked tendency occasionally exists in certain individuals to transmit their special individual characters to the majority of the offspring. It has often been observed that individual horses, cattle, sheep, and other domestic animals possess this capacity in a high degree; and breeders pay enormous prices for such individuals, which must, it is true, excel not only as regards this supposed special power of transmission, but also in respect of certain particular and desirable characters. It is, however, believed that similar observations have also been made with regard to plants. Vilmorin,* one of the most eminent raisers of plants, at any rate distinguished in his experiments between individuals possessing the capacity of transmitting their own characters to the offspring in a greater and in a lesser degree. The former he called '*bons étalons*,' and made use of them alone for purposes of propagation. He could not, however, find out by a mere examination of the plant whether it belonged to this preferred group. This could only be ascertained by examining the offspring, which therefore served as the guides in the selection of the plants for purposes of propagation.

Darwin,† Prosper Lucas,‡ and Settegast§ give many instances of this kind, one of the best known of which is that of the 'otter sheep.' This race was descended from a ram which was remarkable for having short, crooked legs and a long body. It transmitted this peculiarity to many of its descendants, and so enabled the owner to breed a special race of sheep with crooked legs, the advantage of this peculiarity being that they were unable to leap over fences. Similarly, English thoroughbred

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* Quoted from de Vries, *loc. cit.* p. 88.—L. Lévêque de Vilmorin, 'Notices sur l'amélioration des plantes par le semis,' Nouvelle édition, 1886, p. 44.

† Darwin, 'Animals and Plants under Domestication,' Vol. II., p. 40, *et seq.*, London, 1888.

‡ Prosper Lucas, 'Traité philosophique et physiologique de l'hérédité naturelle dans les états de santé et de maladie du système nerveux,' Paris, 1850.

§ Settegast, 'Die Thierzucht,' Breslau, 1878, p. 197.

horses owe their superiority to three individuals,—viz., to the Turkish horse 'Byerley,' and the Arabs 'Darley' and 'Godolphin'; and the celebrated race of Orlow trotters can be traced back to the stallion 'Bars the First.'

If these animals really possessed a stronger 'force of heredity' in the sense indicated, it must not be confounded with the property of *faithful transmission* in a race. This property of 'breeding true' must be due to the presence of a large majority of homodynamous determinants in the germ-plasm, or, what amounts to the same thing, to the existence of similar, *i.e.*, of 'racial,' determinants for every character in most of the ids. The longer a pure race has been kept up, all the individuals which exhibit variations being carefully eliminated, the greater will be the number of ids containing 'racial' determinants, and the more rarely will variations appear in individuals.

At present, however, we are concerned with *individual*, and not with *racial* characters. These cannot possibly have been contained in a preponderating majority of the ids of the germ-plasm from which the individual arose, for the germ-plasm is composed of paternal and maternal ids. The transmission of the proper 'type' can in this case therefore only be due to the fact that the group of idants which preponderated in the development of the parent is once more present in the germ-cell. I should consequently prefer to account for the so-called *prepotency in transmission* by assuming that in some individuals the reducing division simply occurs in such a manner as to separate the paternal and maternal groups of idants, while ordinarily it results in combinations of idants of all kinds. It is impossible to say at present on what peculiarity of the idants themselves or of the apparatus for nuclear division, this must depend; but it can at any rate be stated that the dominant group of idants cannot possibly be contained in every germ-cell of such an individual, even in the most favourable case. On the contrary, it can only be present in half of them; for, according to our assumption, the reducing division always causes the dominant group of idants to pass into *one* of two germ-cells only, the subsidiary group passing into the other. This supposition is in accordance with the facts; for, so far as I know, it has never been observed that *all* the offspring resemble the parent which exhibited 'individual prepotency,' but this, on the contrary, was only the case as regards some of them. In fact, it is expressly stated as regards the 'otter sheep,' that the offspring of the first ram 'closely resembled either the mother sheep of the ordinary breed, or the ram'; and this statement is in correspondence with the theory. Those spermatozoa of the ram which contained the dominant group of idants preponderated over the group of idants of the egg-cell, and an 'otter sheep' thus resulted; while those which contained the subsidiary group of idants could only tend to produce an ordinary sheep of the ancestral breed.

A greater 'force of heredity' is also spoken of in the sense of the prepotency of one race over another. According to Darwin, the short-horn race of cattle seems to possess a particularly marked power of transmission in contrast to other races; and this power is more marked in the pouter pigeon than in the fantail, so that when these two races are crossed, the characters of the pouter preponderate in the offspring. This preponderance of one race over the other must be due to the same causes as those which produce a much greater resemblance to one of the parents in the case of plant-hybrids, which were discussed in another section of this chapter. In both cases the preponderance may be due to the presence of a larger number of idants, of ids, or possibly even of biophors only, in the individual determinants.

5. Summary of Chapter IX

It may be advisable before proceeding further to give a short summary of the results arrived at in the present chapter, and to test the soundness of the assumption on which they are based.

According to my view, the co-operation of the hereditary substances of the two parents in the fertilised egg depends on the presence in each parental germ-plasm of a large number of units, and not of a single one. These units or ids are, moreover, not all similar to one another in the case of each parent, and although in *normal* sexual reproduction they all contain homologous determinants, they exhibit slight *individual* differences. The differences between the ids of the two parents need not in any case be greater than those existing between the ids of the father or the mother alone; it may, indeed, happen that individual ids derived from both parents may be similar to one another, and this is more likely to be the case the oftener inter-breeding has taken place in previous generations.

Each id of the germ-plasm passes through all the ontogenetic stages; that is to say, the number of paternal and maternal ids remains constant throughout ontogeny, and every cell is therefore controlled by an equal number of ids from both parents; and, moreover, in normal reproduction between individuals of the same species, the same number of paternal and maternal ids take part in the process.

The fact that the structure of each cell, organ, or part of the body of the offspring is nevertheless not exactly intermediate between that of the corresponding parts of the parents, must be due to the following causes.

In the first place, an exactly intermediate structure need not necessarily arise even if all the active paternal and *maternal determinants of a cell were exactly alike, or homodynamous*; for even in such a case, the 'controlling forces' of the maternal determinants might preponderate over those of the paternal ones, owing to a superiority as regards the rate of assimilation and multiplication, or in some other respect. The cell-body would then become filled more rapidly by the biophors of the maternal determinants which pass into it from the nucleus, and the multiplication and distribution of the paternal determinants would thus be checked. Hence the controlling force itself may be different with regard to the homologous paternal and maternal determinants.

The differences are, however, still further increased, owing to the fact that the ids, and more especially the homologous determinants derived from either parent, are not always homodynamous, but are, in part at any rate, almost always heterodynamous. The controlling force of the homodynamous determinants must, however, necessarily be cumulative, and the inequality in the force of heredity of the father and mother at any particular stage in ontogeny, is essentially due to the fact that although the number of ids is the same, the number of homodynamous determinants—*i.e.*, those which have a cumulative effect—is different.

It was deduced from the consideration of the phylogeny of variation, that the determinants must have varied *independently* of each other in the different ids of a germ-plasm, so that the homologous determinants may be present in very different variants in their ids; and that, moreover, these variants of the determinants in the different onto-idic stages may be combined in a special way in each id. It therefore results that the number of homodynamous determinants may vary in the different stages of ontogeny, and consequently the paternal and maternal hereditary tendencies may preponderate according to the stage or organ under consideration.

The fact that the offspring may resemble one parent much more closely than the other, is not incompatible with the fact that only half the total number of ids of this parent are present in each of its germ-cells, for *all* the ids only co-operate when strictly intermediate structures are formed; but in those cases in which the ids of *one* parent are overpowered and rendered inactive by a preponderating majority of homodynamous ids of the other parent, *the control of the cell is effected by the successful or 'dominant' ids*, and the others exert no influence. If, therefore, the determinants of one parent, in very numerous stages of development, preponderate in this manner over those of the other, an instance of apparently *monogonic heredity* will result, and the offspring will bear a closer resemblance to this parent; and if, moreover, the 'reducing division' should happen to take place in one of the germ-cells of this offspring in such a way as to result in those ids which were 'dominant,' and controlled the development of this offspring remaining together in the germ-cell, they might possibly preponderate in the next generation over the ids introduced by another parent in the process of amphimixis.

The problem concerning the possibility of the offspring bearing a much closer resemblance to one parent than to the other in spite of the fact that the hereditary substance of both parents is contained in the fertilised ovum, has already been stated in my essay on 'Amphimixis,' and its solution is to be sought in the struggle of the ids which takes place in every cell in the entire course of ontogeny. This struggle, however, only occurs when the determinants become active, and presumably concerns the biophors which pass into the cell-body, the stronger ones annihilating those with a lesser power of assimilation. It does not concern the determinants which are still 'unalterable,' and are inactive as regards the control of the cell. Moreover, the struggle does not occur between the elements of the '*reserve germ-plasm*,' which brings about the formation of the germ-cells of the offspring; and we can therefore understand that the offspring does not by any means only produce germ-cells containing the group of ids which controlled, or was 'dominant' at, its ontogeny, but many other combinations of ids may be contained in its germ-cells.

In this connection I should like to call attention to an interesting essay which appeared when I had almost finished putting the final touches to my manuscript. It bears the pseudonym 'Josef Müller'* on the title-page, and contains in particular an attempt to solve the problem discussed above. The ingenious author, who is accurately acquainted with the subject he treats of, doubts my hypothesis of the ids, but endeavours to account for the very remarkable disappearance of the hereditary tendencies of *one* of the parents in 'pseudo-monogonic' heredity by supposing that the two homologous primary constituents ('Anlage') of the father and mother respectively take part in a struggle ('gamomachia'), which results in the destruction and complete consumption ('gamophagia') of one of them. In principle this explanation of the problem approaches very closely to the solution I have attempted to give, and though I consider the fundamental idea it contains to be correct, I do not think that we may suppose, as the author does, that this struggle occurs at the *beginning of ontogeny*. Basing this conclusion on a statement made by Oscar Hertwig, from which it is conceivable that the homologous 'primary constituents' of the parents unite in the process of fertilisation, he further concludes that the struggle takes place during this union, and leads to the destruction of one of them. Apart from the fact that the paternal and maternal idants remain separate during fertilisation, it seems to me that a large number of the phenomena of heredity contradict the idea of such a union and subsequent struggle. The reappearance of the 'destroyed' primary constituent in the germ-cells — and consequently in the next generation, the phenomena of reversion — which show that every primary constituent must be present in more than two variants in the germ-plasm, and, finally, sexual dismorphism, the occurrence of a large number of very different hermaphrodite structures in certain cases, and sexual reversion, — all tend to disprove such a hypothesis. Moreover, apart from my theory of the ids, I believe that this struggle of the homologous primary constituents

* Josef Müller, 'Uber Gamophagie, ein Versuch zum weiteren Aufbau der Theorie der Befruchtung u. Vererbung,' Stuttgart, 1892.

must occur in the individual cells, in which the decision both as regards the preponderance or suppression of certain of the primary constituents, and the *number* derived from each parent which are to become effective, takes place. For it does not appear to me to be essential that any one of them *must* be entirely suppressed, although this will probably occur in most cases.

If I am not mistaken in my interpretation of a statement made by de Vries, there is no doubt that the primary constituents from *both* parents may undergo development in *one and the same* cell. By crossing a red-flowered with a white-flowered species of bean, this observer obtained a hybrid with *pale red* blossoms, on which the red colouring matter could be recognised in solution in the vacuoles of the cells.* If *parts* only of the cells were coloured, while other parts were colourless, it proves that at least two different (heterodynamous) kinds of biophors, derived from both parents, may control the same cell. There is here, however, an extensive field for further investigation.

My explanation of the process of mingling of the parental characters is based on the assumption of hereditary units or *ids*, each of which contains the whole of the 'primary constituents' of the species, which are, however, modified in the individual. In this connection it may therefore be as well once more to summarise the reasons which lead to this assumption.

In the first place, such an assumption naturally follows from the view that the germ-plasm is made up of 'determining parts' or determinants, for the latter necessitate a definite architecture of the germ-plasm. There must therefore be at least one limited unit of the germ-plasm, to which nothing can be added and from which nothing can be removed without producing an alteration in its capacity for directing ontogeny. But since the process of amphimixis unites the paternal and maternal germ-plasms, *each of which contains all the primary constituents of the species*, each being which is produced sexually must contain *at least two ids* in its germ-plasm.

The phenomena of reversion, which will be treated of in greater detail in the following chapter, show that there must be

* *Cf.* de Vries, *l.c.*, pp. 177, 178. The two species referred to are *Phaseolus multiflorus* and *Phaseolus vulgaris nana.*

several, and indeed many, ids in the germ-plasm of each individual. We know that the personal characters of the grandparents, as well as those of the parents, may reappear in the offspring, and we may therefore conclude that hereditary units or ids derived from the grandparents must be present in the germ-plasm of this offspring, and that it must therefore be composed of more than two ids.

A similar conclusion is arrived at on other grounds. If the assumption of hereditary units in the form of ids is once made, it follows as a matter of course that their number must be doubled in each process of amphimixis; and it becomes evident that this number must have increased enormously, in arithmetical progression, if the 'reducing division' had not intervened and reduced it to the half before each occurrence of amphimixis. This 'reducing division' must have appeared at a certain stage in the phylogeny of amphimixis. If it arose in the germ-cells of the first animal which was produced sexually, — supposing that the germ-plasm of each of the parents previously consisted of only *one* id, — it would always have caused the removal of the id of *one* parent from each germ-cell of the offspring, and thus no grandchild could ever have inherited characters from *both* grandparents. According to our theory of the presence of a large number of ids, such a case would seldom occur, although it is apparently not impossible. A further consequence, however, would be seen in an unusually great uniformity in the structure of consecutive generations; for if only two ids were present, one of which was always removed in the next generation, the same individual ids would pass through a great number of generations, and the diversity of the individual, such as occurs to so great an extent in the human race, would be extremely limited. It is, however, just this extraordinary individual diversity which seems to me to be due to the multiplicity of the ids; it could not have been produced by only two ids taking part in the process of amphimixis.

Finally, as soon as we have recognised, on theoretical grounds, the existence of ids at all, the fact that a number of them exist in the cell is supported by direct observation. For whether they correspond to the 'chromosomes' of other writers, which I speak of as idants, or to the 'microsomes,' of which the chromosomes are composed, as I assume to be the case, a large number of ids may always be observed to be present in the cell.