CHAPTER X

THE PHENOMENA OF REVERSION IN THEIR RELATION TO AMPHIMIXIS

1. REVERSION TO RACIAL CHARACTERS IN PLANT-HYBRIDS

BY the term reversion, is meant the appearance of characteristics which existed in the *more remote* ancestors, but were absent in the *immediate* ancestors — *i.e.*, the parents.

The facts relating to these phenomena are familiar enough, and I shall therefore only refer to as many of them as are necessary for the further development of my theory.

The simplest case of reversion occurs in hybrids. It occasionally happens that hybrids which have been fertilised by their own pollen, produce offspring some of which more or less resemble only *one* of the two ancestral species. In such cases, therefore, a simple reversion to a grandparent takes place. Instances of this kind certainly occur, though not in all hybrid-plants; nor are they often met with even in those species in which they do occur. On this point Darwin quotes two contradictory statements made by Wichura and Naudin respectively, the former of whom never observed instances of reversion in his specimens of willow-hybrids, while the latter insisted strongly on the frequent occurrence of reversion in the *Cucurbitaceæ*. Darwin thought that this contradiction is explained by Gärtner's statement that reversions seldom occur in hybrid-plants raised from wild species, but are of frequent occurrence in those produced from cultivated species. Opinions on this point have since undergone some modification, for Focke states that 'without the influence of the pollen of the parent-species, complete reversions to the ancestral form occur practically only in hybrids of closely allied races.' Instances of reversion of this kind *do* therefore at any rate occur.

Such cases can easily be explained on the basis of our theory. The germ-mother-cells of the hybrid contain a group of idants derived from the paternal, and another from the maternal an-

cestral species. If therefore the 'reducing division' halves the germ-plasm of these mother-cells in such a manner that idants of the mother alone reach one ripe germ-cell, and those of the father alone are contained in another, it is possible that two such germ-cells may unite when fertilisation takes place between these hybrids. In such a case a plant completely resembling one of the ancestral forms would arise, for it would have been produced from a germ-plasm which contains idants of this species only. As however such cases do not often occur, we may conclude that the reducing division only rarely effects such a complete separation of the paternal and maternal groups of idants, and that, in fact, as a rule, both paternal and maternal idants are distributed to each of the four germ-cells produced by the mother-germ-cell. As this halving of the germ-plasm occurs, as we have seen, in a different manner in different instances, we may presuppose that it will also exhibit differences with regard to the proportion of paternal and maternal idants which come together in each germ-cell in consequence of the reducing division; and this supposition is most satisfactorily borne out by the facts, for it is well-known that the offspring of *hybrid-plants, produced by fertilisation with their own pollen, become very variable in the following generation*. It is evident, indeed, that they *must* vary greatly, according to whether each one has received a greater number of maternal or paternal ids, or an equal number of both, from the two germ-cells which combined in the process of fertilisation to produce this particular individual. Thus Focke describes the offspring of hybrid-plants of the first or second year as being 'as a rule unusually diverse and rich in forms,' and gives as examples the genera *Pisum, Phaseolus, Lactuca, Tragopagon*, and *Datura*, mentioning especially in this connection the hybrid of *Nicotiana alata* and *N. langsdorffii*. De Vries * also refers to these facts, and describes them very aptly in the following passage : — ' The hybrids of the first generation have perfectly distinct characteristics in the case of every pair of species. If a hybrid is produced from two species which have already been crossed successfully by previous experimenters, we may be sure that the description given by them will as a rule apply exactly to the intermediate form in question. If the hybrid is fertile without the help of the parent-

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* Hugo de Vries, ' Intracelluläre Pangenesis,' Jena, 1889, p. 25.

forms, and if in a few generations thousands of specimens of its offspring are raised, it will always be found that scarcely two of them are alike. Some revert to the paternal and some to the maternal form, while others, again, are intermediate between the two. The remainder present the most varied alternation of paternal and maternal characteristics, and show almost every degree of mutual intermingling.'

De Vries states this merely as a proof of what he calls the 'free miscibility of the characters,' without attaching importance to the fact that the hybrids of the first generation behave quite differently from those of the second, or attempting to account for this fact theoretically.

Professor Liebscher * has recently brought forward the following interesting instance, in which the details were very accurately investigated. He crossed two species of barley, *Hordeum steudelii* ♀ and *Hordeum trifurcatum* ♂, in the former of which the spikelets are arranged in two rows and are black, while in the latter they are arranged in four rows and are white. The hybrid is as nearly as possible intermediate between the two forms, '*all the ears*,' moreover, '*being strikingly uniform*,' as one would be led to expect theoretically. In all the hybrids the spikelets are arranged in two rows, and in the main spikelets the tips are black, while in the lateral ones they are white, and the 'Löffel '— which are peculiar to *Hordeum trifurcatum* — are black and white. The offspring produced from these hybrids *were exceedingly variable in the first, as well as in the second generation.*

Liebscher has attempted to account for this variability by assuming that a 'loosening ('Lockerung') of the structure of the germ-plasm,' as well as 're-combination of the individual characters,' is produced by the process of reproduction. The former results in 'a weakening of the power of faithful transmission in the generative products,' *i.e.*, 'an inclination to individual variation in the descendants.' This statement indicates that Liebscher certainly had some kind of idea of the actual process which occurs in the idioplasm, although it is not made clear in what this 'loosening' consists.

A definite meaning, however, underlies this expression as soon as it is recognised that the germ-plasm consists of a large

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number of ids. The 'loosening' depends on the repeated removal of half of the ids, which occurs every time the germ-cells are formed. Half the germ-plasm of the hybrid consists of maternal ids of the species A, and the other half of paternal ids of the species B; in the formation of the germ-cells, this per-fectly uniform composition becomes extremely diversified, owing to the fact that the 'reducing division' halves the germ-plasm in different ways. If we suppose that the ids, or even idants, are arranged in a circle, the plane of division will sometimes cut the circle across one diameter, and sometimes across another, and the combination of the germ-plasm in the germ-cells containing ids of A and B will thus be very diversified. If the hybrid is then fertilised by its own pollen, so that amphi-mixis occurs between two of the differently constituted germ-cells, a still greater diversity in the idic combinations will result, and a high degree of variability in the offspring must inevitably ensue.

The offspring of hybrids are also very variable, even in those cases in which they are produced by *a recrossing with one of the ancestral species*. 'Fairly dissimilar offspring generally result from the fertilisation of a hybrid with the pollen of an ancestral form ; intermediate forms between the hybrid and the ancestral species in question are as a rule the most numerous ; while a smaller number of examples resemble either the original hybrid or the ancestral species.' * This statement agrees perfectly with our theory, for a consideration of the reducing division renders it evident that in recrossing with one of the ancestral species, a very dissimilar numerical proportion of idants of the two ancestral species must prevail in the fertilised egg-cell of the following generation. Such hybrids are generally spoken of as '¾ hybrids,' because in them the force of transmission of one of the ancestral species is assumed to be one-quarter only, and that of the other three-quarters. This term is probably indispen-sable in practice, but is obviously totally inaccurate. 'Three-quarter hybrids' do not by any means contain all the hereditary substances of the two ancestral species in the proportion of three to one; the proportion is in fact a very variable one. A '¾ hybrid' is produced, for instance, from two species of pink, *Dianthus chinensis* and *D. barbatus*, by fertilising the hybrid

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* Focke, p. 485.

D. chinensis ♀ × *barbatus* ♂ by the pollen of *D. barbatus*. The formula of this hybrid would therefore be — *Dianthus (chinensis × barbatus)* ♀ × *barbatus* ♂, or in more general terms by $(A + B)$ ♀ × A ♂.

For the sake of simplicity let us assume that the number of idants and force of transmission is similar in the case of both ancestral species. We will suppose that sixteen idants* are arranged in a circle, as represented in Fig. 22, I. In the production of the ½ hybrid, eight idants of A combine with
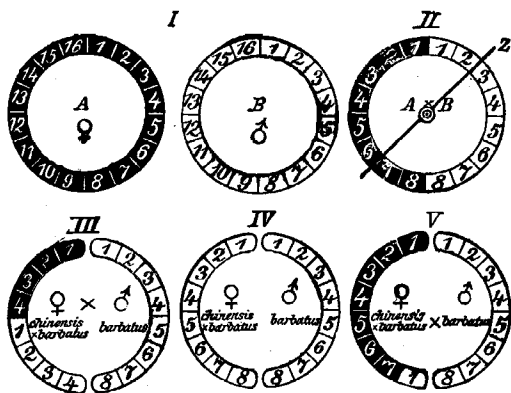

FIG. 22. — *Diagram of the composition of the germ-plasm in hybrids.* — I. The germ-plasm of the parental species, each composed of sixteen idants; A, *Dianthus chinensis;* B, *Dianthus barbatus.* II. Germ-plasm of the hybrid, composed of eight idants from A and eight from B: z, the plasm of section, which may be rotated. III., IV., V. Three of the possible combinations of the germ-plasm which might arise by crossing hybrid II. with the parental species B. III. A true three-quarter hybrid. IV. Contains idants of the parental species B only. V. Contains nine idants from B and seven from A.

eight idants of B; the mother germ-cells of this hybrid will therefore always contain 8A × 8B idants (Fig. 22, II.). The reducing division then occurs, and bisects the circle at some point. Fig. 22, II., will make it apparent that by rotating the

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* We might just as well speak of 'ids' as 'idants' in this illustration. I have referred to the idants simply because they are visible units, and not merely hypothetical structures, and also because the number of idants may be assumed to be less than that of the ids, and is thus more easily controllable.

plane of section, the circle may be separated into nine dif-
ferent combinations of the black idants A of *D. chinensis* and
the white ones B of *D. barbatus*, viz.: 8A; 7A + 1B; 6A + 2B;
5A + 3B; 4A + 4B; 3A + 5B; 2A + 6B; 1A + 7B; and 8B.
Nine kinds of germ-cells, differing in quality, may therefore be
formed, the egg-cells only being taken into consideration in this
connection.

In the formation of the so-called ¾ hybrid, one of these egg-
cells unites with a germ-cell of the pure ancestral species B.
The following combinations of idants may then result:—
8B × 8B, which would produce the pure ancestral species B;
(7A+1B) ♀ ×8B ♂ ; (6A+2B) ♀ ×8B ♂ ; (5A+3B) ♀ ×8B ♂ ;
(4A+4B) ♀ ×8B ♂ ; (3A+5B) ♀ ×8B ♂ ; (2A+6B) ♀ ×8B ♂ ;
(1A+7B) ♀ ×8B ♂ ; and 8A ♀ ×8B ♂ . Theoretically, therefore,
all stages from the pure ancestral form B (Fig. 22, III.) to
the form which is intermediate between the ancestral species
may occur, but no individual can arise which inclines more
strongly towards A than does the exactly intermediate form.
Whether all these are actually produced, and in what relative
frequency they occur, can only be decided by further researches
carried out from this point of view. Those which have till now
been made are insufficient, as the number of seedlings raised
has always been too small. We may, however, infer from the
facts we already possess, that the different combinations of the
two kinds of idants *do not occur with equal frequency*, and that
the intermediate combinations are the most usual. Were this
not the case, 'the form which is intermediate between the ½
hybrid and the ancestral species' could not be 'the most fre-
quent.' This is also most probable theoretically, and becomes
more so as the number of idants is greater. The cells of many
Phanerogams possess far more than sixteen idants, and even if
we also assume that the position of the line of section is entirely
a matter of chance, the rarest case will always be that in which
it accurately separates the idants of A from those of B, and it
will happen much more frequently that it divides them in some
other plane. This is equivalent to saying that germ-cells of
½ hybrids rarely contain idants of A or of B *only*, and that in
most cases there is a combination of the two.

If the so-called ¾ hybrids are again crossed with the ancestral
species B, ⅞ hybrids (the third hybridised generation) are
obtained, and these 'as a rule bear a close resemblance to that

species of which ⅞ths is represented, although the individual specimens still display considerable differences in form.'* The result of these observations also agrees with our theory, for even in the second generation of hybrids, eight was the highest possible number of ids of the ancestral species A in the mature germ-cells of the hybrid, and in the process of fertilisation these met with the same number of idants of the ancestral species B, which was used for recrossing. The germ-mother-cells of the ¾ hybrid cannot contain more than 8A × 8B, and, as a rule, a smaller number of the idants of A will be present. The reducing division then again halves these sixteen idants in various ways ; and in the case which is most favourable for the preservation of the hereditary substance of A, the halving of one of these germ-mother-cells, which was most favourable for A, might again lead to the formation of germ-cells with eight idants of A and eight of B. But in all other ¾ hybrids the germ-mother-cells already contain more idants of B than of A, as is shown in Fig. 22, III., and the reduction therefore results in the germ-cells containing either idants of B only, or, at any rate, some of B in addition to those of A. If these egg-cells are then fertilised by germ-cells of the pure ancestral form B, the largest conceivable number of idants of A which can be contained in the fertilised egg-cell will again be eight. Hence the form exactly intermediate between the two ancestors may possibly also appear in the third generation, but this will occur *much more rarely* than in the second generation. On the other hand, those individuals the idioplasm of which contains only a few idants of A will preponderate ; and in others, even idants of B only may be present, for the idants of B were in the majority in most of the mother-germ-cells of the second generation : the halving due to the reduction must therefore have frequently resulted in the distribution of idants of B *only* to one of the germ-cells, and these then once more combined in the third generation with idants of the pure species B. Theoretically, therefore, the ⅞ hybrids must in part revert to the ancestral form B. This conclusion is supported by facts, inasmuch as Kölreutter and Gärtner, who made a large number of experiments on recrossing, found 'that three to six generations (four to five as a rule) were required for the complete transformation of the

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* Focke, p. 485.

occur; and only those instances are possible in which the rever-
sion concerns more or less extensive groups of characters which
already existed in an individual of a former generation.

We have now discussed the question of transmission from the
parents, grandparents, and great-grandparents, to the child; and
it will be as well, before going further, to summarise the various
possible cases, and to see whether observation and theory con-
tradict one another in any respect.

The most frequent case seems to be that in which the child is
a mixture of the types of the two parents, the characters of both
of which are either completely united, or else they alternate with
one another in the different cells, parts, and organs, and even in
the systems of organs themselves. In all such instances, the
group of idants which predominated in the ontogeny of the
parent, or rather of both parents, must have been contained in
the germ-cell from which the child arose.

The question might here be asked as to how it can so fre-
quently happen that only the dominant group of idants is
present in the germ-cell destined to undergo amphimixis. We
must, however, remember that a perfectly equal blending of the
types of the two parents in the child occurs much more rarely
than is generally supposed; and that it is difficult, and frequently
in fact impossible, to say whether the maternal portion of a
character is really derived from the type of the mother, and not
from that of her father or mother. General characters only, of
the mother's family are most usually combined with others
derived from the family of the father. But those characters
which have been peculiar to many members of a family for
several generations are the most likely to occur in numerous ids
and idants, and they therefore reach the germ-cells in larger
numbers in many of the modes of ' reducing division.' Theo-
retically the dominant group of idants of the parent would not
be necessary for such a transmission of a general family resem-
blance, but only a majority of the idants of this group.

The case, however, is different when the resemblance refers
mainly to the type of *one* parent; and we must then assume that
the dominant group of idants of this parent is present, and is
opposed to another weaker group derived from the other parent,
and provided with a smaller number of homodynamous deter-
minants.

place with the pollen of the hybrid; and even by continued recrossing with one of the ancestral species, the combination of the germ-plasms of the first generation would gradually become weakened, and perfectly pure germ-plasm of the one ancestral species could never be produced. But as soon as we assume that the germ-plasm consists of units which remain separate in the form of idants or ids, it is evident that the whole of the units of one species may be removed from the germ-plasm of the hybrid-offspring, either with or without the occurrence of recrossing; and even if recrossing does take place, reversion *must* occur sooner or later in individual descendants.

Our theory also enables us to make certain predictions, which, as far as my knowledge extends, have not up to the present been confirmed by facts. If sometimes, though rarely, all the idants of A pass into one germ-cell, and all those of B into the other, in the process of halving of the germ-plasm of the primary hybrid A × B a reversion to both the ancestral forms will occur when the second generation is fertilised with the pollen of the hybrid, as has just been shown: that is to say, such a reversion will take place when a pollen-grain containing idants of A only *comes in contact with an egg-cell which also contains idants of* A only, or when idants of B meet with others of similar origin. The same must also be possible in the hybrids of the third generation, even when all the complete reversions of the second generation are left out of consideration, simply for the reason that certain individuals of the second generation are produced from the combination of nA with nB idants, and are therefore exactly intermediate forms like all the hybrids of the first generation. The occurrence, even if only in individual cases, of such intermediate forms, renders it possible that germ-cells may again arise which contain idants of A or B only, so that ultimately reversion to one or other of the two ancestral forms becomes possible. These reversions will certainly be of rare occurrence; and as it is entirely a matter of chance that germ-cells which *contain the most infrequent combinations of idioplasm should* come together in the process of fertilisation, it would be necessary to examine a very large number of seedlings before such cases would be found.

Before passing on to the consideration of reversion to individual characters, it should be remarked that the same law of reversion which can be recognised in the case of plant-hybrids,

holds good as regards the crossing of the different human races. According to this law, the intermingling of a racial character is uniform in the first generation, but subsequently becomes quite irregular when recrossing with one of the original races occurs. The skin of mulattoes, which are a cross between white races and negroes, is never quite white, its colour being as a rule an approximate mean between that of the two parents. When mulattoes and white races are recrossed, the skin does not regularly become less black, but the descendants of the third and fourth generations are sometimes white and sometimes fairly dark: this fact indicates the absence of uniformity in the process of 'reducing division.'

2. REVERSION TO INDIVIDUAL CHARACTERS IN MAN.

The essential difference between the process of reversion in plant-hybrids and in Man, consists in the fact that the former is concerned with the intermingling and subsequent separation of *specific* or racial characters, while in the case of the reproduction of human beings of the same race *individual* characters only are intermingled. As regards hybrid-plants, the idants of each parent might be assumed to be similar, — although this may not be strictly true in all instances, as will be seen later on, — but in the case of individual differences the idants of each parent cannot be regarded as similar. Each of these idants consists of a number of separate ids, which may differ in many respects. In all of them the determinants are as similar as the retention of the specific character renders necessary: that is to say, all the determinants of the same ontogenetic stage are homologous, though at the same time they are never all homodynamous, but differ in many respects owing to slight individual deviations. Hence different ids may contain different variations of any particular homologous determinant. In the following examples, each homologous determinant is indicated by a letter, and variants of a determinant are distinguished by dashes after each letter. Thus id i. of the germ-plasm might, for instance, contain the determinants a, b, c, d, e, - - - n; id ii., the determinants a, b', c, d', e, - - - n' ; id iii., a', b'', c', d'', e', - - - n, and so on. The total effect of the idants is decided by the struggle of the ids; the laws which regulate this struggle cannot at present be determined more precisely, and until we know more about them, we may suppose that those variants

which are present in the largest numbers always have the best prospect of controlling the cell entirely, or at any rate chiefly; their effect must be cumulative, and a small minority of homo-dynamous determinants will not be able to take effect against a large majority of some other variant. The control of the cell therefore results from this struggle of the determinants, which must naturally not be conceived to take place in such a manner that the group of paternal ids struggles with the maternal group, but so that all the active determinants which are contained in the idioplasm migrate into the cell body and there strive to obtain the control. If the parents of the organism in question are closely related, the same homodynamous determinants may very possibly be contained in the idants of both parents, and the forces of these will then combine just as would be the case if they had been contained in one idant of the father or mother. It will, however, happen more frequently that homodynamous determinants are present in the ids of *each* parent respectively, and a majority of homodynamous maternal determinants will then compete with a majority of paternal ones; they will then either control the cell together, or the prepotency of one of the parents will be so great as to suppress the influence of the other entirely.

In order to test to what extent these ideas of the co-operation of parental idioplasms may be applied to the phenomena of reversion in Man, we must again consider the simplest of these phenomena, viz., that of *reversion to a grandparent*.

It is well known that a child not infrequently resembles its father or mother in a high degree, and it is also assumed that a father may beget a child which does not resemble him, but it and its father's mother are as 'like as two peas.' This pre-supposes that the father himself bore no resemblance to his mother, for otherwise it would not be an instance of reversion of the child to the grandmother.

This case may be explained theoretically by assuming that the 'reducing division' of the respective germ-cells of the two generations accurately separated the paternal from the maternal idants, and that, as was shown above, the group of idants of one of the parents may possibly have had no influence on the formation of the child, the other group being the dominant one. The fertilised egg-cell from which the father was developed must therefore have contained the two groups of idants A and

C, A being derived from the grandmother, in the development of whom this group dominated. C was derived from the grandfather, and preponderated to such an extent over A that it alone determined the type of the son. Hence A remained latent in the idioplasm of the father, who therefore resembled the grandfather and not the grandmother. If now, that germ-cell of the father, from which the child of the third generation was developed, just happened in the reducing division to receive the group of idants of A only, which remained without influence on the development of the father, but which was dominant in the grandmother, a reversion to the grandmother would then become possible. It would occur when this sperm-cell unites with an egg-cell in which the group of idants D has a much weaker controlling force than A. The child would then resemble neither the paternal nor the maternal type, but would be like his grandmother, for the group of idants A determined the type of the grandmother.

I nevertheless consider it doubtful whether reversion of this kind ever occurs so thoroughly and completely as is conceivable theoretically. The facts are unfortunately by no means so decisive as one could wish. No one, so far as I know, has hitherto attempted to ascertain whether *complete* reversion to a grandparent ever occurs, and from a theoretical point of view I should consider this to be improbable. Similarity to a grandparent may undoubtedly often be observed, but it does not therefore by any means follow that a correspondence exists between all, or at any rate the greater majority of individual characters, such as is seen in 'identical' twins. All the parts of the child and grandparent have never been carefully compared, not to mention the fact that such a comparison has never been made at corresponding ages. Moreover, to use the same example, only those cases could be utilised in questions of reversion in which the father bears no resemblance to the type of the grandmother. Cases of this kind are, however, not quite reliable, and are certainly not common.

I am therefore inclined to think that in all these cases we are only concerned with a partial and not a complete reversion to the grandparent, — that is, with the reappearance of a more or less extensive aggregate of characters of the grandparent; and this is certainly sufficient in many cases to produce what appears to be the type of the latter. More or less extensive

aggregates of the characters of the grandparents undoubtedly reappear in the child, and these may be more easily explained theoretically, without the necessity of supposing that chance plays so great a part. For in order that perfect reversion may be possible, numerous most infrequent occurrences must take place together. To use the same example, in each individual of three consecutive generations, only one of the two groups of parental idants could determine the type of the child, and the reducing division, moreover, must affect one of the mother-germ-cells of each of four individuals — *i.e.*, the two grand-parents and the two parents — in such a manner as to separate the two groups of parental ids. All these possibilities may sometimes concur, but we can only imagine this to be so if it is proved that an exact resemblance exists between the child and grandparent.

A *partial* resemblance is theoretically far more likely to occur. Let us suppose, for instance, that the germ-plasm consists of sixteen idants, eight of which are derived from the mother and eight from the father, and that the reducing division causes six idants of one parent and two of the other to be present in one germ-cell: the former might possibly contain many of those determinants to which the type of this particular parent was due. This need not necessarily be the case, for all the sixteen idants may have had a farely equal share in the production of this type, and six out of the sixteen idants could not then possibly give rise to the same type even approximately.

It might, on the other hand, happen that the type of the parent was essentially determined by the group of idants derived from the father or mother of this parent only, and a resemblance of the child to its father could then only occur when the whole or a great part of that group which controlled the development of the father was also present in the germ-cell from which the child was developed. Even then, the production of the type of the father would not absolutely be ensured, for in the process of fertilisation by the other parent a group of idants might be added, in which the controlling force preponderates over those already present, either entirely, or at any rate as regards many or most of the determinants.

We may, however, conclude from all these considerations, which are unfortunately still very vague, that a large number of idants of the grandfather, for example, may be present in the

germ-cell which will give rise to the father, and still may not result in the production of the type of the grandfather; and that these may then pass into a germ-cell of the next generation, and partially determine the type of the son, provided that they are opposed to a group of idants which has a weaker controlling force. At every ontogenetic stage, then, the struggle of the ids and idants decides which group of the latter is to control the cell. According to the hypothetical principle on which we have supposed this struggle to take place, the majority of homodyna-mous determinants would always represent the greatest con-trolling force, so that certain of the more comprehensive or special characters of the grandparent might very well reappear in the grandchild, even if only six or eight idants which con-trolled the development of the grandparent were present in the germ-plasm from which the grandchild arises.

We may even assume that, as regards Man, *ontogeny is hardly ever passed through without reversions occurring to one or other of the grandparents*; for determinants of one of the grand-parents will almost invariably have been suppressed in the development of the parent by stronger ones derived from the germ-cell of the other grandparent, and will predominate in the formation of the grandchild, because they are here again opposed to other combinations of ids over which they may pre-ponderate under certain circumstances. It may therefore happen that some of the individual characters of the grandparent may reappear in the grandchild, although there may be no general resemblance between the two.

The answer to the above question relating to the causes on which reversion to a grandparent depend, may be briefly stated as follows : — *such a reversion is due to the fact that the whole or part of the group of idants which determine the type of the grandparent were present in that germ-cell of the parent from which the grandchild was developed, and that it was there opposed to a weaker group derived from the other parent.*

We do not know what number of the controlling idants of the grandparent must be present in the germ-plasm of the grand-child in order that reversion to the grandparent may occur. *Complete* reversion can only take place if none of the deter-mining idants are absent; but, as we have seen, such complete reversion has not by any means been proved to occur in Man. Still less is this the case in *the next following generation, viz.,*

as regards the great-grandparent. Instances of a descendant of an ancient family reverting to a great-grandparent whose characteristics were not present in the intermediate generations, are certainly occasionally mentioned in novels, but it is only natural to doubt the accuracy of such cases, even when they claim to be true. A great-grandchild certainly often resembles its great-grandparent, but when this is so, *this resemblance had not disappeared entirely in the intermediate generations.* As has been shown above, it would certainly not be incredible, from a theoretical point of view, that the group of idants which controlled the development of the great-grandparent should remain intact in certain germ-cells of two generations, and should be suppressed by more powerful groups derived from germ-cells of other parents, once more to predominate in the third generation. If reversion of this kind could be proved to occur, it might be explained in this manner, and we should be justified in assuming that in many cases the idants of the two parents may again be separated into their original groups by the reducing division. The great variability of hybrids of the second generation proves that this only occurs very rarely, and in most instances not at all.

We have seen that the difference between reversions in hybrids and in human beings of the same race is simply due to every idant of one parent, in the case of hybrids, containing specific characters, so that all the idants of the one parent are similar, and all the homologous determinants may also be considered homodynamous. When therefore an ontogeny is directed by the ids of *one* of the parent species *only,* the type of this species is produced. The type of a human being, on the other hand, is constituted by ids of very many different kinds, no two of which are exactly alike, for each of them contains determinants of a somewhat different kind from the rest; and, speaking generally, the type is in all cases only the resultant of all these different components. The same type, or combination of characters, can only appear for a second time if the same components are again brought together. Except in the doubling of the fertilised egg in the case of 'identical' twins, this can, however, never occur, for a new combination of ids and idants which never existed before arises every time fertilisation takes place. Hence cases of complete reversion as regards individual characters to a previously existing form, can never

occur; and only those instances are possible in which the reversion concerns more or less extensive groups of characters which already existed in an individual of a former generation.

We have now discussed the question of transmission from the parents, grandparents, and great-grandparents, to the child; and it will be as well, before going further, to summarise the various possible cases, and to see whether observation and theory contradict one another in any respect.

The most frequent case seems to be that in which the child is a mixture of the types of the two parents, the characters of both of which are either completely united, or else they alternate with one another in the different cells, parts, and organs, and even in the systems of organs themselves. In all such instances, the group of idants which predominated in the ontogeny of the parent, or rather of both parents, must have been contained in the germ-cell from which the child arose.

The question might here be asked as to how it can so frequently happen that only the dominant group of idants is present in the germ-cell destined to undergo amphimixis. We must, however, remember that a perfectly equal blending of the types of the two parents in the child occurs much more rarely than is generally supposed; and that it is difficult, and frequently in fact impossible, to say whether the maternal portion of a character is really derived from the type of the mother, and not from that of her father or mother. General characters only, of the mother's family are most usually combined with others derived from the family of the father. But those characters which have been peculiar to many members of a family for several generations are the most likely to occur in numerous ids and idants, and they therefore reach the germ-cells in larger numbers in many of the modes of 'reducing division.' Theoretically the dominant group of idants of the parent would not be necessary for such a transmission of a general family resemblance, but only a majority of the idants of this group.

The case, however, is different when the resemblance refers mainly to the type of *one* parent; and we must then assume that the dominant group of idants of this parent is present, and is opposed to another weaker group derived from the other parent, and provided with a smaller number of homodynamous determinants.

A third case may also occur in which *the type of an uncle or aunt* is more or less accurately reproduced in the child, or in which this type is blended with the characters of the parent on the other side. I know a man who closely resembles a maternal aunt, but nevertheless possesses many general characters of his father's family. This fact may in all probability be explained in terms of the idioplasm as follows : — the egg-cell from which this person was developed contained the group of idants which was dominant in the ontogeny of the mother's sister, and not that which predominated in the case of the mother. Theoretically this might very well be the case. Let us suppose that the primary germ-cells of the maternal grandfather (m p) contained the idants a, b, c, d, e, f, g, h, and those of the grandmother the idants i, k, l, m, n, o, p, q ; and also that the fertilised egg-cell from which the mother was developed contained the idants a, b, c, d × i, k, l, m, and that from which the aunt was developed the idants *a, b, c,* f × *l,* n, o, p. We will further assume that the group of idants which was dominant in the ontogeny of the aunt were those indicated by the letters *a, b, c,* and *l,* printed in italics. It will then be seen that the same combination *a, b, c, l* can also be formed from the germ-plasm of the mother by means of the reducing division, for all four of them are present in this germ-plasm (*a, b, c,* d × i, k, *l,* m). It is doubtful whether such a case ever occurs so accurately, and I know of no instance which renders this hypothesis necessary : the resemblance is always an imperfect one.

We must also consider a fourth case, in which the child neither specially resembles its father or mother, presents a recognisable combination of the characters of both, nor bears a striking resemblance to one of the four grandparents, but displays an entirely new combination of characters. Such a child would probably always bear some resemblance to both, or at any rate to one, of the parental families, but it would not exhibit certain marked characters of the respective fore-fathers.

These cases do not contradict our theory, for by means of the reducing division it may possibly happen that none, or only certain of those very idants which were dominant in both parents are present in the germ-cells of the parents which undergo amphimixis.

If, for instance, the germ-plasm in the ontogeny of the father had the composition *a, b, c, d, e, f,* g, h, of which the idants a, b,

d, f, were dominant, and the germ-plasm in the ontogeny of the mother consisted of the idants *i*, k, *l*, m, *n*, *o*. p, q, of which i, l. n, o essentially determined her type. If the reducing division then resulted in an egg-cell containing the idants k, m, p, q, and a spermatozoon was formed which contained the idants c, e, g, h, and these came together in the process of amphimixis, the resulting germ-plasm would certainly contain characters of both families, but it could not possibly produce the type either of the father or mother, or a mixture of both.

I have already discussed the question of reversion of the child to one of its four grandparents in detail, and need not return again to this point. I should, however, like to call attention to the fact that, theoretically, *a child can never exhibit a combination of the types of two of its grandparents*, simply for the reason that at least half of the idants of a germ-plasm determine the type of the child, the germ-plasm of which can only contain one quarter of the idants of *two* grandparents. An exception to this rule could only occur in cases of close interbreeding, in which both grandparents in part contained the same idants.

No case has, however, ever come before my notice in which a child bore no resemblance to its parents and yet exhibited a combination of the types of that of two of the grandparents.

3. *Reversion to the characters of ancestors far removed in animals and plants.*

We will now consider the question of reversion *to remote ancestors*. Cases of such reversion are so well known through Darwin's researches, that a more detailed description of the mere facts might almost be considered superfluous. But such a description is nevertheless necessary, and I must even express the opinion that the facts have not been so accurately investigated from all points of view as is desirable in order that a theoretical explanation of them may be arrived at. Darwin was the first to point out that in cross-breeding, either of species or of mere varieties, characters not infrequently appear in descendants which were not present in the parents, in some of which cases, indeed, it can be proved, and in others shown to be very probable, that they have been derived from remote ancestors. Mules, for instance, sometimes exhibit distinct stripes, like those of the zebra, on the fore-legs and shoulders,

while such stripes are very seldom present in the horse and ass, and are even then only very faint; but we must nevertheless suppose them to be derived from the ancestral form of the two species. And, again, when certain races of pigeons are crossed, offspring are produced in which the plumage has the slaty-blue colour of the wild rock pigeon, although the races used for crossing were of quite another colour; in this case, moreover, the descent from the wild rock pigeon is certain. Similar instances also occur in plants. The hybrids of *Datura ferox* and *D. lævis*, in both of which the flowers are white, regularly bear blue (purple?) flowers, and Darwin * has shown that this is to be looked upon as a reversion to ancestors which possessed blue flowers, as, in fact, is the case at the present day in an entire group or species of *Datura*.

I will now attempt to explain these three instances in accordance with my theory. In them, as is universally the case, reversion must be attributed to the presence of old unmodified determinants in the germ-plasm, which take the place of the younger homologous determinants as regards obtaining the control of the cell or region of cells in question. Similar assumptions must be made in every theory of heredity. In his theory of pangenesis, Darwin makes use of old gemmules for this purpose, while de Vries assumes that reversion is due to the presence of old pangenes. Some unmodified portion or other of the hereditary substance must always form the starting-point in attempting to explain the problem; and the only question is, whether we are to remain satisfied with such a statement, and leave everything else in obscurity, or whether it is possible to obtain a certain insight, in principle at any rate, into the question as to why these minute parts can remain unmodified, and why and under what circumstances they can suddenly obtain control precisely in the region of transformed parts which are homologous to them.

A solution of the first of these problems has already been given above. It has been shown that, according to the principle of selection which controls the whole, a transformation such as is required by the vital conditions of a species never necessitates the transformation of *all* the determinants relating to the parts to be transformed, but that this process is only necessary in the

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* Darwin, ' Animals and Plants under Domestication,' Vol. II. p. 254.

case of a majority of them, which is sufficient to ensure the occurrence of the modification in question in every ontogeny, — *i.e.*, in every individual of the species. This is all that is required, and consequently *the processes of selection cannot accomplish more*. After every transformation of the body in the process of development of the species, the germ-plasm will thus contain some unmodified determinants in addition to those which have been transformed in any part, and these will only disappear very gradually in the course of the further history of the species.

The existence of the *material* by means of which reversions to all specific characters operate, can therefore be proved on the basis of the theory of selection : *every germ-plasm must contain a larger or smaller number of old determinants corresponding to the characters of the ancestral species*.

The solution of the second problem, as to why these ' ancestral determinants ' always exert their influence at the right spot in the body, naturally follows from our theory, in which the mechanism of ontogeny is referred to the gradual disintegration of the germ-plasm.

The third problem then only remains : *how can the ancestral determinants, which are present in a minority, gain control over the majority of younger ones ?*

We have seen that reversions to the ancestral form occur in the offspring of hybrid plants, — even if they are fertilised by their own pollen, — when those cells to which the *entire* group of idants of the ancestral species of the *same* parent has been distributed at the reducing division happen to come together in the process of fertilisation. Whenever the germ-plasm of the fertilised egg-cell contains idants of the species A *alone*, an organism of the species A can alone arise. But this occurrence is out of the question in cases of reversion to the characters of remote ancestors. The germ-plasm can then never consist entirely of idants of the ancestral species ; and, in fact, we may doubt whether entire ancestral idants exist at all in the germ-plasm of any individual of a long-established species. For the number of idants (nuclear rods) is not extremely large in any species ; and if, as in the instance given above, we assume this number to average sixteen, even the proportion of *one* unmodified to fifteen modified idants would be rather large, and would render an occasional reversion to the ancestral form possible in the ordinary reproduction of the species. Fertilisation need

only occur eight times successively, two of the unmodified ancestral idants being added each time to those already pres ent, in order to produce a germ-plasm consisting of pure ances- tral idants, and the organism developed from it would then agree with the ancestor in question in all its characters. Under particularly favourable circumstances the process might even be completed in four generations, as is shown in the following table : —

Generation I. $\begin{cases} a', & b, & c, & d \mid e, & f, & g, & h = \male \text{ germ-cell.} \\ a', & i, & k, & l \mid m, & n, & o, & p = \female \quad \text{``} \end{cases}$

Generation II. $\begin{cases} a', b, & a', & d \mid c, & i, & k, & l = \male \quad \text{``} \\ a', & q, & a', & s \mid t, & u, & v, & w = \female \quad \text{``} \end{cases}$

Generation III. $\begin{cases} a', & a', a', & a' \mid b, & d, & q, & s = \male \quad \text{``} \\ a', & a', a', & a' \mid a, & \beta, & \delta, & \epsilon = \female \quad \text{``} \end{cases}$

Generation IV. $\begin{cases} a', & a', a', & a', a', & a', a', & a' = \male \quad \text{``} \\ a', & a', a', & a', a', & a', a', & a' = \female \quad \text{``} \end{cases}$

The letters in the above table indicate the idants, which — with the exception of a', which represents the unmodified ances- tral idant, and only occurs *once* in the first generation — are only individually different from one another. The vertical line represents the reducing division of the mother-germ-cell, which in the most favourable case we are now considering, always causes this ancestral idant a' to pass into the germ-cell about to undergo amphimixis. For the sake of simplicity, the con- jugating germ-cells are assumed to be similar in respect to their contained ancestral idants. It would thus follow that germ-plasm consisting of ancestral idants only, would be pro- duced in the fourth generation.

Although we must certainly admit that so favourable a com- bination of events can hardly ever occur, it cannot be doubted that an accumulation of ancestral idants may take place in *one* germ-cell in the course of a large number of generations, and that a *majority* of these ids may consequently come together in fertilisation. In this case a more or less complete reversion to the ancestral form must take place. As such reversions to the complete type of the ancestral species cannot be observed to occur in the normal reproduction of pure and long-established species, we must conclude that *all the idants have become modified in such old and pure species,* each of which produces

the type of the species, and not that of an ancestor, in case it alone has to control the ontogeny.

The foregoing considerations seem to me to afford a good explanation of the *frequent occurrence of reversion in young species which are not yet definitely established.* Cultivated varieties of flowers, such as the Heartsease (*Viola tricolor*), always produce, among a large number of seedlings, certain plants which bear flowers more or less resembling those of the wild species. Evidently only a portion of the idants have become transformed in this modern form, another and smaller portion having remained unmodified. Since the reducing division separates the idants into two groups of all possible combinations, germ-cells, both male and female, containing a preponderance of unmodified ids, must also occur; and if two such germ-cells come together in fertilisation, reversion must result.

Let us suppose that, of the sixteen idants in the germ-plasm, ten were modified and six unmodified. Under favourable circumstances a case might then occur in which the majority of idants would remain unmodified, without further accumulation taking place in the course of generations — *i.e.*, at every fertilisation. This may be illustrated by the following table, in which the letters with a dash represent the unmodified, and those without one the modified idants, the line dividing the letters indicating the reducing division :

Maternal germ-plasm $\{$ a', b', c, d', e, f', g', h $|$ i, k, l', m, n, o, p, q.
Paternal   " $\{$ f, r', s, t', u', v', w', x $|$ y, z, a, b', c, d, e, g.
Germ-plasm of offspring I. : — a', b', c, d', e, f', g', h × f, r', s, t', u', v', w', x.

Owing to the manner in which the reducing division takes place, the maternal and paternal germ-cells each contain five unmodified idants, so that in the germ-plasm of the offspring ten unmodified and six modified idants are present. If, on the other hand, we suppose that the other two cells produced by the reducing division from the same mother-germ-cell undergo fertilisation, the germ-plasm of the offspring II. will have the following composition : —

i, k, l', m, n, o, p, q, y, z, a, b', c, d, e, g.

It therefore only contains two unmodified idants, and must consequently give rise to the modified form of the plant.

A large number of cases of heredity which have not hitherto been understood can thus be explained in a very simple way. Take, for example, the *varying degrees of certainty with which varieties of cultivated plants transmit their peculiarities.* The extent to which such peculiarities are transmitted must depend on the number of idants in the germ-plasm which have remained unmodified, and the greater this number, the more easily will reversion occur.

These theoretical considerations will probably account for the first of the three cases which were mentioned above as types of reversion to more remote ancestors, viz., that of *Datura ferox* × *lævis.* The two species of *Datura* have white flowers, but produce hybrids in which the flowers are blue; and this is not only occasionally the case, but occurred in every one of the 205 plants which Naudin raised from this cross,* and also in all those cases which had been observed previously by Kölreutter and Gärtner.† If we assume that, in addition to their own specific idants, the two species of *Datura* contain a certain number of ancestral idants, the latter might be relatively increased in individual germ-cells in consequence of the reducing division; and when these met with germ-cells of the other species, which also contain numerous ancestral idants, a germ-plasm possessing a larger number, and perhaps even a majority, of these idants would be constituted. Individual cases of reversion to the common ancestral form might thus occur. But this assumption is evidently insufficient to account for the facts, for the blue colour of the flower appears in *all* the hybrids. The reversion in these cases must therefore be independent of a greater accumulation of ancestral idants which may possibly occur in individual germ-cells in consequence of the reducing division. These idants must, on the contrary, *come together in each fertilised egg-cell in a sufficient number to preponderate over the modified idants,* and to control the ontogeny. They cannot possibly, however, be stronger *numerically* in every case, and another factor must therefore take part in the process, which causes the ancestral primary constituents to preponderate in every case; and this is in all probability *the specific diversity of the modified idants.* We have assumed from the first that

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* Darwin, 'Animals and Plants,' Vol. II., p. 254.
† *Cf.* Focke, ' Pflanzenmischlinge,' p. 269.

homodynamous determinants have a cumulative effect, while heterodynamous determinants tend to counteract one another. The same must be true of the *groups* of determinants, — the ids and idants; similar idants must increase the effect produced, while dissimilar ones will interfere with one another to a greater extent the more diversified their composition out of ids and determinants is. Let us confine our attention for the present to the groups of determinants for the flowers. The two species of *Datura* certainly contain determinants which tend to form *white* flowers, and we might therefore be disposed to infer that these are homodynamous, and that their effect must be cumulative. But this conclusion would be erroneous, for it is quite possible that these determinants only correspond as regards the production of a 'white' *colour*, and differ widely in respect of many other characteristics of the cells, such as those relating to their size and minute structure. On the other hand, the 'blue' determinants are actually homodynamous, and correspond not only with regard to the colour to which they give rise, but also in respect of all the other characters of the cells of the flowers, for they are derived from the common ancestral species. When the hybrid begins to develop flowers, the structure of the cells in the latter will depend on the determinants of the two white species and of the blue ancestral form. Although the 'blue' determinants are in the minority in the idioplasms of either parent, they may nevertheless, if they all combine, possess a greater power of transmission than the 'white' ones, if the latter are not homodynamous, *i.e.*, do not possess an exactly similar force of heredity, and consequently cannot produce an intermediate effect. They interfere with one another in their action, as they act in different directions to a greater or less extent. Many cases of reversion can be understood — even though only in principle — by means of this law. They can, moreover, easily be rendered comprehensible in individual cases if we have recourse to figures.

Let us suppose that the 'blue' ancestral determinants are not only contained in individual ids, but are present in all the ids of entire idants: a minority of old ancestral idants would then be opposed to a majority of modern ones, half of which, however, would correspond to the type of *D. lævis* and half to that of *D. ferox*. We assume that there are in all sixteen idants, six of which are 'blue' and ancestral, and ten 'white.' Since, therefore,

five of the latter belong to *D. lævis* and five to *D. ferox*, and these are consequently dissimilar, the six similar ancestral idants, which have a cumulative effect, will preponderate, because the 2 × 5 different idants of *D. lævis* and *D. ferox* do not produce the cumulative effect of 10.

Hitherto I have assumed that we are in this case dealing with a *complete* reversion to the ancestral form, and not merely with reversion to *individual ancestral characters*. I cannot, however, judge with certainty in this respect from the facts known to me concerning these hybrids; and as this instance was not chosen for its own sake, but merely as an example in which complete reversion to more remote ancestors might be accounted for, it must remain undecided whether it really belongs to the above category, and whether such instances of complete reversion actually occur. The blue colour of the flowers is at any rate not the only apparently new character in these hybrids; the stem, for instance, is brown, while it is green in the two pure species. In only one of these species (*D. ferox*) is the stem brown at first, and this colour is only retained as a brown ring around the base of the stem. I must leave botanists to decide whether the shape of the leaves, and the structure of the stem or fruit, afford any reason for considering these parts as intermediate between those of the two parental species, or whether they are to be regarded as deviations from both, and presumably, therefore, as reversions to the ancestral species.

It may in all probability be assumed that the process is not a complete one in the above-mentioned cases in which reversion to the wild ancestral form in different races often occurs when the latter are crossed. Darwin certainly gives one instance of a pigeon which ' was hardly distinguishable from the wild Shetland species,' but which was, nevertheless, descended from four grandparents which differed very considerably from the wild species (*Columba livia*).* This bird, which was blue, and possessed the typical black bars on the wings and tail, was descended from a red spot, a white fantail, and two black barbs. These breeds, as is well known, differ from the wild pigeon in colour as well as in many other details, such as the length of the beak and number of tail feathers; and it would therefore be interesting to ascertain whether these racial characters had all disap-

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* 'Animals and Plants under Domestication,' p. 14.

peared in the grandchild, and had become retransformed into the corresponding characters of the wild species. Were this so, the reversion might be considered complete, and the same theoretical explanation could be given for it as in the case of the *Datura* hybrid. Unfortunately Darwin leaves this point untouched, as he devoted his attention chiefly to the coloration so characteristic of the species. It seems to me to be very probable, however, from several of his statements, that this was also essentially a mere case of reversion as regards the coloration of the plumage. I conclude this principally from the fact that the blue or original coloration of *Columba livia* occurs in all the principal breeds of pigeons, although these blue sub-varieties are rare in some of them. The other racial characteristics do not at any rate exclude the possibility of a blue coloration ; and thus, on the other hand, reversion to the blue colour is not necessarily accompanied by a reversion to all the other characters of the ancestral form.

It is perfectly certain that in most cases the reversion produced by cross-breeding is not complete, even as regards the coloration, but gradually becomes more marked, so that at first very faint and hardly perceptible indications of the wing-and tail-bars are seen, and these become more pronounced by degrees, so that a partial blue coloration with perfect bars, and finally the perfect slate-colour and complete bars of the ancestral form are produced. The greater number of reversions in pigeons must consequently be *incomplete*, — *i.e.*, they must refer to individual *characters or groups of characters* only, and we are here concerned with the theoretical explanation of such cases as these.

I take for granted the facts that all valuable races of pigeons breed true, that all the main breeds are characterised by differences in *form*, and that sub-breeds differ merely as regards *colour*. In my opinion this implies, in the first place, that the germ-plasm of the main breeds has become essentially modified from that of the rock-pigeon, and that only lesser portions of it correspond to that of the ancestral form ; and also, that *all the determinants have not become modified to an equal extent*, — those for the coloration having undergone the least, and those for the whole body the most, alteration. I therefore suppose that the germ-plasm of one of the main breeds consists of a number of modified idants, none of which any longer correspond exactly

to those of the ancestral form, so that no one of them, did it control the ontogeny, could result in the development of a rock-pigeon. This conclusion depends entirely upon the race breeding true, for a germ-plasm which still contained individual unmodified idants of the ancestral form would also necessarily, or at any rate probably, once in a way, contain a majority of ancestral idants at the same time, in consequence of the incessant recombination of the idants in the reducing division and in fertilisation; and this must result in reversion to the ancestral form. Such a reversion, however, never occurs in purely bred races, but only when crossing takes place.

The germ-plasm of a race of pigeons therefore consists, according to my view, of a certain number of idants, each of which represents the type of the race. The majority of the ids of which each idant is composed must consequently virtually contain this type; or, expressed more accurately, *the whole of the racial determinants — as compared with those unmodified determinants which may still be present — are in the majority in all the ids of every idant*.

The fact that races breed true can in this way be thoroughly explained.

As regards reversion to the coloration and markings of the wild pigeon, we must suppose that, in the process of artificial selection to which the different races owe their origin, only just as many ids have become completely transformed into racial ids as were required to ensure the desired object, viz., the preservation of the racial characters. A larger or smaller number of determinants in many or perhaps all the ids must have remained unmodified in all, or at any rate in many, of the idants. The determinants on which the coloration depends, must have remained unmodified in larger numbers than did those relating to any other characters, for the coloration is the most liable to revert.

Reversion in the coloration will therefore occur when the ancestral determinants for any particular region of the bird's plumage gain a predominance over the racial determinants in the course of development; and in cross-breeds it will take place *when the racial determinants are so different that their forces counteract one another instead of being cumulative.* Although the ancestral determinants are in the minority in the germ-cells of the two different breeds which unite at fertilisation,

their controlling forces will nevertheless be cumulative, and if
they are sufficiently numerous, they will determine the colora-
tion in question, and thus produce reversion.

In this way we may, I think, account not only for the phenom-
enon of reversion in general, but also for many special details,
and more especially for *the different degrees of reversion in
different races of pigeons*. A sufficient number of experiments
has certainly not been made with regard to this point, but it is
nevertheless recognised that reversion occurs more easily and
more markedly in some races than in others. Darwin, for
instance, by crossing two black barbs with two red spots
obtained dark hybrids, of which ' no less than six presented
double-wing bars.' * On the other hand, the mongrels derived
from two black barbs and two snow-white fantails showed no
trace of reversion. This must have been due to the retention
of a different number of unmodified specific determinants in
the germ-plasm of the two races, as well as to the difference of
the modified racial determinants ; for the more marked the
difference between the two crossed races, the more easily will
the ancestral determinants gain the predominance over them.

The last-named experiment by Darwin was continued by
pairing two of these hybrids, one of which was brown and the
other black. The first brood (it is not stated how many there
were) displayed wing-bars ' of a darker brown than the rest of
the body.' This must have been due to the accumulation of a
larger number of unmodified determinants in individual germ-
cells in consequence of the reducing division, and to the subse-
quent union of two of these cells in the process of fertilisation.
We should therefore expect that reversion would not occur in
all the offspring of this pair, for the reducing division must also
result in certain germ-cells containing a majority of the modified
determinants. In the second brood of the same parents, in
fact, a brown bird was produced which possessed no trace of
wing-bars.

It is easy on the basis of our theory to account for the fact
that a simple crossing of two species did not in many instances
produce any traces of reversion, although reversion resulted
from *the subsequent double crossing*. The most complete case
of reversion obtained by Darwin was produced as follows. A

* Darwin, *l.c.*, Vol. I., p. 208.

mongrel female barb-fantail and a mongrel male barb-spot were paired. Neither of these birds 'had the least blue about them, nevertheless the offspring' (the number is not stated) 'from the above two mongrels was of exactly the same blue tint as that of the wild rock-pigeon from the Shetland Islands over the whole back and wings; the double black wing-bars were equally conspicuous.' * In this case the ancestral determinants evidently prevailed all the more strongly because they were opposed by racial determinants of three or four different kinds, the controlling forces of which could not simply be cumulative, like those of the ancestral determinants, but could only partially weaken and neutralise one another.

The fact which may be deduced from Darwin's observations, viz. that the offspring of simple crosses display practically a very similar tendency to reversion, can also easily be explained theoretically. For the germ-plasm of a well-established race will contain a certain percentage of ancestral determinants, and the germ-cells of an individual will be liable to but few fluctuations in this respect. In such simple cases of crossing, an almost similar number of ancestral determinants, as well as of racial determinants, must therefore come together at each fertilisation; and the struggle between these different kinds of determinants must always produce approximately the same result. A perfect uniformity in the offspring of the same cross cannot be expected; but if reversion does occur in some cases, it will be absent in others, and if it occur partially in some, certain parts in others will revert. An instance of the former kind is seen in the above-mentioned cross between a black barb and a white fantail, and of the latter in the case described by Darwin on p. 207 of his 'Animals and Plants under Domestication,' Vol. I. He crossed a white nun with a red tumbler, and reared five young, all of which presented traces of reversion. One possessed a blue tail; the second and third 'presented a trace of the bar at the end' of the blue tail; the fourth 'was brownish, and the wings showed a trace of the double bar'; and the fifth 'was pale blue over the whole breast, back, croup, and tail, but the neck and primary wing-feathers were reddish, and the wing-bars presented two distinct bars of a red colour.' Thus all the five young had reverted — some more and some less markedly —

* *Loc. cit.*, Vol. I., p. 209.

in one part or another. The differences between the young
support the theoretical assumption that the number of ancestral
determinants, which determined the type of the five young ones,
was by no means the same in the different germ-cells of the
two parents. Their dissimilarity, moreover, admits of a further
conclusion, which could likewise be foreseen theoretically, viz.,
*that the determinants for the coloration of the different regions of
the body are represented in the different germ-cells in fluctuating
numbers.* Not only should we naturally suppose this to be the
case from the structure of the germ-plasm as here assumed, but
we can hardly even imagine it to be otherwise. If the various
idants in the germ-plasm of a hybrid together contain twenty
ids with ancestral determinants, it does not follow that the latter
only are present in each id. There is no reason why in any one
id the determinants for the colours of the wings, for instance,
should not be ancestral, while those for the colours of the tail
are racial, or *vice versa*. The bird would display reversion in
the tail or wings, according to whether the former or the latter
kind of determinants is in the majority in the germ-cell: for
our theory shows that the struggle of the determinants takes
place independently in every cell, and consequently also in
every part of the organism ; and the result will therefore be
independent in each part, and will depend solely on the com-
bination of homologous determinants which contend with each
other in the cell or group of cells under consideration. It can
thus easily be explained how it comes about that though all the
offspring of a certain cross show reversions, the latter are never-
theless combined in very different ways with the racial characters
of the parents.

We must now consider the third type of reversion mentioned
at the beginning of this section, viz., that which concerns *in-
dividual characters of very remote ancestors, and is seen, for
instance, in the stripes on the legs of horses and asses, and
more especially of mules.*

It will not be necessary to repeat the arguments which Darwin
used to show that the horse was primitively dun-coloured and
striped. Indications of such a coloration are seen at the present
day in horses of different colours in all parts of the world, in the
form of a dark stripe down the back, and of transverse markings
on the legs and shoulders ; such markings, however, are not
common, and most frequently occur in dun-coloured horses.

The ass has been proved to be descended from a species pos-
sessing stripes on the legs, and corresponding to the existing
wild species (*Asinus tæniopus*) of Abyssinia. The domesticated
ass has, as a rule, only retained the crossed stripe on the back
and shoulders, but occasionally transverse markings occur on
the legs, and this is most often the case in animals of a pure
grey ground colour. The stripes on the legs are very rare both
in horses and asses, as I know from personal observation, and
even when present they are very faint.

In mules these stripes occur much oftener and much more
distinctly — particularly in light grey animals, and are some-
times seen on the hind-legs as well as on the fore-legs and
shoulders. Thus reversion occurs to the ancestral form of both
sides.

The theoretical explanation of this fact must be based on
the assumption that a certain number of unmodified ancestral
determinants for the hairy coat have been retained in the germ-
cells of the two species ; and that these, when they are brought
together in the germ-cells of the two parents, may predominate
over the modified determinants of the parents. The fact that
such reversion does not by any means always occur in mules,
points to the conclusion that the number of ancestral deter-
minants varies very considerably in the germ-cells of individuals,
and that these may even be entirely absent, or only sparsely
represented, or, on the other hand, may be present in large
numbers. In the latter case, when two of these germ-cells come
together in fertilisation, partial reversion will occur, and will be
more marked and extensive the greater the number both of the
ancestral determinants which meet together and the parts of
the body to which these belong. The determinants for the
stripes on the hind-legs are evidently much less numerous in
the combined germ-plasm of the two existing species than are
those for the marks on the fore-legs as is shown by the manner
in which these stripes have been relatively retained by several
existing wild species of *Equus*. All these determinants must,
however, be present in very varying numbers in the germ-plasms
of different individual horses and asses, for, as already stated,
reversion does not by any means always occur in mules ; in Italy,
where these animals are used in large numbers, it is not common,
and, as far as my experience extends, is perhaps only exhibited
in one or two animals out of a hundred. Gosse, however, states

that in the United States of America nine mules out of every ten are striped.

Before concluding this section, I will analyse a case of reversion to remote ancestors in plants in greater detail. My reason for so doing is not because different principles are necessary for its explanation, but because we possess the results of experiments which render a closer examination of the theory possible.

I will select as an example the case of the reversion of *irregular or unsymmetrical flowers to a regular or peloric form*. Many instances of reversion of this kind have been described, but they are very exceptional: their origin cannot be connected with any external causes, and must evidently be due to purely internal ones, viz., to the composition of the germ-plasm.

If my opinion concerning the transformation of the germ-plasm in the course of phylogeny is correct, it follows, as has already been shown, that individual unmodified determinants of an old character must always appear here and there in the germ-plasms of the modern species, even after an enormous number of generations. Such ancestral determinants — those of the original regular flowers, for instance — need not by any means be contained in the germ-plasm of every individual plant; and the older the modern species is, the fewer will be the number of these determinants, which we will call 'peloric.' They must gradually be displaced by the 'asymmetrical' determinants; for the latter, being better adapted to the existing conditions, have a better chance in the struggle for existence. A large number of plants, such as *Corydalis tuberosa*, for instance, will thus no longer contain any 'peloric' determinants, and this makes it apparent why reversion so seldom occurs in these cases. The fact that it can occur at all, is to be accounted for by the processes of reducing division and amphimixis in two germ-cells, the latter of which always follows on after the former. For if a small number of 'peloric' determinants still remained in various idants of individual plants of the species in question, they might occasionally come together in one germ-cell owing to the reducing division; and if two such germ-cells meet one another in the process of fertilisation, this group of determinants may predominate, and reversion will then occur — provided that the combined power of these 'peloric' deter-

minants is sufficient to predominate over the 'asymmetrical' determinants.

The experiments which have been made with respect to the transmission of characters in such abnormally peloric flowers, prove that this explanation must be correct in principle. Darwin crossed the peloric snapdragon (*Antirrhinum majus*) with its own pollen, and from the seeds thus obtained raised sixteen plants, which 'were all as perfectly peloric as the parent plant.'* We need not be surprised that the pelorism was inherited, for the 'peloric' determinants were in the majority in the parental germ-plasm on either side; it may, however, have been due to chance that *all* the sixteen plants which were reared proved to be peloric. If a larger number of offspring had been raised, some of them would certainly have produced asymmetrical flowers, for the reducing division would in most cases divide the 'peloric' determinants unequally amongst the two resulting cells, and consequently two germ-cells containing no, or only a minority of, 'peloric' determinants might meet together in fertilisation. Reversion to the ordinary form of the flower must then occur.

The result of Darwin's counter-experiment is particularly interesting. The peloric snapdragon was crossed with the common form, and 'two great beds of seedlings' † raised, '*not* one of which was peloric.' And in ninety plants which were carefully examined there was not a trace of pelorism, 'except that in a few instances the minute rudiment of the fifth stamen, which is always present, was more fully or even completely developed.' Darwin attempted to explain this fact by the assumption that in this case the common form of the flower possessed a 'prepotent force of transmission;' but apart from the fact that this statement is merely another formulation of an observed fact, and can hardly be looked upon as a real explanation, it does not hold in the case of Darwin's subsequent experiments. For the plants obtained by crossing the common snapdragon with the peloric form, 'which perfectly resembled the common snapdragon, were allowed to sow themselves; and out of a hundred and twenty-seven seedlings, eighty-eight proved to be common snapdragons, two were in an intermediate

* 'Animals and Plants,' &c., Vol. II., 1888, p. 46.
† *Loc. cit.*, Vol. II., 1888, p. 46.

condition between the peloric and normal state, and thirty-seven were perfectly peloric.' * If now, the character of asymmetry possessed a ' prepotent force of transmission,' we should expect it to become more apparent when the flowers of both parents were asymmetrical, than when this was the case as regards one parent only. In the chapter of the same book which treats of pangenesis, Darwin has attempted to give a special explanation of the fact ' that a character gains strength by the intermission of a generation' in which this character is not present.

My own explanation of the above-mentioned facts follows almost directly from what has already been said. The production of so many individuals of the ordinary kind by the crossing of ·the common snapdragon with the peloric form, and the fact that a large number of 'perfectly peloric' offspring, as well as of the common form, were produced when those obtained by the first cross were fertilised with their own pollen, is due simply to the reducing division of the germ-mother-cells occurring in different ways, so that sometimes only 'ordinary' and sometimes only 'peloric' determinants reach the germ-cell, and sometimes, again, a combination of both, in which either the 'peloric' or the 'ordinary' determinants preponderate. The daughter-plant will produce flowers which are either quite of the common form or more or less peloric, according to whether the determinants which are brought together by the two germ-cells in the process of fertilisation are chiefly 'peloric' or chiefly of the 'ordinary' kind. It is evident, however, that most of the parents of this generation, which possessed flowers of the ordinary form, must have contained 'peloric' as well as 'ordinary' determinants in their germ-plasm before the reducing division, for they were all derived from a peloric father or mother. The predominance of the ordinary form in the next generation may be explained as being due to the peloric grandparents possessing only a slight majority of 'peloric' determinants in their germ-plasm, in addition to a considerable number of 'ordinary' determinants. The whole of the germ-plasm of the germ-cells from which the parent generation arose must have contained very many more 'ordinary' than 'peloric' determinants.

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* *Loc. cit.*, Vol. II., p. 46.

4. *Reversion to Rudimentary Characters.*

It is well known that organs which have lost their value for the preservation of the species become rudimentary in the course of generations: they diminish in size, become stunted, and ultimately disappear altogether.

This may be expressed in terms of the idioplasm as follows. The group of determinants in the germ-plasm for the organ in question becomes reduced in one id after the other, first in one determinant and then in another, until finally it disappears completely; and the process is repeated in an increasing number of ids, until eventually this group of determinants is no longer contained in any of them. It cannot be stated how long a time and how many generations are required for this process, but it may at any rate be asserted, and even proved, that individual ids still contain determinants for the organ in question long after its disappearance from the mature individual. The fact that the organ occasionally reappears, and that consequently *reversion may take place*, proves that this is the case.

The supernumerary nipples which occasionally occur in human beings are an interesting example of this kind. The two normal nipples generally occur in a rudimentary form in men, but, in addition to these, very diminutive ones are occasionally met with in parts in which they are normally present only in the lower orders of mammals, such as carnivores, rodents, and lemurs : — a pair may be present above the normal teats near the axillary region, and two or three others lower down on the abdomen. All of them certainly never occur in the same individual, but usually only a single one or a pair are present: these, however, are found both in men and women. They are undoubtedly to be looked upon as reversions to extremely remote characters possessed by our lower mammalian forefathers. We owe an accurate account of their occurrence in the male sex to the numerous and detailed investigations of Otto Ammon,* who found them in three per cent. of our recruits.

As Ammon's researches only extend over two, or at most three generations, and only refer to individual cases, we cannot form a precise estimate as to the degree and extent to which these structures are transmitted. We may, however, attribute the

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* I am indebted to Mr. Ammon for these details, which are not yet published.

stimulus to reversion in these instances to interbreeding; that is to say, to the amphimixis of such germ-cells as contain a certain number of ancestral determinants in their germ-plasm on either side for those regions of the skin in which the nipples were situated in remote ancestors. Merely in consequence of the reducing division, these determinants may possibly accumulate in one germ-cell in sufficient numbers to produce the character in question. The same may be said with regard to many small individual marks, and such very ancient hereditary parts as supernumerary nipples usually follow the same rule as do individual characters; they have to a certain extent degenerated so as to come under the same category, and for a long time past have not been contained in the germ-plasm of every individual; their determinants, on the contrary, are entirely absent in most cases, and are only found in a certain number of ids in certain individuals. These determinants, like those of individual characters, may be transmitted for several generations without attaining development, and may then suddenly become manifest in consequence of a favorable combination of two conjugating germ-cells. The only difference between these ancestral characters and ordinary individual peculiarities is, that the determinants of the latter are contained in a larger number of ids, and we must therefore conclude that they become developed far more frequently and regularly.

Although in the case of the supernumerary nipples in the human race we cannot definitely indicate the ancestor from which they were derived, or the length of time during which they have been transmitted, it is at any rate possible to do so approximately in the case of *the supernumerary toes of horses*. For, thanks to the excellent researches of Kowalewsky, followed by those of Marsh, we are well acquainted with the phyletic development of the horse: we now know that horses belonging to the genera *Mesohippus, Miohippus,* and *Protohippus* or *Hipparion*, which possessed two smaller lateral toes in addition to the large median ones, existed in the middle Tertiary period. When horses are occasionally born at the present day in which one or two such accessory toes are present on two or even on all four feet, we are perfectly right in considering the development of these toes to be due to reversion to an ancestor of the Miocene period. We must therefore assume that in certain series of generations of the existing horse, some idants have

been retained in which ancestral determinants of the fore and hind-feet are present, but that these are in the minority, and a large number of them can only accumulate in one germ-cell when a particularly favourable reducing division occurs. This, however, would not in itself be sufficient to produce the character in question : chance must also play a part, in order that such an egg-cell, containing an abundance of ancestral determinants, may be fertilised by a spermatozoon in which a certain number of these determinants are also contained. Then, and then only, will there be a likelihood that the entire number of the latter will be sufficiently large to preponderate over the modern determinants of the foot in the process of ontogeny.

Cases of reversion of this kind occur very rarely. Marsh has, however, brought forward a small series of such instances, the oldest of which relates to a horse belonging to Julius Cæsar, and the most recent was observed by him in a living animal.*

5. *Preliminary Summary of Sections* 1-5.

All the phenomena of reversion which have so far been considered can be explained on the supposition that every germ-plasm is composed of a large number of equivalent units or ids, each of which possesses all the determinants required for the development of an organism ; every character is therefore produced by the co-operation of many determinants of the same region (homologous determinants). The transformation of a species or race into a new one, moreover, never depends primarily on a simultaneous modification of all the ids and determinants : when the modification begins to take place, even entire groups of ids (idants) may remain unmodified, and this will subsequently be the case as regards a minority of ids, and still later at least with regard to certain of the determinants in individual ids. The characteristic form of every individual cell which takes part in the process of ontogeny is the result of the struggle of the ids which occurs in this cell ; and as some amongst the mass of determinants which constitute every id in the germ-plasm may become modified and others not, and the proportion of modified to unmodified determinants may vary from id to id, we can understand that in crosses between species

* O. C. Marsh, ' Recent Polydactyle Horses,' *American Journal of Science*, Vol. xliii., April 1892.

or races, reversion is sometimes more and sometimes less marked — in some cases restricted and in others very extensive. In those cases, therefore, *in which rudimentary and insignificant characters only are concerned, such as stripes in mules, pelorism in flowers, and rudimentary nipples in the human race, individual variations must frequently occur in all degrees, from the complete absence of reversion to the most marked form of it.*

Conversely, it is just as easy to explain why reversion occurs *without exception* in other cases, such as in that of *Datura*-hybrids, if we assume that entire groups of ids or idants, as well as certain determinants in individual ids, have remained unmodified. For if the former are present in such numbers as to preponderate in a hybrid over the two kinds of modified ids, which counteract one another, they must be contained in nearly equal numbers in the germ-plasm of every individual.

We can in principle understand the whole series of the phenomena of reversion, if we represent the transformation of the germ-plasm as being due to the majority of the ids in most of the idants becoming modified first, while a minority of them remain unmodified : in the course of generations the number of these unmodified ids then gradually becomes smaller, owing to the action of natural selection, until the ancestral species is only represented by a number of scattered ids ; and finally, by continued selection, these ids also become modified in the same direction, to such an extent that eventually only the determinants of those individual characters escape modification which are less important or quite meaningless for the life of the organism. We know that complete reversion to the ancestral form may occur in young species in the case of favourable crosses between allied species (*Datura*) ; and that in the further course of phylogeny, that is, in older species, total reversions can no longer occur, although reversion to single characters, or even to entire groups of characters, may still take place, and does so with certainty under certain conditions — as is exemplified by the reversion of *certain* hybrids between different races of pigeons. In its last stage, then, reversion occurs as an entirely uncertain and apparently capricious re-appearance of an individual ancestral character, such as, for instance, that of the occasional striping in mules.

By means of our theory much may also be deduced and rendered comprehensible in principle concerning the *external causes*

of reversion. It can easily be understood that the crossing of different species and races is liable to lead to a preponderance of those ancestral idants, ids, or determinants which are common to the two parents. We might, however, also infer from the theory that certain of the offspring of hybrids are very liable to revert in the next generation to one of the ancestral species; for the germ-cells of the hybrids are very dissimilar as regards the germ-plasm they contain, in consequence of the reducing division which every germ-cell undergoes at its formation : most of them will contain idants of both parents in every conceivable proportion, while in others, idants of only one of the parents will be present. *The 'reducing division' is therefore one of the most efficacious of the primary causes of reversion*, for it renders possible the uneven distribution of the different qualities of the idants which were contained in the germ-plasm of the germ-cells of this parent. This principle applies equally to the cases in which not a single entire idant remains untransformed in the germ-plasm, which then only contains a minority of unmodified ids or even merely of determinants, scattered amongst several idants.

Reversion in any degree therefore depends, in the first instance, on the process of amphimixis, for without sexual reproduction the reducing division would not have been introduced into the organic world, and the second extremely important factor in reversion — viz., the crossing of different germ-cells — would also not exist. Reversion is, however, not of necessity connected with *actual* amphimixis, but may, as I shall show later on, occur in con-nection with parthenogenesis and gemmation ; although this is only true in the case of those organisms in which amphimixis formerly occurred, and the germ-plasm of which may therefore contain ancestral ids or ancestral determinants. It is evident, however, that the chance of reversion occurring must be much greater when amphimixis takes part *directly* in the process of reproduction ; for the relative proportion of modified and un-modified units of the idioplasm of this order may be quickly or suddenly altered in favour of the unmodified units, and thus the ancestral units which were originally present may undergo accumulation, and predominate over the somewhat dissimilar homologous units of the modified kind.

Our comprehension of the problem just discussed is certainly increased by the above considerations, and the following passage

from Darwin's 'Animals and Plants under Domestication'* will best show how much our insight has since then advanced: — 'In purely-bred races, occasional reversion to long lost characters of the ancestors often occurs without our being able to assign any proximate cause.'

6. REVERSION IN ASEXUAL REPRODUCTION

(a) *Reversion in the Process of Gemmation*

As already stated, *reversion does not entirely depend on amphimixis*, and may in fact, also occur apart from the crossing of two individuals. The *bud-variations* of plants form a well known instance of this kind.

For many years I possessed in my garden a maple (*Acer negundo*) with variegated leaves which were almost entirely white, and one branch of this tree bore ordinary green leaves, flowers, and seeds. Owing to the greater amount of chlorophyll, this branch grew and bore flowers and seeds far more luxuriantly than the main branch from which it arose. If we look upon the offshoots of a tree as persons, this would be an instance of a person of the plant-stock produced asexually, which reverted to the ancestral form.

We must go back to the origin of variegated species in order to find a theoretical explanation of this phenomenon. Like most similar varieties, indeed, of our trees and shrubs, this form must have arisen by *bud-variation;* in other words, a normal maple, from certain unknown causes, gave rise to a branch bearing variegated leaves. The cause of this modification, traced to the idioplasm, must have been due to the determinants of the leaves and other green parts of the shoot becoming modified in such a way as to result in the production of organs deficient in chlorophyll. If, however, only the majority, and not all the ids in the apical cells of the first variegated shoot became modified in this manner, a reversion of the variegated variety to the green ancestral species would become possible.

Another assumption, however, which cannot yet be proved to be true, is required in order to account for the appearance of a green branch upon a variegated tree: we must suppose that even in ordinary cell and nuclear divisions, the division of the idioplasm may take place in an irregular manner, so that all the

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* Vol. II., p. 25.

ids do not reach both the daughter-nuclei; but that both the halves of some of them which result from the division pass into the *same* daughter-nucleus. On the other hand, it might even perhaps be possible for an entire idant to be transmitted to only *one* of the daughter-nuclei. It must be possible for some such irregularity to occur in the distribution of ids during nuclear division, for otherwise the occurrence of a different combination of the primary constituents in the course of growth — such as, indeed, actually occurs in cases of bud-reversion — would be inexplicable.

Let us distinguish between those ids which correspond to the original form, and those which have become modified, by describing them respectively as 'green' and 'variegated' ids. The reversion of a shoot must then be due to the unequal distribution of the ids amongst the daughter-nuclei during the divisions of the apical cells of the shoot, so that a majority of 'green' ids were distributed to a cambium cell containing 'blastogenic' germ-plasm, or even also to an apical cell of a young lateral bud. Conversely, a variegated shoot might subsequently originate from a green one, as in fact actually occurs.

I should be inclined to offer a similar explanation of the re-versions to the ancestral form which so frequently occur in all the numerous varieties of our trees and shrubs, such as, for example, the oak-leaved heterophyllous hornbeam, the fern-leaved oak, the varieties of the maple and birch which possess greatly subdivided leaves, and the copper-beech and copper-hazel. The tendency to revert is very varied even in the different varieties of the same species. The golden-striped variety of *Euonymus japonica*, for instance, is very liable to revert, while in the silver-striped variety of this plant reversion rarely occurs.

This difference would simply depend on the relative minority of ancestral ids in the variety in question. Reversion will never, or only rarely, occur when the idioplasm only contains a few ancestral ids; if, however, there are so many of these that the unmodified ids only form a small majority, reversion can easily take place.

In this connection I must mention another instance, which has very frequently been discussed since Darwin's time, viz., that of the peculiar 'graft-hybrid' *Cytisus adami*. The com-

bination of the characters of the two ancestral species con-
tinually varies in this plant, which sometimes bears the yellow
clusters of flowers characteristic of the common laburnum
(*Cytisus laburnum*), and sometimes purple flowers like those
of *Cytisus purpurea*, or, again, both these colours may be
present in the same flower. I will here quote Darwin's descrip-
tion of the plant * : — ' To behold mingled on the same tree
tufts of dingy-red, bright yellow, and purple flowers, borne on
branches having widely different leaves and manner of growth,
is a surprising sight. The same raceme sometimes bears two
kinds of flowers, and I have seen a single flower exactly divided
into halves, one side being bright yellow and the other purple,
so that one half of the standard-petal was yellow and of larger
size, and the other half purple and smaller. In another flower
the whole corolla was bright yellow, but exactly half the calyx
was purple. In another, one of the dingy-red wing-petals had
a narrow bright yellow stripe on it ; and lastly, in another
flower, one of the stamens, which had become slightly foliaceous,
was half yellow and half purple.'

The result of the struggle of the parental idants evidently
cannot depend in the case of *Cytisus adami*, as it does in that
of the individual characters of the human race, upon the fact
that the number of homodynamous determinants varies in the
parental idioplasm according to the part concerned ; for were
this the case the same parts of the flower could not sometimes
be yellow in some instances and red in others, — all the flowers,
on the contrary, would display the same composition as regards
the parental hereditary parts, even though slight variations might
occur, such as would be produced by a dissimilarity in the con-
ditions of nutrition. As in the case of the hybrids of *Oxalis*
already mentioned, the flowers would at least display a certain
combination of parental characteristics which would be uniform
in one and the same plant. The fact that this is not the case,
seems to me to afford a decisive proof that *Cytisus adami is a
real graft-hybrid, and not an ordinary seminal hybrid*, as in
fact was stated to be the case by the nurseryman Adams, who
first produced it. I therefore consider the controversy ended
as to whether graft-hybrids exist at all, and offer the following
explanation of the hereditary phenomena concerned.

* *Loc. cit.*, Vol. I., p. 414.

Cytisus adami was obtained from a young bud on a portion of the bark of *Cytisus purpurea*, which was grafted into the stem of *C. laburnum*. This bud developed into a shoot which exhibited an intimate combination of the parental characters. The shoot was afterwards propagated, and the plants raised from it exhibited 'reversions to both of the parental forms,' as well as dingy-red, *i.e.*, mixed blossoms, so that the pure characters of the parents were displayed in more or less extensive regions of the hybrid.

From a theoretical point of view, it can obviously be granted that a mongrel-plant may originate by contact of the living tissues of the parents, only if the transformation of the rudiment of an existing shoot is out of the question, and if the rudiment then appears for the first time. An existing dormant bud, which contains all parts of the shoot, cannot become modified as regards the idioplasm which it contains by the stock of another species which nourishes it: its apical cells, from which further growth proceeds, cannot receive a supply of extraneous idioplasm from the supporting stock; for the nuclear rods alone contain idioplasm, and this is a solid substance, and can only undergo combination by the fusion of two cells and their nuclei. It is therefore also worthy of notice that Adams did not observe that a hybrid was developed from the *single* dormant bud which was from the first present on the graft, but that the hybrid arose from *one of the later buds which were formed in the second year*; moreover, only *one*, and not *all*, of these buds produced bud-hybrids. The formation of this single hybrid-bud must have been regulated by an unusual and accidental occurrence, for all efforts to produce the hybrid a second time have so far been in vain. This accidental occurrence must have been that the cambium-cells of the two species came to lie close together, so that they could both enter the same bud arising from the cambium. Botanists must decide whether two cambium-cells, belonging to different species, can conceivably become united into one by a process of conjugation similar to that which occurs in the union of the male and female cells in fertilisation, and whether the foundation may in this way be laid for a new growing point.* If such a process

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* A *fusion of nuclei*, apart from that seen in the process of fertilisation, actually occurs in plants in the case of the embryo-sac. Guignard (*loc. cit.*) describes this process in detail as follows: — The 'upper and lower pole-nuclei' of the embryo-sac approach one another, each accompanied by

occurred in this case, *the number of idants of Cytisus adami must be as large as that of the two ancestral species taken together;* for, as far as we know, a process of reducing division only occurs in the formation of sexual cells. The correctness of my assumption can therefore be controlled by observation.

It is hardly conceivable that two young plant-cells could, without fusing, have formed the growing point of the hybrid-shoot; for probably only one of these cells could have performed the function of an apical cell, and consequently the hereditary influence of the other could not have extended to countless daughter-shoots, as was actually the case. In the course of growth, every cell below the apical cell must necessarily have gradually come to be situated further away from the growing-point. Such an intimate combination of characters as actually occurred could not have been effected in this way.

I am therefore inclined to suppose that the unusual phenomena exhibited by *Cytisus adami* were due to an abnormal kind of amphimixis, so that the idants of both species were combined in the apical cell of the first shoot; but that in the subsequent cell-divisions an unequal distribution of the two kinds of parental idants amongst the daughter-nuclei took place, thus producing the variations in the combination of the characters.

Such an unequal distribution of the superabundant idants might also occasionally occur in an apical cell itself. This process may, moreover, be connected with the frequent complete reversion of an entire branch to *one* of the ancestral species, as well as with the fact that a modification tending to make the parental characters more and more distinct has occurred in the course of time in many examples of hybrids. Shortly after the first appearance of the *Cytisus*-hybrid, the colour of all the flowers was a dingy-red, — that is, an intimate mixture of the two ancestral colours, yellow and purple; but by degrees this mixture became less perfect, until eventually pure yellow and pure purple flowers, and even entire clusters of flowers and entire branches possessing almost the pure character of one or other of the parent-species,

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its centrosome, which has already become doubled by division. The nuclei then come to be situated close together, the centrosomes uniting in pairs, just as in the ordinary process of amphimixis; and finally the two nuclei fuse together completely. A spindle of division is then formed, and several divisions follow close after one another.

were formed. It seems only possible to explain this circumstance by supposing that the connection of the two idioplasms was easily severed, and that differential nuclear divisions occurred in such a manner as to cause a larger number of idants of *C. purpureus* to pass into one daughter-nucleus, and a larger number of those of *C. laburnum* into the other; or, at any rate, to cause the one or the other idant to pass completely into one of the daughter-nuclei, instead of dividing longitudinally and one of the resultant halves entering each daughter-nucleus. Though this is certainly only a conjecture, it is, however, not altogether an unjustifiable one, for the apparatus for division in each of the two species is certainly concerned with a smaller number of idants than that which must be present after the fusion of two nuclei; irregularity might therefore easily occur at the division. It is possible that unknown forces of attraction may also play a part in the process: the idioplasms of the two species do not at any rate exhibit a marked attraction to one another, as might perhaps be conjectured from the negative results obtained by Darwin, Reisseck, and Caspary in ordinary experiments on hybridising. By fertilising *C. laburnum* with the pollen of *C. purpureus*, Darwin obtained pods which dropped off 'in sixteen days after the withering of the flowers,' and the reverse cross resulted even less successfully.

However this may be, — and the point can be settled by determining the number of idants, — the phenomena of heredity at any rate indicate that the idioplasms of the two parents can easily again become separated in the course of cell-divisions. This separation might perhaps begin with the passing over of *one* idant only from one side, which would result in the preponderance of one parent in many of the blossoms, &c. This preponderance would have increased considerably in the course of growth, so that far larger groups of cells now frequently contain pure idioplasm of *C. laburnum* or *C. purpureus*, and new shoots are formed which apparently contain idioplasm of one or the other species only. The fact that the plants raised by Herbert from seeds of pure yellow flowers of *Cytisus adami*, which, although they bore yellow flowers, showed a purple tinge on the flower stalks, proves that even these shoots may still contain some individual idants of the other ancestral species. The idants of *C. purpureus* seem, however, to have disappeared entirely from certain shoots; for Darwin raised plants from

the seeds of yellow flowers, which resembled *C. laburnum* 'in every character, with the exception that some of them had remarkably long racemes.'

My explanation of the fluctuation in the combination of parental characters in *Cytisus adami* rests on the fact that we are not here concerned with the subtle differences in the forces which, in the reproduction of the human race, cause either the maternal or the paternal idants to predominate, and which we have attributed to the number of homodynamous determinants, which differs according to the characters concerned : this fluctuation depends on the grosser differences, and on the number of idants on the two sides. Sometimes the idants of *C. purpureus*, and at others those of *C. laburnum*, predominate in the idioplasm of a cell ; and, under certain circumstances, even only the *one* kind of idant may be represented in a cell, in which case it alone will also be present in all the offspring of this cell.

My theory is not therefore rendered less likely by the case of *Cytisus adami* ; we can, on the contrary, even explain the most minute details of such phenomena by its means, although it was not formulated for this purpose.

6. *Reversion in Parthenogenesis.*

Reproduction by means of unfertilised ova occurs regularly in some plants and in many animals — more especially in crustaceans and insects. We might be inclined to expect, *a priori*, that no great degree of deviation between the mother and daughter could occur at all in this monogonic form of reproduction, and that at most a reversion to more remote ancestors could take place.

Such a supposition is not, however, borne out by experience. A series of experiments with parthenogenetic species, which I have made during the course of the last eight years, have shown that although the expected uniformity between parent and offspring generally results in a very high degree, exceptions occur occasionally, and that these must be regarded as exhibiting reversions to an ancestral form many generations removed.

The facts are briefly as follows. Two varieties of a small Ostracod (*Cypris reptans*), possessing a very marked coloration, occur in certain ponds in the neighbourhood of Freiburg. The colour of one variety A, is light yellow ochre, five green spots being present on either side of the shell ; the other variety B,

appears dark green, owing to the yellow-ochre ground colour being reduced in extent by the presence of six large green patches. These patches exactly correspond as regards position in the two varieties, and are merely much smaller in A than in B, the sixth spot being wanting in A. Both varieties are reproduced parthenogenetically in the neighbourhood of Freiburg, and males never appear.
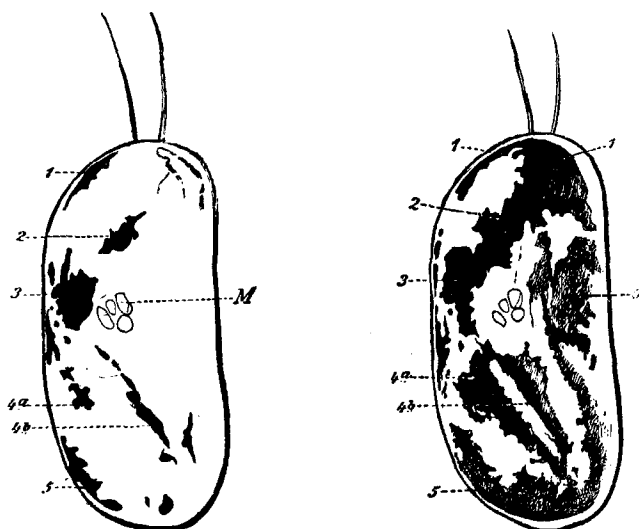

Fig. 23. — The two varieties of *Cypris reptans*. 1-6, indicate the six main patches of colour on the shell.

My experiments were made by isolating one female of each variety in a small aquarium, feeding them well, and allowing them to multiply until each vessel was filled with their mature descendants, which in their turn produced eggs. The individuals of the colony were then examined, and the greater number killed and preserved, one or more of them being kept alive and placed separately in fresh aquaria for breeding purposes.

These animals breed very rapidly throughout the year, and thus in the course of the last eight years many thousands of individuals have passed through my hands.

The first result obtained by these experiments confirmed

my expectations: *the descendants of the same mother resembled one another as well as the parent with which the experiments began, even as regards minute details of the markings.* The differences were mostly as small as those which may be observed in identical human twins: it cannot be stated whether these were due to a want of similarity in the germ-plasm, or whether they were to be accounted for by accidental differences in nutrition.

Apart from the exceptions about to be mentioned, no modifications occurred even in the course of many generations. I now possess colonies of A and B which cannot be distinguished from their ancestors in the year 1884. Reckoning that from five to six generations were produced each year, about forty generations have been passed through since then.

In 1887, some individuals of the dark-green variety B appeared for the first time in an aquarium containing the typical yellow-ochre-coloured variety A; and since then I have twice observed a similar occurrence in other broods of A. In the last of these cases, examined in May 1891, it could be proved that only a single Cypris out of 540 adults contained in one aquarium had changed into the dark variety *suddenly, and without apparent cause.* In another case, intermediate forms between the two varieties were found, as well as ordinary individuals of the variety B; and this fact is not only of interest theoretically, but it also removes all doubt as to the trustworthiness of the experiments.

For a long time I waited in vain for the occurrence of the reverse transformation from the dark variety to the light-coloured one, and was inclined to consider that the former was the ancestral form. But in the winter of 1890–91, a colony of B appeared in which a few typical individuals of the variety A were found, together with typical specimens of B which had been bred in this aquarium for many years.

It is out of the question that these sudden transformations were due to external influences, for *both* forms made their appearance together in the same small aquarium, under precisely the same conditions. We can only suppose that *modifications in the composition of the germ-plasm* must have taken place, and I think it is possible to prove that this was the case.

Parthenogenesis, using this term in the strict sense, has in all cases been derived from sexual reproduction, as is proved in

this case by the fact that the unmated females retain the receptaculum seminis, which is unused and always empty.

The two varieties must have originated at a time when sexual reproduction occurred — at any rate periodically : were this not so, primary constituents of A could not be present in the germplasm of B, and *vice versa*. The co-existence of both kinds of primary constituents in the same animal, can only be understood if we suppose that sexual reproduction had occurred at no very distant period.

The explanation of the process of reversion naturally follows from the fact that *in species in which parthenogenesis regularly occurs, a reducing division nevertheless takes place*, but only a *single* one : *one* polar body is separated off from the egg, and not two, as in sexual reproduction. This single halving of the idants in the ovum must undoubtedly be preceded by a doubling, just as occurs in sexual reproduction ; for a reduction of the number of idants to one half would otherwise take place from generation to generation, so that ultimately only a single one would be left. If, however, a reducing division preceded by a doubling of the number of idants takes place, reversion becomes possible.

Let us take a case of the simplest possible kind, and suppose that there are four idants in the germ-plasm, three of which are entirely composed of ids of the type A, and the fourth of ids of the type B. The four idants a, a, a, b, first become doubled, so that eight idants, a, a, a, a, a, b, b, result. Let us assume the most favourable case for reversion towards the variety B to occur, the reducing division resulting in the separation of these idants into the groups a, a, a, a, and a, a, b, b, the latter of which forms the nucleus of the egg-cell : the daughter individual arising from this egg would then produce primary ova containing the group of idants a, a, b, b. After the process of doubling in the ripe ovum, this group would then have the composition a, a, a, a, b, b, b, b ; and if the reducing division occurred in such a manner as to result in the combination a, a, a, a, passing into the polar body, and the combination b, b, b, b, remaining in the nucleus of the ovum, an individual of the variety B would undoubtedly arise from the egg, and reversion would ensue.

These processes would in reality be much less simple, and would take place much more slowly. For the number of idants is doubtless in most cases much larger, and the addition of a

single idant of the other form would result in a much smaller percentage. I have been able to prove the existence of 24–26 idants in the case of *Artemia salina*, a crustacean which multiplies parthenogenetically. If even several of these belonging to one of the two ancestral varieties were present in a minority, it is questionable whether they would ever become accumulated in one and the same germ-plasm in the course of generations and the corresponding reducing divisions, so as to form a preponderating majority : such an accumulation is, however, conceivable. This would partly depend on chance, for the majority of the ova produced by an individual always perish, and rare combinations which would produce reversions are therefore also usually lost.

We may thus account for the fact that reversion only occurred rarely in my experiments and only in certain individuals of a colony at the same time, as well as for its appearing either suddenly, or else after the production of intermediate forms. The latter case is to be explained theoretically by supposing that a balance of the two kinds of idants was first produced, and that this then in the offspring partially led to the preponderance of the idants on which reversion depended.

The possibility of reversion in parthenogenesis therefore depends upon two factors : firstly, upon the composition of the germ-plasm out of different kinds of ids and idants, — *i.e.*, upon the occurrence of sexual reproduction in a previous generation ; and, secondly, upon the ‘ reducing division ’ which always takes place at the formation of germ-cells.

7. *Proof that the Determinants become Disintegrated into Biophors*

I will conclude this chapter with some remarks which might have been more suitably inserted in the chapter on *the control of the cell by the idioplasm*, but in that place they would have been unintelligible, as they depend upon a knowledge of the phenomena of maturation of the ova and spermatozoa.

The fact that actual germ-plasm is removed from the animal-ovum by means of the cell-divisions occurring before maturation, — that is, in the process of *the separation of the two polar bodies*, — was not by any means easily determined, and was only proved after at least ten years of prolonged and difficult investigation and reasoning. I have not thought it advisable to give

an account of the whole history of the development of our
knowledge of this subject,* as this is unnecessary for under-
standing the phenomena of heredity. I must, however, refer
to a period of this history, which is instructive as regards the
method by which the cell is controlled by the emigration of
nuclear matter into the cell-body as enunciated by de Vries and
accepted by myself.

After the so-called 'extrusion' of the polar bodies of the egg
had been shown to correspond merely to a very unequal cell-
division, and convincing proof had been given that the controlling
substance must be situated in the chromatin of the nucleus, it
followed as a logical postulate that the ovum, like every other
cell, must be supposed to contain a special controlling substance,
or *specific idioplasm*, the function of which is to produce the spe-
cial histological nature of the cell in question. This conclusion
I arrived at, and assumed that the ovum, from its earliest stage
to the attainment of its full size and specific nature, is controlled
by a special idioplasm, which differs entirely from the idio-
plasm which becomes active after the completion of maturation.
If the nature of the cell is determined at all by its idioplasm,
the ovum, while still growing and undergoing histological de-
velopment, cannot possibly be controlled by the same idioplasm
as that which serves for embryonic development. I consequently
assumed the existence of an *'oogenetic'* idioplasm in the egg
during the period of its histological differentiation, and also that
after maturation, this substance gives up the control of the cell
to the germ-plasm.

The question then arises as to what becomes of the oogenetic
idioplasm when this change in the control takes place.

My answer to this question was, that the oogenetic idioplasm
is removed from the ovum by means of the polar divisions, and
that it was thus rendered possible for the germ-plasm — which
was already present in the nucleus of the ovum, and had in the
meantime increased considerably in bulk — to obtain control of
the cell.

This conjecture has since turned out to be erroneous. Investi-
gations which I subsequently made soon showed that at least
one of the two polar divisions has a totally different significance,

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* Such an account is given in my essay on 'Amphimixis,' and in still
greater detail in the previous 'Essays upon Heredity.'

inasmuch as it results in the halving of the germ-plasm itself. It became apparent subsequently that *both* divisions serve this purpose, and each of them causes the removal of germ-plasm, and not of oogenetic idioplasm from the ovum.

My hypothesis must therefore be given up, but I nevertheless believe that the conclusion on which it was based was a correct one, and that it may be further utilised in the light of the theory of heredity here developed. The oogenetic idioplasm must exist, and, using the terminology I have now adopted, it may be spoken of as the oogenetic 'determinant.' This determinant will consequently be the first to become separated from the mass of germ-plasm of the young egg-cell, to disintegrate into its constituent biophors, and to migrate through the nuclear membrane into the cell-body. In this way alone can we account for no trace of it remaining in the nucleus, and for embryonic development not being subsequently impeded by its presence. *This determinant is used up, and disappears as such;* and the fact that it is not expelled from the egg strongly indicates, if it does not prove, that the control of a cell by a determinant is accompanied by the absorption of the latter, and a further support may thereby be obtained for the hypothesis of emigration.

A precisely corresponding process must be assumed to occur in the formation of the sperm-cells, in which also the function of the idioplasm during the histological differentiation of the cell differs widely from that of the germ-plasm of the mature spermatozoon. The necessity for assuming the existence of 'histogenetic' determinants is perhaps rendered still more evident in the case of the egg-cell, as in some animals two kinds of eggs are produced which are very different as regards size, the relative quantity of food-yolk, colour, and nature of the shell. The assumption of *two kinds* of oogenetic determinants cannot be avoided in this case, for we cannot suppose that the same germ-plasm can have such different effects on the cell. In the section on alternation of generations, it was shown to be necessary to assume that such species contain two kinds of germ-plasm, containing determinants which are in part similar and in part dissimilar. Thus the germ-plasm from which the winter-eggs of the *Daphnidæ* are developed must contain an oogenetic determinant which is quite different from that of the germ-plasm in the summer-eggs, for these two kinds of ova are entirely dissimilar.

I know of no instance in which there is such a wide difference as regards the activity of the idioplasm in successive cell-generations as is the case in the germ-mother-cells and the mature germ-cells arising from them. If, however, even in this very striking instance of a sudden change of function of the idioplasm, the idioplasm which was active at first is not removed from the cell, such a process cannot occur in any other case; and we are consequently justified in applying to all other cells the conclusion derived from the behaviour of the germ-cells, and in considering it as proved that the *active idioplasm of a cell becomes used up in consequence of its activity*.