The Theory of Genotypic Parallelism as a Basis of Group-variability[1]

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I
INTRODUCTION

In his Monograph[2] the writer has enumerated 2077 titles of papers published during the years 1900–1929 which are principally concerned with gene-analyses in the flowering plants. Since the field of genetics was opened to exploration in its real scientific method with the rediscovery of Mendel's Laws in the year 1900, the list of literature in that Monograph, though it does not pretend to be complete, may serve approximately to represent the magnitude of works now available in this line of research carried out during the past thirty years.

The species which have been used as materials for gene-analysis are numerous. The Monograph has dealt with 373 species, belonging to 55 families (*v.* 'Monograph', p.777–786). Most of them are crop or ornamental plants, because of their numerous variations and easy breeding, and further

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1) The MS. of the present paper was actually accomplished in 1933. Owing to some unavoidable circumstances, its publication was so far delayed.

2) 'A Bibliographical Monograph on Plant Genetics (Genic Analysis). 1900–1929. 2nd edition. 1933'. This work is cited abbreviatedly as 'Monograph' throughout the present paper.

because of the number of geneticists who have, in view of applying genetics to agriculture, confined themselves to these. It is surprising to see how large a portion of the literature on gene-analysis in plants has been occupied by these plant-breeders, horticulturists and pomologists. The present writer fears that this has led some persons of the practical side to an appreciation of Mendelian analysis only in the practical combination of it with agricultural or horticultural requirements for the creation of new varieties of economic value.

On the theoretical side, modern geneticists have expanded the subject-matter in fundamental researches involving the interrelations of their science with other branches of biology, especially cytology. This of course is the natural direction of development of genetics and much more fruitful achievements are to be expected in this direction. At the same time, however, the writer fears, this has caused some geneticists to lose the original interest in gene-analysis and to consider that most of the data so accumulated are nothing more than repeated confirmations of Mendel's principles.

The writer believes that all the data thus acquired should have their significance for insight into the process of 'group-variability'. They become valuable first only when one attempts to utilize them in constructing a coherent whole of a higher order. Up to the present, to our regret, no attempt has been made to gather up such scattered facts in order to unite them into an integral system. This lack of generalization has naturally resulted in the establishment of a number of independent systems of plant genetics, such as *Triticum*-genetics, *Nicotiana*-genetics, etc. In the mode of symbolizing the genes, therefore, there is no standardization. In this connection, Prof. FUJII says (in his Foreward to 'Monograph'):

"..... in chemistry symbols for elements are used each with a definite name with its quantitative and qualitative attributes, which is universally adopted among all chemists, while in genetics of the present day, one and the same symbol is often used by different authors for different genes, and the same author uses different symbols in different plants, and even on different occasions for the same gene,—a state of affairs which should not be allowed in an exact science, and the very cause of the impression that genetics is a play of numbers and arbitrary symbols."

The control of this anarchy now prevailing in genetics is attainable only by the establishment of a certain integral system which is to cover the ground principles concerning genotypic variability in general, that is, in higher groups as well as within each species.

Accordingly in this paper an attempt is made to present a general survey of the present status of a problem: is it justifiable to consider characters varietal, specific, generic, etc. under one category; and if so, to what extent?[1] From such a survey it is to be hoped that some light may be shed upon the direction in which further research and new evidence are most urgently needed.

II
MENDELIAN SEGREGATION IN INTERSPECIFIC CROSSES

In the early stage of development of genetics, problems on eventual differences between the behavior of specific and varietal crosses were subjects of lively discussion. In 1903, DE VRIES advanced the hypothesis that Mendel's principles hold true only for varietal crosses, but not for interspecific crosses. This idea came naturally from the pre-Mendelian conception of interspecific hybridisation, as represented by WICHULA and GAERTNER. Both the investigators, WICHULA working on *Salix* and GAERTNER on *Aquilegia, Verbascum, Geum, Dianthus, Nicotiana,* etc., obtained results indicating that interspecific hybrids remain constant in further generations. It is interesting to note, however, that NAUDIN on the other hand observed wide-range segregations in F_2 of numerous interspecific crosses (*cf.* BLARINGHEM).

MENDEL's work on the cross, *Phaseolus vulgaris* (described as *Ph. nanus*) $\times$ *Ph. multiflorus,* is of historical significance. He observed monogenic segregation as to growth habit and color of unripe pods. The occurrence of one white-flowered plant among 31 F_2 offsprings led him to assume that in this case the flower pigmentation is probably due to at least two 'elements', an idea which was later fully accepted as gene polymerism. With this as the first instance demonstrating Mendelian segregation in interspecific crosses, the experiments since 1900 subsequently disproved the idea of constant species hybrids. Numerous cases of crosses between two distinct species which behave in the same manner as varietal crosses have been accumulated very extensively. A general survey of them, as represented in tabular form as follows, may serve as an indication of the extent of plant groups where these instances have been known.

1) Here the terms, specific, varietal, etc. are used in the taxonomist's sense. In this connection, it might be objectionable to open the discussion without giving any consideration of the conception of species, but this may be justified by the reason that the present discussion as a whole has naturally an intimate connection with this problem.

Salicaceae
Salix
Urticaceae
Urtica
Chenopodiaceae
Spinacia
Nyctaginaceae
Mirabilis
Caryophyllaceae
Dianthus
Lychnis
Ranunculaceae
Aquilegia
Papaveraceae
Papaver
Brassicaceae
Brassica
Capsella
Raphanus
Saxifragaceae
Ribes
Rosaceae
Fragaria
Geum
Rubus
Amygdalaceae
Prunus
Fabaceae
Medicago
Mucuna
Phaseolus
Pisum
Tropaeolaceae
Tropaeolus
Linaceae
Linum
Vitaceae
Vitis
Malvaceae
Gossypium
Malva
Violaceae
Viola
Oenotheraceae
Epilobium
Godetia
Rhodoraceae
Rhododendron
Primulaceae
Primula
Hydrophyllaceae
Phacelia
Laminaceae
Mosla
Origanum
Solanaceae
Datura
Nicotiana
Petunia
Solanum
Rhinantaceae
Antirrhinum
Mimulus
Rubiaceae
Richardia
Campanulaceae
Phyteuma
Asteraceae
Lappa
Poaceae
Avena
Hordeum
Triticum
Secale
Cannaceae
Canna
Orchidaceae
Cattleya
Odontoglossum

As far as these cases are concerned, there is in the mechanism of inheritance no *essential* difference in inter-specific crosses from that which exists in varietal. This implies that the features which are regarded by taxonomists as 'essential' ones in distinguishing species are also subject to the same principles as are the varietal characters. Notwithstanding this, the assertion is still occasionally made that characters inherited in a Mendelian manner are of minor importance.

Several investigators have succeeded to express the differentiating specific characteristics in definite genic terms. For instance, HONING working on the hybrid between *Canna glauca* and *C. indica* clearly indicated that the characters distinguishing the parental species involve 18 allelogene

pairs. They are: *A* originating red corolla color and also acting as the base gene for anthocyanin pigmentation, *B* and *C* responsible for red leaf margin, *D*, *E* and *F* intensifying the effect of *A* and *R*, *G* extensifying anthocyanin in the leaves, *K* and *L* responsible for the wax layer on the leaves, *M*, *N* and *O* responsible for the third staminodes, *H* and *I* responsible for deep yellow plastids, *J* intensifying vein-coloring, *P* extensifying the central red coloring in a yellow margin, *Q* acting as a lethal, and *R* producing red patches in yellow flowers. In these genic terms, the parental species were expressed as:

C. indica = *AABB*(*CC*)*DDEEFFggHHIIjjkkll*(*mmnnoo*)*ppqqrr*,
C. glauca = *aabb*(*cc*)*D*.*eeffG*.*hhiiJ*.*K*.*LL*(*M*.*N*.*O*.)*PpQqRr*.

In these schemes, doubtful genes are put in brackets and marked with a point, when it is unknown whether the character is in homo- or heterozygous condition.

Another striking instance may be cited from KRISTOFFERSON's experiments on an extensive series of inter-specific crosses in the genus *Malva*, especially between four species, *M. oxyloba*, *M. parviflora*, *M. neglecta* and *M. pusilla*. As to the five allelogenic pairs identified, *O* producing serrated leaves and pointed sepals as contrasted with *o* producing serrated leaves and round sepals, *A* and *B*, each producing the raised margin of the carpels as contrasted with *ab* for round margin, *F* intensifying the effect of either *A* or *B* and *E* causing rosette-stage flowering, these species were represented as:

oxyloba = *OOAABBFFee*,
parviflora = *ooAABBFFee*,
neglecta = *ooaabbffEE*,
pusilla = *ooAABBffEE*.

These are only a few instances out of many which might be cited, but may be enough to show that such analysis of the specific characters offers biologists a basis for a much clearer understanding of the fundamental constitution of the species and of the nature of the limits of taxonomic groups.

Sometimes inter-specific crosses reveal some differences of minor[1] importance in genetical behavior from that in intra-specific ones. One of the differences which is met with rather frequently is discrepancies in segregation which are imagined to be caused by disturbances in the distribution mechanism of the chromosomes. For instance, CLAUSEN found

1) Of course, from the view-point of genotypic homology.

in the cross, *Viola tricolor* × *V. arvensis* that the chromosome containing a gene, *W*, which bleaches the yellow corolla pigment and is possessed by *V. arvensis*, is eliminated in about 60% of the pollen mother-cells, resulting in a segregation ratio much differing from what would be expected from the ordinary segregation. Since, as is well-known, the normal conjugation of chromosomes is a *conditio sine qua non* for the normal segregation, it is quite natural that disturbances in the former would cause disturbances in the latter. Another kind of difference is met with an cases where the genotypic differences between parental species first become apparent when they are brought together in a cross, but do not in intra-specific crosses. Such is the case of *Gossypium*. In the inter-specific cross with American cottons, segregation of some characters such as color of the corolla and pollen usually takes places continuously, making a marked contrast to the varietal cross where segregation occurs in a definite, sharp manner. The cause of this difference in segregation between intra- and inter-specific crosses was clearly explained by HARLAND on the assumption that "in varietal crosses there is segregation of the main gene alone, whereas in the inter-specific cross there is segregation of modifiers which may partially, or in some cases entirely, obscure the distinction between dominant and recessive." On a similar basis cases might also be expected in which different inter-specific hybrids differ in the mode of inheritance for the same character. Thus BALLS and KEARNEY showed that in the Upland-Egyptian cotton cross the more deeply lobed leaf type of the latter dominates in F_1 and segregation occurs in F_2 in a continuous form, indicating a number of modifiers involved in this character, whereas MCLENDON working on the cross between broad-lobed Upland and narrow-lobed Sea Island cotton observed a monogenic difference, the hybrid being intermediate and the F_2 segregation taking place in a definite 1:2:1 ratio.

III

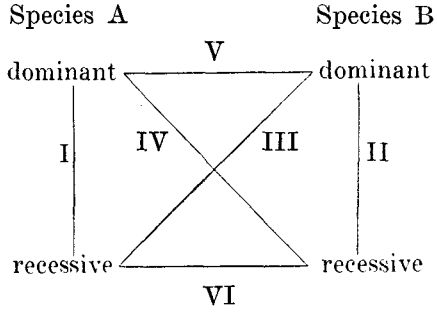
PHENOTYPIC PARALLELISM AND GENOTYPIC PARALLELISM

It is a well-known fact that different species which are morphologically similar are also similar in their variability, thus resulting in the production of parallel variations. The fact was emphasized by VAVILOV and led him to a generalization, "Law of Homologous Series in Variation". It states: "in general, closely allied Linnean species are characterized by similar and parallel series of varieties; and as a rule, the nearer these Linneons are genetically, the more precise is the similarity of morphological and phy-

siological variability''.

The existence of such remarkable correspondence among different species seems to indicate by itself a similarity of their germinal composition and organization. Critically speaking, however, it is quite doubtful whether it is justifiable to predicate merely from similarity in character effects that parallel variations are conditioned by identical genotypes. There are numerous cases demonstrating that different genes within a species may produce identical character effects. Before going further, it is therefore desirable to give some accounts of the method of testing the identity of genes in two species.

The reliable method is to compare the results from all the possible combinations within and between two species, as represented by the following diagram:



This is the method of Diallel Crossing which was originally introduced by SCHMIDT for testing quantitative differences between different individuals. By this means, it is possible to disclose genotypic differences, if any, between the parental species, even though they are phenotypically alike, or at the same time to discover genetypic identity between them, even though they are phenotypically dissimilar. For example, let a case be taken where the crosses, I, II and III (or IV) (in the preceding diagram) were made and proved to give the same monogenic segregation ratio in F_2 as to the character pair in question. Such a case will be found of comparative genetics of *Brassica Napus and Braccica rapa* (KAJANUS, HALLQVIST. *v.* 'Monograph', Tables II–IV). This is, however, insufficient to afford conclusive evidence that the corresponding recessive characters in these species are genotypically identical, because they might have been different in that one of them was of such a constitution as Xy and the other xY, where X and Y are *complementary genes* standing for the dominant character. To detect such genotypic difference, the VI cross is necessary, for it would give

the dominant character in F_1 and segregation of the digenic ratio in F_2 (Diagram 1). Let it further be supposed that the cross VI gave nothing but the recessive character in further generations, thus indicating that the materials are genotypically identical. Even in such a case, the definite proof for the identity of the genes is wanting, unless cross V is made, because the corresponding dominant parents might have differed in their genotype in a way that one of them had a constitution *Xy* and the other *xY*, where *X* and *Y* are *duplicate genes* for the character. In this case cross V should give the digenic segregation in F_2 (Diagram 2). Furthermore, by introducing the reciprocal cross between two parental species, cases would be disclosed where the phenotypic expression differs by a dissimilarity in the cytoplasm of the parents, and not by genic differences. Such a case was fully demonstrated by CHITTENDEN and PELLEW in two lines of *Linum usitatissimum*. Here the same recessive gene proved to react normally in the plasm of one of the lines, but to react abnormally in the plasm of the other, producing sterility in the male side. The possibility of plasmic differences may be possibly greater in inter-specific hybrids than in varietal ones. Indeed there are many known cases demonstrating plasmic differences in different species, *i.e.*, *Digitalis* (JONES), *Epilobium* (LEHMANN, MICHAELIS, RENNER, etc.), *Aquilegia* (SKALINSKA), *Oenothera* (RUDLOFF), and also in cryptogamous plants, *Funariaceae* (WETTSTEIN) and *Basidiomycetes* (HARDER).

It is rather surprising to see that with these strict limitations, in no case hitherto has the genotypic identity of parallel variations in different plant species been demonstrated in the exact sense. Not only in inter-specific crosses, but in intra-specific ones, the identification of genes in different lines has not been very frequently carried out through the critical analysis. The lack of this diallel analytic method naturally results in serious confusion in consolidating the results of different investigators working on different lines into one general scheme. These cases may be found even in such an extensively investigated material as *Pisum*. We are quite uncertain, for instance, whether or not RASMUSSON's *V*, a gene intensifying the effect of *P* which is responsible for the production of

parchmented membrane in the pod is really identical with WELLENSIEK's *V* for the same character, because they have not as yet been tested with each other. Another difficulty in identifying them is offered in this case by the contradictory data that *V* of the former is linked with *P*, while *V* of the latter is independent of *P*. Of course to determine by linkage experiments the exact loci of genes on the chromosome is useful as a supplementary tool for the identification of the genes, as achieved by STURTEVANT in *Drosophila melanogaster* and *D. simulans* which yield completely sterile hybrids, but we must be very cautious on this point, because recent works on plant genetics, especially on *Pisum*, present some affirmative deta indicating the possibilities of (1) genotypic variability in linkage values, (2) linkage of more than 50% crossing-over and (3) chromosomal linkage. Consequently many difficulties will be met with in determining the loci of genes, as the linkage between the two allelogenic pairs may escape observation owing to 50% crossing-over, unless they prove to be linked with the third allelogenes, (2), (KAPPERT, WELLENSIEK), or they may show different percentages of crossing-over in different lines used for experiments, (1), (RASMUSSON), or they may be closely linked together in a line but independent in another, (3), (HAMMARLUND, WELLENSIEK). The possibility of (1) has been more clearly indicated by COLLINS & KEMPTON in *Zea mays* in respect to two genes, *C* for colored aleurone and *wx* for waxy endosperm. The possibility of (3) is also suggested in TAKAHASHI & FUKUYAMA's experiments on *Phaseolus chrysanthos* where two genes, *C* for black seed coat color and *M* for mottled seeds, were completely coupled together in certain strains, but independent of each other in another. Thus the linkage phenomena in plants are sometimes very complicated, as contrasted with those in *Drosophila*, and make the immediate application to them of MORGAN's principles rather doubtful.

From these considerations it may be stated that the diallel analysis of parallel variations provides the only one reliable method for their genotypic identification, and as pointed out in the above statement, we have no case as yet of fertile inter-specific crosses to which this method has been applied. Therefore at the present there is no definite proof for parallel variations in different species which are conditioned by the same genotypic situations.

In spite of this lack of proof, however, its possibility may be presumed from *a priori* reasoning, because in any species which freely cross-breed with each other as enumerated in the preceding chapter, the Mendelian segregation will naturally result in the production of parallel variations

in each species which are unquestionably conditioned by the corresponding same genotypes. In this way any genotypic variation in one species will be easily transferred to the other which lacks it. If the complex of genes for the characters which distinguish the species one from another be distinguished from those for varietal characters, and the former be expressed by R_1, R_2 etc. and the latter by V_1, V_2, V_3 etc., (corresponding recessives, v_1, v_2, v_3, etc.), a species R_1 in which all the possible combinations of 'varietal' genes are present may be represented as:

$$R_1\begin{pmatrix} V_1\ V_2\ V_3\ \ldots\ldots \\ v_1\ v_2\ v_3\ \ldots\ldots \end{pmatrix}.$$

Let it be taken that another species R_2 is not provided with variations in 'verietal' genotypes, thus:

$$R_2(V_1\ V_2\ V_3\ \ldots\ldots).$$

The cross-breeding between these two species will lead to the production of a series of forms of R_2 corresponding to those of R_1, such as R_2 ($v_1\ V_2\ V_3\ldots\ldots$), $R_2(V_1\ v_2\ V_3\ldots\ldots)$, $R_2(V_1\ v_2\ v_3\ldots\ldots)$, etc. Thus species R_2 becomes quite equivalent with R_1, namely,

$$R_2\begin{pmatrix} V_1\ V_2\ V_3\ \ldots\ldots \\ v_1\ v_2\ v_3\ \ldots\ldots \end{pmatrix}.$$

An illustration may be cited from the classical work by SHULL on *Capsella*. He showed that the four biotypes as to leaf form found within *Capsella bursa-pastoris* are determined by the interplay of two allelogene pairs, *A* and *B*, and the triangular form of capsule is governed by duplicate genes, *C* and *D*, giving 15:1 ratios in F_2 from crosses with *C. Heegeri* which is characterized by round, top-shaped, uninflated capsules. As far as these genes are concerned, *C. bursa-pastoris* has the constitution of $CD\begin{pmatrix} AB \\ ab \end{pmatrix}$, while the original *Heegeri* had the constitution of $cd(AB)$. Now in the experimental garden of SHULL, however, the four biotypes of *C. Heegeri* corresponding to those of *C. bursa-pastoris* are commonly found, thus indicating that *C. Heegeri* is now to be expressed by $cd\begin{pmatrix} AB \\ ab \end{pmatrix}$.

IV

GENOTYPIC PARALLELISM WITHIN A GENUS

For the conclusive demonstration of true homology in different species, a condition is thus demanded that the two species in question are mutually crossable and yield fertile hybrids, permitting genic analysis. When inter-specific hybrids are entirely sterile, certain difficulties are naturally

imposed upon this, and when species are not crossable, more difficulties, rather fatal, are met with. The only one resort upon which one is able to rely in such cases is to compare genetical behaviors of parallel variation within each species.

A priori it can however be presumed that different species, although they are not crossable, may contain a considerable amount of germinal material in common. The reason for this is that cross-sterility is not regarded on any reasonable basis as a criterion of genetical relationship between species (*cf.* Chapter VII). In other words, cross-sterility does not mean eventual differences in the germinal system as a whole. Furthermore it has been shown in the above discussion that where two species proved fertile together, a definite evidence for true homology is *always* expected. Based on these considerations, parallelism in genetical situations of corresponding variations in different species may be considered as strongly suggestive of homology. A survey of literature indicates that the following are such cases:

i) *Althaea* : doubleness of flowers in *A. rosea* and *A. ficifolia* (*v.* 'Monograph', p. 2).

ii) *Dianthus* : doubleness of flowers in *D. barbatus* and *D. caryophyllus* (*id.* pp. 89–90);

iii) *Digitalis* : peloric flower formation in *D. gloxiniaeflora* and *D. purpurea* (*id.* pp. 90–94);

iv) *Fagopyrum* : heterostylism in *F. emarginatum* and *F. esculentum* (*id.* p. 96);

v) *Nicotiana* : leaf surface characters, height of plants, and time of flowering in *N. Tabacum* and *N. rustica* (*cf.* HOWARD, *id.* pp. 227–228, 229);

vi) *Oxalis* : heterostylism in *O. rosea* and *O. valdiviana* (*id.* pp. 265–266);

vii) *Papaver* : flower color in *P. somniferum* and *P. Rhoeas* (*cf.* NEWTON, *id.* p. 267);

viii) *Phaseolus* : certain seed characters (mottling and 'eye' pattern) in *Ph. chrysanthos* and *Ph. vulgaris* or *Ph. multiflorus* (*id.* pp. 296–309);

ix) *Primula* : heterostylism in various *Primula* species (*id.* pp. 327–373, 376).

More interesting works on parallel variation have been carried out on polyploid species in connection with their chromosomal situations. Three

genera have hitherto been investigated, both genetically and cytologically, viz., *Capsella* (*id.* p. 66 *et seq.*), *Gossypium* (*id.* p. 112 *et seq.*), and *Triticum* (*id.* p. 419 *et seq.*).

x) *Capsella*: SHULL divided the genus into two genetic groups: (1) the diploid group (n=8) and (2) the tetraploid group (n=16). Intra-group crosses yield more or less fertile F_1 hybrids, but inter-group crosses result in sterile hybrids. The genic analysis in *Capsella* has been mostly concerned with the tetraploid group, especially *C. bursa-pastoris* and *C. Heegeri,* and only a few analyses have been reported on the diploid group. Some results from crosses in the latter group, however, were explaind by assuming the same genes which were identified in the former group. Thus in the cross, *C. grandiflora* × *C. Viguieri,* both being members of the diploid group, SHULL states that the leaf characters of *C. Viguieri* "are produced by three Mendelian factors, *a* and *B* of *rhomboidea* together with a recessive inhibiting factor, i_2, which nearly suppresses the *rhomboidea* lobing". The genes, *A* and *B,* are those primarily identified in *C. bursa-pastoris.*

xi) *Gossypium*: The genus *Gossypium* is divided into two genetic groups: (1) the diploid group (the Asiatic cotton group, n=13) and (2) the tetraploid group (the American cotton group, n=26). Crosses between these two groups are only made with difficulty and usually result in completely sterile hybrids. The genic analysis so far carried out in both the groups exhibits a striking similarity in genetical behaviors of certain characters. LEAKE & PRASAD using Asiatic cotton varieties identified two gene pairs for corolla color: *Y* for yellow (*y*: white) and *R* for red (*r*: white). In American cotton varieties, a similar monogenic difference between yellow and white has been demonstrated by several investigators (BURD, GRIFFEE & FAIRCHILD, HARLAND). With respect to red pigmentation, MCLENDON observed in American cotton crosses a monogenic difference between corresponding color contrasts. The gene *R* identified by LEAKE & PRASAD is described as imparting anthocyanin to the entire plant body. The same situation was also revealed in MCLENDON's case.

The inheritance of petal spot offers another instance. In the Asiatic cotton, LEAKE & PRASAD demonstrated a monogenic difference between the presence and the absence of petal spot, the spotted condition being completely dominant. In the American cotton group, KEARNEY, GRIFFEE & FAIRCHILD, GRIFFEE & LIGON and CARVER—all found monogenic segregation as to the same character pairs in varietal crosses with Upland or Pima cottons. Results from inter-specific crosses within the latter group indicate also that one main allelogenic pair is involved, although the segregation is

less clear cut than in varietal crosses, because of the action of many modifying genes derived from the parental species.

xii) *Triticum*: As well known, the genus *Triticum* comprises three genetic group: (1) the diploid or Einkorn group (n=7), (2) the tetraploid or Emmer group (n=14) and (3) the hexaploid or vulgare group (n=21). The genus offers very favorable material for the comparative study of genetical behaviors of parallel variations, as rather extensive investigations on genic analysis have been made in parallel in both the tetraploid and the hexaploid group, and also in inter-group hybrids which are fortunately comparatively fertile. A survey of literature indicates that both the groups are characterized by a striking similarity in the series of genotypic variations. The following genetical features are common amongst them[1]:

1) Mono- and dimeric dominance of red grain color over white;
2) Monomeric dominance of brown glume color over yellow, of black over yellow and of black over brown;
3) Monogenic difference between dense and lax spikes;
4) Mono- and dimeric dominance of pubescent glumes over glabrous;
5) Monogenic difference between large and small glumes;
6) Monogenic difference between soft and hard structures of the endosperm;
7) Multigenic nature of stature of plants;
8) Mono- and digenic dominance of resistance to *Puccinia graminis tritici* over susceptibility;
9) Mono- and multigenic difference between early and late maturing time.

It is interesting to note that tetraploid species are characterized by duplicate genes and hexaploid species by triplicate genes. If WINGE's hypothesis on the origin of allopolyploids be admitted, one comes to the logical conclusion that n-ploid species should contain n-sets of genomes, and therefore many of its characters should depend on genes, at most n-plicate, but not more.

In *Capsella,* SHULL demonstrated that while no indications of duplicate genes have been found in the diploid group, several but not all genes in the tetraploid group, proved to be usually or occasionally duplicated, namely, (1) triangular form of capsules (*C* and *D*), (2) sinuses of the leaf-lobes reaching to the midrib (*B* and *B'*), (3) non-coriaceous texture

1) Full references are to be made to the section of *Triticum* in the 'Monograph'.

of the leaf (*K* and *L*), and (4) capacity to produce pollen (*Sp* and *Sp'*). The analysis by CORRENS of chlorophyll defects in *C. bursa-pastoris* likewise points to the existence of two duplicate genes, H_1 and H_2, which stand for the normal distribution of chlorophyll.

In *Gossypium,* duplicate genes are also suggested, though not so conclusively, in the tetraploid group, as to corolla color (BALLS), presence vs. absence of the fuzz on the seed (BALLS, MCLENDON), pitted vs. smooth boll surface (MCLENDON), pubescent vs. glabrous boll surface (PEEBLES) and chlorophyll defects (STROMAN & MAHONEY). No cases of duplicate genes however have been described in the diploid cotton group.

Still further informative data have been accumulated in *Triticum* genetics. The dimeric nature of segregation has been found in the following characters:

1) Grain color: red *vs.* white,
2) Glume color: brown *vs.* yellow,
3) Seedling color: colored *vs.* colorless,
4) Ears: spelting *vs.* non-spelting,
5) Glumes: pubescent *vs.* glabrous,
6) Ears: shattering *vs.* non-shattering,
7) Ears: awned *vs.* awnless,
8) Endosperm: soft *vs.* hard,
9) Chlorophyll: green *vs.* albino,
10) Chlorophyll: green *vs.* yellow,
11) Stature: tall *vs.* dwarf,
12) Resistance to black stem-rust *vs.* susceptibility,
13) Habit: spring *vs.* winter,
14) Maturing time: early *vs.* late.

Most of these cases, viz., (2), (3), (4), (5), (6), (7), (8), (9), (11), (13) and (14) have been reported in the hexaploid group, (8) and (10) in the tetraploid group and (1), (5) and (12) in both the groups. The trimeric nature of segregation has been reported in the following cases:

1) Grain color: red *vs.* white,
2) Ears: shattering *vs.* non-shattering,
3) Chlorophyll: green *vs.* albino,
4) Stature: tall *vs.* dwarf,
5) Maturing time: early *vs.* late.

It is a remarkable fact that these trimeric cases, in contrast with dimeric ones, are all confined to the hexaploid group or inter-group crosses involving hexaploid species. Again, recent excellent works by WATKINS on the

exact analysis, both genetical and cytological, of an pentaploid hybrid, *turgidum* × *vulgare*, indicate that paired (7_{II}) and unpaired (7_{I}) chromosomes carry a similar series of genes. Thus the tetraploid *turgidum* was assumed to have a constitution of *e.g.* A_1A_2 and the hexaploid *vulgare* to be of *e.g.* $A_1a_2A_3$. A_3 is here supposed to be carried by an unpaired chromosome.

It may be noted *en passant* that *Avena* which occurs as diploids, tetraploids and hexaploids, similarly to *Triticum*, is likewise characterized by a number of characters which are found to be governed by duplicate or triplicate genes (*v.* 'Monograph', p. 18–43). Only one contradiction to the cytological findings in *Avena* is the occurrence of a tetrameric character, *viz.*, ligulelessness. Only one such case, however, has been reported by NILSSON-EHLE who suggested it from a few F_2 progeny, and is not regarded as absolutely convincing, because all other investigators touching the inheritance of this character have shown that the character is of either mono-, di- or trigenic nature.[1] On the other hand, in *Herdeum* (*v.* 'Monograph', pp. 135–162) and *Secale* (*v. id.* pp. 395–399) which occur as diploids only, no duplicate genes have been definitely demonstrated (disregarding MIYAKE & IMAI's work on *Hordeum* which is not accurate). Further in *Oryza* which is cytologically regarded as a secondary tetraploid species (*cf.* LAWRENCE), several characters proved to be dimerous, but no one to be more (*v.* 'Monograph', pp. 240–265).

In view of these considerations on allopolyploids, it can be understood why cytological complexity is correlated with genetical complexity and why genetical complexity is of a nature to indicate that differences between diploids and tetraploids or between tetraploids and hexaploids are those of degree rather than of kind. It may be concluded therefore that the occurrence of genotypic parallelism of variability in polyploid species is a natural consequence.

V

DISSIMILARITY OF GENETICAL BEHAVIORS OF PARALLEL VARIATIONS

One meets rather often with cases of corresponding variations behaving differently in different species. The yellow color of *Cattleya Dowiana aurea*

1) After the MS. of this paper was prepared, the writer came across a report by ÅKERMAN & MÜHLOW (*Hereditas* 18, '33) who have reworked the same materials as NILSSON-EHLE had used before and found that the character, ligulelessness, was really of a trimeric (not tetrameric) nature.

behaves as a recessive to the rosy-purple color of other Cattleyas, while the yellow color of *Laelia Cowanii* and others are dominant to the same, though in most cases the dominance is incomplete (HURST; *v.* 'Monograph', p. 73). In *Pharbitis purpurea,* the double flower which is due to the feathering of the corolla, proved to be a monogenic dominant over the normal single form, while in *Ph. Nil* the corresponding double form was found to be a monogenic recessive (IMAI; *v. id.* pp. 285, 295). In European pears, the green skin color is dominant over russet color (WELLINGTON), but in Japanese pears, the condition is the reverse (KIKUTI) (*v. id.* pp. 321, 323). In *Linaria alpina,* the presence of the orange colored area in the palate is recessive to its absence, while in *L. vulgaris* the opposite proves true (SAUNDERS; *v. id.* pp. 173, 174). A more striking case is that reported by SALAMAN in *Solanum* (*v. id.* p. 402 *et seq.*). In *S. etuberosum,* he found that the white tuber color is dominant over purple, round tuber form over long, shallow eyes over deep, and susceptibility to the attacks to wart disease over immunity from the same, while in *S. tuberosum* all the corresponding characters exhibited the exactly opposite behaviors.

These cases might be taken as opposing the view of genetypic parallelism in variability of different species. Really PHILIPTSCHENKO discussing fundamental bases of parallel variability has set forth his belief as follows: "Bei verschiedenen Arten wird aber auch eine andere Form von Parallelismus beobachtet, den man zum Unterschied von dem genotypischen am besten den ökotypischen nennen kann. Dabei handelt es sich nicht so sehr um das Vorhandensein von gleichen Genen, als vielmehr um die Ausarbeitung bei verschiedenen Formen einer gleichen Reaktion auf bestimmte Standorts- und klimatische Bedingungen". He cites several examples favoring his view, one of which is: "Der Eisbär ist doch—was die konstante weisse Farbe anbetrifft—eine dem Polarhasen (*Lepus arcticus* LEACH) durchaus parallele Form; bekanntlich aber dominiert bei Kreuzung von Eis- und Landbär die weisse Färbung, während sie bei Nagetieren stets rezessiv ist".

It is evident that his claim is based upon a view that any character effect exhibited by the organism is the result of the action of a particular gene, and therefore any change in the former means directly the existence or operation of another gene. This is nothing but an old conception of heredity that every character or every organ has its own factor in the germplasm, that is, a "determinant" in the sense originally introduced by WEISMANN in his idioplasm doctorine. Instead of such a naïve idea that the characters and genes are directly connected, however, geneticists are

now convinced with an abundance of affirmative data that the character effect is the final product resulting from the reaction of a chain of genes upon the intra-cellular substratum and the external environmental factors. Taking this point of view, one is not necessarily driven to such a conclusion as PHILIPTSCHENKO has drawn that these cases of dominance reversal involve different genetic systems, characteristic to each and independent from one another, but on the contrary one finds several reasonable possibilities of interpreting these cases on the same basis which he is able to deduce from intra- and inter-specific crossing experiments. Firstly, *e.g.* in *Pisum,* the existence is known of two kinds of yellow cotyledon color which are not phenotypically distinguishable from each other, but are genotypically dissimilar, one being dominant over green, the other recessive to the same geen variety (*cf.* 'Monograph', pp. 328–329). It is realized from crossing experiments between these two yellow varieties that one of them is yellow because it contains a dominant gene for green cotyledon and a gene suppressing the action of the former, and the other is also yellow because it lacks both the dominant genes. Similar cases have been very often met with in many plants, and seem to indicate that such a mode of interaction of genes is not of an unusual occurrence. It will then not be unreasonable to expect similar occurrence in different species. In cases, as enumerated above, where one species is provided with a dominant variation, and another with one corresponding to it but recessive in nature, it would not be regarded as too much to expect that real homology would be proved, were more extensive researches carried out. In reality on the basis of a known fact that there are two kinds of awned varieties of *Triticum,* one dominant and the other recessive, VAVILOV attempted to discover the same occurrence in other genera of *Poaceae,* and succeeded in obtaining two different kinds of awned varieties of oats, one dominant and the other recessive to the same awnless variety.

Secondarily cases are known, although they are similar in essential nature to those given above, of dominance reversal of a gene according to differences in the 'residual' genotype with which it co-operates. For example, TAMMES found in *Linum usitatissimum* that when the genes for blue corolla color (*B′, C′* and *D*) are present, a gene *A* which acts as an intensifier of the color, dominates over *a,* but when only the genes for pink (*B′, C′* and *d*) are present, *a* dominates over *A*.

Thirdly cases are known which show that the plasm has an important influence upon the action of genes. According to RENNER & KUPPER, differences in reciprocal hybrids between *Epilobium* species are due to

plasmic differences between the parents. In the hybrid, *E. parviflorum* ♀ $\times$ *E. roseum* ♂, the activity of the *roseum*-genes is entirely suppressed in the *parviflorum*-plasm, but in its reciprocal cross, *E. roseum* ♀ $\times$ *E. parviflorum* ♂, they are able to act more strongly in their own plasm. Thus for example, a gene for the recurved position of the peduncle possessed by *E. roseum* or *E. montanum* can exhibit its activity in hybrids with *E. parviflorum* only when these species were used as the female parent, but in the reciprocal crosses, the unbalance of it with the *parviflorum*-plasm makes its expression very highly obscure.

It may be realized then that the same 'dominant' gene may result in a 'recessive' expression when it combines with another intra- or extra-nuclear substratum, and therefore differences in phenotype can only coincide with those in genotype when all other factors, genetic and non-genetic, are the same.

It is a striking fact that each of parallel variations in *Solanum etuberosum* and *S. tuberosum* is entirely characterized by the opposite genetical behaviors, in so far as SALAMAN's work goes. It would be rather difficult to imagine that different series of genes are here operating and nevertheless producing so remarkable a series of parallel variations in each species. A more simple interpretation would be rather founded on an assumption that we are here dealing with different reaction systems, both the species containing the same series of genes but differing in the intra-cellular substratum upon which they react.

VI

GENOTYPIC PARALLELISM WITHIN A FAMILY

It can be further expected that similar regularity of genotypic variability also exists even in quite different genera belonging to the same family. For example, MENDEL in his classical work has already shown that three character pairs of *Phaseolus,* tall (twinning) *vs.* dwarf (bush) stature, yellow *vs.* green unripe pod and inflated *vs.* constricted pod form behaved just like those found in *Pisum.* Similar instances might be cited in different species within a family where parallel variations were dealt with genetically. The existence of two genetically different types of yellow cotyledon in *Pisum* and *Glycine* will be a good example (*cf.* 'Monograph', p. 104).

The writer will not however attempt to make a further comparative survey on this subject, because in most cases works on genic analysis in plants are very fragmentary and sometimes different workers dealing with

the same varietal characters have come to different, even contradictory conclusions. To prepare a consistent integration of genetic data would be impossible until coherent genic systems are devised for all varietal characters and existing varieties within a species.

It is more important theoretically that, on the basis of the belief in genotypic parallelism, one would be able to expect similar genotypic differences in parallel variations of different species. Let us compare, for instance, the mode of inheritance of plant pigmentation in *Zea* with that in *Oryza,* both being members of *Poaceae.*

In *Zea,* the genic analysis of plant colors, that is, colors in several plant parts, such as stem, anthers, husks, leaf-sheaths, leaf-blades, etc., has been completely carried out by EMERSON (*v.* 'Monograph', p. 492). He explained the results by assuming four pairs of genes, *A, B,* $\underset{\smile}{Pl}$ and *R.* *A* together with $\underset{\smile}{Pl}$ gives the purple coloration which is modified by the series of multiple allelogenes of *R.* Thus for example, R^r causes the purple pigments in the entire plant body, but R^{rg} ensures colorless anthers and silk, the other parts being purple. The gene *B* is responsible for the production of a brown flavone and is independent of the basic gene for anthocyanin formation *A* in its action.

In *Oryza,* the inheritance of purple pigmentation has received most attention, but many different workers using different lines and adopting different modes of denominating the genes involved have caused serious confusions and ambiguities. There has not been built up here such a coherent system as in *Zea.*

Combining together the divergent results hitherto obtained on the inheritance of purple pigmentation of *Oryza,* one finds however a strong possibility of interpreting it on the same basis which was deduced in *Zea.* Firstly, it was several times demonstrated that the purple pigments in *Oryza* are caused by the basic gene for the production of anthocyanin (*A* in *Zea*) together with the gene for purple color ($\underset{\smile}{Pl}$ in *Zea*), although here the genetic situations are more complicated owing to the existence of complementary and duplicate series of these genes. Secondarily, intimate genetic connection between colors in different organs has been very often observed. Most workers ascribed this to different genes which are completely linked together. For example, PARNELL *et al* from a cross between a variety with purple internodes and glumes but colorless stigmas and axils and another variety with colorless internodes and glumes but purple stigmas and axils, obtained F_1 plants having purple pigments in all these parts and in F_2 a monogenic 1:1:2 ratio for the two parental forms and

the F_1 type respectively. They explained these results by assuming that four genes, *L, G, S* and *A* are responsible for the purple coloration in the internode, glume, stimga and axil, respectively, and that *L, G, s* and *a* on one side and *l, g, S* and *A* on the other side are completely linked together. The results however strongly point to the existence of a modifying gene (*R* in *Zea*), the allelogenic series of it exerting different actions, that is, causing the purple pigments in different vegetative parts. Thus the parental forms used by PARNELL would be, in analogy with *Zea,* assumed as: $\underset{\smile}{AAPlPl}R^1R^1$ and $\underset{\smile}{AAPlPl}R^2R^2$ respectively, where R^1 originates the purple coloration in internodes and glumes, and R^2 originates it in stigmas and axils. The F_1 plants have then a constitution of $\underset{\smile}{AAPlPl}R^1R^2$, segregating in F_2 into three forms, R^1R^1, R^1R^2 and R^2R^2, in a $\overset{\smile}{1}:\overset{\smile}{2}:1$ ratio. On the same basis, the intimate association of colors in different parts, *e.g.* the association of glume apiculus color with the color in the stigma and leaf-sheaths, as observed by several workers (NAGAI, YAMAGUTI, HECTOR, CHAO, etc., *v.* 'Monograph', p. 248 *et seq.*) may be sufficiently interpreted. Let other allelogenic members of *R* now be presumed, *e.g.*, R^3 standing for the production of pigments in the apiculus and leaf-sheaths and R^4 standing for the color formation in the stigma in addition. Then a cross, $\underset{\smile}{AAPlPl}R^4R^4$ (purple apiculus, leaf-sheaths and stigmas) $\times$ $\underset{\smile}{aaplpl}R^3R^3$ (colorless) would give in F_2 a segregation ratio of 27 (purple apiculus, leaf-sheaths and stigmas) : 9 (purple apiculus and leaf-sheaths, but colorless stigmas) : 28 (colorless in all these organs), which are to be genically represented as $--\underset{\smile}{APl}R^4 : \underset{\smile}{APl}R^3 : (\underset{\smile}{aPl}R^3, \underset{\smile}{Apl}R^4, \underset{\smile}{aPl}R^3$, etc.). The case is that really obtained by HECTOR. Another cross, $\underset{\smile}{AAPlPl}R^4R^4 \times \underset{\smile}{aaPlPl}R^3R^3$, would give a F_2 ratio of 9 (purple apiculus, leaf-sheaths and stigmas) : 3 (purple apiculus and leaf-sheaths but colorless stigmas) : 4 (colorless in these parts). In a similar way, if one assumes R^5, another member of *R,* for the color production in stigmas only, plants heterozygous for these genes, such as $Aa\underset{\smile}{Plpl}R^5R^3$, would on selfing give the following segregation : 9 (colored apiculus, colored stigma) : 3 (colorless apiculus, colored stigma) : 4 (colorless apiculus, colorless stigma). These cases are those really obtained by CHAO. Furthermore the existence in *Oryza* of a gene similar in effects to *B* of *Zea* is strongly suggested in the experiments of some workers (*e.g.,* NAGAI, YAMAGUTI).

Many suggestions of this kind might be found in other instances. In reality, HAASE-BESSELL explained her data on the inheritance of flower color in *Digitalis purpurea* by assuming a similar series of genes as those described by BAUR in *Antirrhinum majus* (*v.* 'Monograph', p. 92).

The writer believes that such a speculation would facilitate the comprehension of genetic behaviors of parallel variations and lead to useful generalizations under which they ought to be subjected.

VII

RELATIONSHIP OF THE DEGREE OF INTER-SPECIFIC STERILITY TO THE DEGREE OF GENOTYPIC SIMILARITY

Statements have been very often made to the effect that the degree of sterility between two species represents a criterion for the estimation of the degree of their genotypic similarity. Parent species which give distinctly sterile hybrids when crossed are said to be less and those which gives a negative results from crossing to be far less related with each other than those which are able to cross-breed freely. A critical survey on the phenomenon of sterility however discloses its very complicated nature which necessitates cautiousness in accepting such a statement. A number of cases of sterility are known which represent a continuous series of transitions ranging from complete cross-sterility to the production of fully fertile hybrids.

The extreme case of cross-sterility may be caused by a lack of harmony between the haploid pollen tissue and the diploid stylar tissue of the foreign species. This however does not mean genotypic dissimilarity between the parental species, but it may be merely based on certain physiological or histological discrepancies. An unbalanced condition, such as slower rate of the pollen tube of one species and quicker withering of the style of the other will naturally result in non-achievement of fertilization. Furthermore, as fully substantiated by numerous instances, *e.g. Linaria* (*v.* 'Monograph', p. 174), *Nicotiana* (pp. 231–233), *Verbascum* (p. 467), *Capsella* (p. 70), *Antirrhinum* (pp. 6–7), etc., the mode of inheritance of cross- and self-incompatibility within a species has been found in every case to be governed by a multiple allelic series of incompatibility genes, in a way that pollen tubes carrying an incompatible gene do not function properly in stylar tissue having the same incompatibility gene. This finding makes one very cautious when he considers cross-sterility between species. The possibility is not therefore entirely excluded that one species is not crossable with another, because both have some incompatibility genes in common which act in the inter-specific cross, in other words, they are genotypically *identical* as to these genes.

There are numerous cases of inter-specific sterility which result in the

development of poor, non-germinating seeds. Even in such cases, it does not necessarily depend upon genotypic disharmony between the two species, because certain evidences clearly indicate that at least in some cases it depends on a lack of harmony between some physiological factors of the embryo and the mother plant tissue. An excellent instance for this will be found in LAIBACH's experiments on *Linum*-crosses. It is known that crosses between *L. perenne* and *L. austriacum* are made only with difficulty and in many cases the seed, if developed, has no germinating power. LAIBACH however introduced a new method and succeeded in obtaining F_1-plants of *L. perenne* × *L. austriacum*. The method was simply to prepare the small embryo from the seed-coat and to bring it to further development on filter-paper. The plants thus obtained showed good vitality and fertility. In a similar way, MÜNTZING obtained fertile hybrids from certain inter-specific crosses with *Galeopsis*. By introducing such a method, therefore, it is highly probable that one can obtain the hybrid plants of many crosses which have hitherto proved failures, the seed being regarded as abortive. These experiments make one very skeptical as to the demarcation hitherto laid down between fertile and sterile hybrids and as to the significance of cross-sterility.

Furthermore numerous cases are known illustrating how the effect of lethal genes varies with the environment. In *Zea* many chlorophyll defects have been found to grow to maturity, when they were brought under favorable conditions (*v.* 'Monograph', p. 508 *et seq.*). In *Hordeum*, two cases of chlorophyll deficiency have been described, in that their expression is dependent on temperature. At high temperatures the materials were able to develop chlorophyll normally and to reach maturity. One of them proved sterile (HALLQVIST, *id.* p. 147), but the other proved fertile, producing well-developed ears (COLLINS, *id.* p. 148). In *Secale*, a peculiar type of chlorophyll defect has been reported, which is light-sensitive (SIRKS, *id.* p. 398). A more interesting instance is that described by HONING in *Nicotiana*. An aberrant form ('deformis', *cf. id.* p. 224) of Deli tobacco which is characterized by short internodes, deformed leaves, no flower and weak vitality was originally found in Sumatra. HONING brought the stock to Holland and found that it grew very vigorously and produced fertile flowers. In crosses with the normal plant, it was found to differ monogenically from the normal type. A conclusion was then reached that the gene for *deformis* exerts a sub-lethal effect under Sumatra conditions, but the effect is considerably decreased in sub-arctic conditions.

On the same basis, a similar behavior can be expected from sub-lethal

inter-specific hybrids. In reality, ÅKERMAN found that the hybrid *Epilobium hirsutum*×*E. montanum* is a stunted dwarf under 'normal' conditions, but in subdued light it grows up to a plant of normal appearance.

Still furthermore cases are known in which the plasm plays an important rôle in determining lethality. For example, DAHLGREN found that the hybrid between *Geranium bohenicum* and its subspecies *deprehensum,* when the latter was used as the male parent, results in green and white marmorated seedlings which usually perish very soon after emergence owing to insufficiency of chlorophyll, while its reciprocal cross gives less spotted seedlings which are able to grow normally, though they are sterile. The results indicate the incapability of normal development of the *bohenicum*-plastids, but the capability of the *deprehensum*-plastids, in cells with a hybrid nucleus. An analogous case has been described by RENNER in certain *Oenothera* crosses. Undoubtedly some of the sterile inter-specific hybrids which proved to be lethal in seedling stages come into the same category, *viz.,* lethality due to an unbalanced relation between the plasm and the nucleus.

Thus understanding the phenomenon of sterility as due to disturbance of a balanced system of reactions, both in the haplo- und diplophases, one can not take the inter-specific sterility as a reliable criterion of a thorough genotypic dissimilarity. Of course, the difference in the chromosome number of the parental species aggravates the degree of sterility in the F_1 plant, if produced. But this is connected with the disturbance in the normal mechanism of meiosis which enables the segregation of genes to occur in the normal fashion, but not with genotypic differences between the parents. Evidences from recent cyto-genetical works indicate a close relationship between chromosome pairing and their homology. Chromosomes pair because they are homologous, and they fail to pair because they are non-homologous. "Homology is a function of the relationship of the parts of the chromosome in terms of chromomeres (cytological) or genes (genetical) according to the attitude, cytological or genetical, with which one approaches the subject" (SANSOME & PHILP). However it is known on the other hand how chromosome pairing is profoundly affected by certain genetic (*e.g. Zea*) and non-genetic (such as temperature, chlorhydrate, etc.) factors. Therefore a possibility may be more than a mere speculation that the same effect as by the asynapsis gene of *Zea* (*v.* 'Monograph', p. 517) would be brought about by the co-operation of two genes, one of one species and the other of another, resulting in non-pairing of chromosomes in the meiosis of F_1, although the parental species are pro-

vided with 'homologous' chromosomes, as well as a possibility that normal pairing would take place, were the parental species which are known to have 'non-homologous' chromosomes brought in other external conditions.

On the other hand, where cytological inspection alone fails, the comparative genic analysis of two species has achieved in some instances a disclosure of real identity (homology) and unidentity (non-homology) of the parts of the chromosome. The most significant illustration is that given by extensive studies of STURTEVANT on *Drosophila melanogaster* and *D. simulans*. These two species are so similar in morphological characters that they were not distinguished from each other until 1919, that is, until the discovery that the hybrids between them are completely sterile. Under laboratory study *simulans* has produced a series of variations parallel to those in *melanogaster*. By a caraful analytic process ('diallel-crossing'), at least 27 of the loci that have mutated in *simulans* proved (most probably, *cf.* Chapter III) to be homologous or 'isomorphic' with those mutated in *melanogaster*. The chromosome linkage maps of them showed that the genes occupy corresponding positions in each chromosome, except chromosome III in which the corresponding loci are in inverse order! Such a finding suggests a possibility that a species may produce sterile hybrids when crossed with another, not because of dissimilarity in their genotypic constitutions, but merely because of different arrangement of the identical genes in the same (morphologically) chromosomes.

VIII
CONCLUSION

In the foregoing chapters, the writer has suggested certain possibilities for different species, even though they are so far related that they can not cross together, thus offering no experimental clues to identify their genotypes, yet of possessing a high amount of germinal compositions and organizations in common, on that the occurrence of genotypic parallel variations is based. This suggestion is deduced from (i) negative proofs against the degree of inter-specific sterility as a reliable criterion for the degree of genotypic dissimilarity between the two species and (ii) positive proofs from comparison of genic compositions of parellel variations in each species.

Concerning the origin of genotypic parallel variations, there are at least two possible procedures. One of them is the parallel loss mutation which may be the only one resort for their production in different species which are cross-sterile, as BAUR already stated in his 'Einführung' ('19,

p. 293): "Ebenso, wie wir hier annehmen, dass homologe Veränderungen verschiedener Ausgangskörper diesen homologen Reihen zugrunde liegen, ebenso müssen wir annehmen, dass homologe Veränderung in Bau der Chromosomen bei den Organismen den homologen Mutationen zugrunde liegen".

The other procedure is hybridization. As already shown, when two species are crossable and yield fertile hybrids, the induction of the whole series of variations of one species into the other as well as the creation of a quite new parallel series in them may be nothing but a natural consequence. On the other hand, the demonstration of profound influences of external factors on lethality in both haplo- and diplophases (*e.g., Epilobium* hybrids, *cf.* p. 161) makes one very skeptic as to the possibility of inter-specific crossing. A conjecture that the changes in the climatic conditions during different geological periods might have in this way influenced the production of fertile hybrids and as a consequence, the production of a homologous series of variations, may be then justified to some extent.

From the comparative genetical work on *Drosophila melanogaster* and *D. simulans,* it has been demonstrated that the arrangement of genes within a chromosome is different in these species. This finding is very significant, because it apparently demonstrates that the identical sequence of genes in the chromosome is not necessary for the identical character effect. In other words, the formation of genotypically parallel variations in different species does not require the identical chromosomal situation, but at any rate the existence of identical (or allelic) genes, no matter how differently they are arranged. What the actual method of producing changes in the order of genes within a chromosome may be is another question about which we have not even the slightest knowledge. But it should be mentioned that such a change is not regarded as a characteristic feature of inter-specific differences, because we are similarly acquainted with the fact that different geographical races of *Drosophila melanogaster* differ in the order of the genes in a chromosome, as determined by means of linkage tests.

All the available data, so far accumulated, on the inter-specific differences indicate that they do not differ in their essential nature from the intra-specific differences. Every kind of difference known to exist within a species,—such as the difference in 'Mendelian' genes, that in extra-nuclear factors ('plasmon' of WETTSTEIN), that in the arrangement of genes in a chromosome, that in the degree of sterility, balanced and unbalanced

differences in the amount of genes, etc.,—has been proved to occur also between species. It may be stated then that the differences between inter- and intra-specific differences are at least of such a nature as to be acceptable as those in degree, rather than in kind.

Nowadays a criticism formerly raised especially by physiologists that genetic workers were dealing with analysis of superficial characters unimportant to plant life, such as color, size and form, can no longer be maintained. Genes controlling the chlorophyll formation in *Zea* are now being analyzed with every accuracy as in chemistry. Genes controlling lethalily and sub-lethality in both the gametophyte and sporophyte, and intensities or velocities of their physiological activities are now being fully demonstrated in several plants. It is needless to give further numerous instances which might be cited in order to illustrate how genetical studies have contributed to the realization of the fundamental constitution of the organism. Similarly a criticism raised especially by taxonomists that geneticists were dealing with only varietal characters and not with more essential ones, such as specific, generic, etc., can no longer be maintained. It is self-evident that the specific characters must be those possessed by each and every individual belonging to that species in common and it is only by their differences that the genes are identified; then as a natural consequence it is not possible to deal with specific characters when inter-specific crosses fail. But in every case where inter-specific crosses succeed, one can expect to deal with the genes for them and it actually is possible, *e.g.,* in *Capsella, Triticum, Malva, Viola* and others. Similarly the characters, generic or even more, are nothing more than the specific or varietal characters in their essential nature.

Taxonomists have succeeded in their effort to schematize or catalogue the vast multitude of different kinds of individuals which now exist on our globe into groups, viz., species, genera, families, orders etc. The catalogue has been made in apparently consistent order by devising a perfectly artificial index of morphological characters to cover all the diversities of the organisms. It must be realized that the present conceptions of taxonomical groups are only schemes which must not be regarded as representing the real nature of multiform life, though such a schematization is useful as a provisional working basis for grasping the natural phenomena. Historically taxonomy has developed first of all branches of biology, whereas theoretically it should come as the last.

The ignorance of the fact that the taxonomical categories are only conventional has led some biologists to attribute to them phylogenical significances and to discuss in vain how a species can attain the rank of a genus, or a genus that of a family and so on, taking as if these systematic categories were separate existences. As a matter of fact, however, all these characters, specific, generic, of families, etc., are not to be distinguished as belonging to different ranks; they are characters composing each and every species, and all should be alike in their genetical behaviors. The distinction between them is merely dependent upon the degree of extent of characters which the organisms have in common. Thus on the principle that *entia non sunt multiplicanda praeter necessiatatem* may be justified our attitude of reasoning that at least the same causes are concerned with genotypic variability within a species as well as in higher groups, and therefore the fundamental laws established to govern the former are also applicable to the latter.

These considerations enable one to suppose how genotypic parallelism comes to exist also in higher groups. Limiting the discussion to the taxonomical groups, Order, Family, Genus and Species, and designating the genes concerning these characters (for simplicity's sake, taking one gene common in each group) as O, F, G and S respectively, each and every species can be represented by the genic term OFGS. Let the possibilitity of free assortment be now conjectured between two members of each gene, O_1 and O_2, F_1 and F_2, G_1 and G_2, and S_1 and S_2 (just as in F_2 of a cross, *e.g.*, $O_1F_1G_1S_1 \times O_2F_2G_2S_2$), then the following 16 different combinations or species will be obtained:

	O_1F_1-series	O_1F_2-series	O_2F_1-series	O_2F_2-series
G_1S_1-series	$O_1F_1G_1S_1$	$O_1F_2G_1S_1$	$O_2F_1G_1S_1$	$O_2F_2G_1S_1$
G_1S_2-series	$O_1F_1G_1S_2$	$O_1F_2G_1S_2$	$O_2F_1G_1S_2$	$O_2F_2G_1S_2$
G_2S_1-series	$O_1F_1G_2S_1$	$O_1F_2G_2S_1$	$O_2F_1G_2S_1$	$O_2F_2G_2S_1$
G_2S_2-series	$O_1F_1G_2S_2$	$O_1F_2G_2S_2$	$O_2F_1G_2S_2$	$O_2F_2G_2S_2$

It will be seen from the above diagram that each of the four families thus arranged (O_1F_1, O_1F_2, O_2F_1 and O_2F_2) is characterized by an entirely corresponding parallel series of genotypic variations as to the variable elements, G and S. At the same time one can see that the four groups, G_1S_1, G_1S_2, G_2S_1 and G_2S_2, are all characterized by the same series of genotypic variations as to the variable elements, O and F. Although genotypic parallelism does not necessarily cause phenotypic parallelism, equally the lack of the latter does not mean the lack of the former, and there is no

definite evidence against this *a priori* reasoning that the organic world is primarily composed of individuals which may be arranged in such a way as just described.

Recent works by paleontologists have emphasized the existence of long parallel phylogenetic trends in different lines of descent. How these parallel roads arose is to be investigated further, but it may be possible to interprete them on a similar basis to that just given. It will be needless and unfruitful of anything but confusion to introduce for these phenomenon any new conception of parallel variability, such as 'morphological parallelism' of PHILIPTSCHENKO.

To conclude: The theory of genotypic parallelism may be recognized as the sole working ground now acceptable for group variability. The possibility of the existence in different species of the identical gene constitution or identical parts of it which has been responsible for genotypic parallel variability has been justified on experimental grounds and, where experimental proofs were not available, from *a priori* reasoning.

The acceptance of the theory may enable geneticists to make more rapid progress in the establishment of genes and linkage relations within a species, if some information on the corresponding variations has already been obtained in a related species, and also make possible the prediction of genotypic variations which have not been as yet discovered in a species, from a knowledge of them in another.

Genetics has developed in its differential field; now the genetics of to-morrow is expected to develop in the integral field. The standardization of gene symbols is possible only when the integral work of all existing variations has been accomplished. The unification of symbols on a formal ground or priority of their designation must be regarded as working merely provisionally.

It would be the writer's great pleasure if the present paper might be accepted as a prolegomenon to future development of Genetics in this field.

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IX

LITERATURE CITED

Note: Since the present paper was originally intended as a part of the same writer's A Bibliographical Monograph on Plant Genetics, 1900–1929, the present discussion has been made on the data compiled in the Monograph, no reference (with a very few exceptions which have intimate connections with the present discussion) having been made to literature of later date. In the following list, papers cited in the Monograph are indicated by the bibliography numbers of the same and those not cited in it are listed below with their full titles.

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