

ON GAMETIC SERIES INVOLVING REDUPLICATION OF CERTAIN TERMS¹.

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IN a paper recently published² we gave a brief account of some peculiar phenomena relating to the coupling and repulsion of factors in the gametogenesis of the sweet pea and of several other plants. The view there stated was that if A and B represent two factors between which coupling or repulsion can exist then the nature of the F_2 generation depends upon whether A and B were carried into the F_1 heterozygote by the same gamete or by different gametes. If the heterozygote $AaBb$ is formed by the gametes AB and ab partial coupling between A and B occurs in F_2 according to a definite system, and it must be supposed that the gametes formed by the heterozygote belong to one or other of the series

$$3AB : Ab : aB : 3ab,$$

$$7AB : Ab : aB : 7ab,$$

$$15AB : Ab : aB : 15ab, \text{ \&c.}$$

If on the other hand the heterozygote, $AaBb$, is formed by the gametes Ab and aB repulsion occurs between A and B , so that only the two classes of gametes Ab and aB are formed. In the account to which we have alluded we supposed that such repulsion was complete, and that the two classes of gamete AB and ab were not formed. Our work on sweet peas during the present summer has led us to modify our conception of the nature of the gametes produced in cases where repulsion occurs, and this modification will perhaps be made clearer if we begin by giving an account of the experiments upon which it is based.

¹ This paper is also appearing in the 49th volume of the Brunn *Verhandlungen* which is to be published as a Mendel *Festschrift*.

² *Proc. Roy. Soc. B*, Vol. 84, 1911, p. 1.

During the years 1906 and 1907 we were engaged upon an investigation of the inheritance of the hooded character in the sweet pea, of which an account appeared in Report IV to the Evolution Committee of the Royal Society, 1908, pp. 7—15. Among several thousand plants bred and recorded in this set of experiments there occurred a single individual (in Exp. 35, R.E.C. IV, p. 15) exhibiting striking peculiarities in the form of its flowers. These were small and much deformed (cf. Pl. XL, fig. 1). The standard failed to become elevated, the keel was cleft distally so that the anthers were partially protruded, while the stigma projected far beyond the petals, and was carried on in the line of the carpels instead of being abruptly bent at right angles to them as in the normal flower. At the time of its discovery, in reference to the open "mouth," and the protruding "tongue" represented by the projecting style, the plant was dubbed "the cretin," by which term we shall subsequently refer to this peculiar malformation. The fact that the style protrudes is due to the malformation of the keel which is unable to curve the growing style and cause it to assume its natural position. Fuller experience of these cretins has shewn us that the petals may sometimes be nearly as large as in normal flowers (cf. Pl. XL, fig. 2), and that the standard may sometimes become elevated in the normal way (cf. Pl. XL, fig. 3). The size of the flowers may vary considerably on the same plant, and hitherto where the larger form of flower has occurred the plant has also borne others more nearly resembling the original type. The degree to which the keel is cleft also shews some variation, but in all cases these cretins have the peculiar and characteristic straight stigma.

Our original cretin was found in 1907 and was used as the pollen parent to fertilise various sterile¹ sweet peas. The F_1 plants, which flowered in 1908, were all indistinguishable from normal sweet peas. The normal form of flower (N) was completely dominant to the cretin (n), and fertility (F) of the anthers was of course dominant to sterility (f). We may draw attention to the fact that the crosses were in all cases of the nature $Nf \times nF$, one of the two factors entering with each gamete. In the following year a single F_2 family was raised and consisted of 51 normal fertile, 30 normal sterile, 33 cretin fertile, and 1 cretin sterile². The cretin character behaved as recessive to the normal flower, but the

¹ In this family and in one of those grown later both light and dark axilled plants occurred. In each case the dark axil went in from the fertile cretin parent, and in F_2 there is some coupling between the dark axil and fertility. The numerical results however are complex and must be left over for discussion until more material is available.

relative distribution of the different characters evidently pointed to some form of repulsion between the normal flower and fertility. Had it not been for the appearance of the single sterile cretin we could have regarded this case as one of complete repulsion between the factors N and F . The problem was to account for the sterile cretin, and at the time we were inclined to regard it as due to an unaccountable failure of repulsion between N and F . Lack of opportunity prevented us from following up this case in 1910, but in the present year we sowed the seed of the rest of the F_1 plants harvested in 1908 and obtained details of eight more families which are set out in the accompanying table (Table I).

TABLE I.

Reference Number	Normal fertile	Normal sterile	Cretin fertile	Cretin sterile
Number 5, 1909	51	30	33	1
„ 72, 1911	26	14	10	1
„ 73, „	21	12	12	1
„ 74, „	24	9	8	—
„ 75, „	22	4	4	2
„ 76, „	30	12	5	1
„ 77, „	78	43	32	3
„ 78, „	59	15	24	—
„ 79, „	25	12	15	2
Total ...	336	150	143	11
Expectation ...	330	150	150	10

These records shew that the appearance of a small proportion of sterile cretins is a constant feature in these families and we suggest that their presence may be accounted for as follows. The repulsion between N and F is to be regarded as partial, and of such a nature that the series of gametes produced by the F_1 plant is NF , $3Nf$, $3nF$, nf . Such a series of ovules fertilised by a similar series of pollen grains would give rise to a generation consisting of 33 normal fertiles, 15 normal steriles, 15 cretin fertiles, and 1 cretin sterile. As the figures given in Table I shew, this expectation is closely realised by the facts of experiment, and we have little hesitation in regarding this explanation as the correct one. Moreover we are inclined to go further and to extend the principle to all cases of repulsion in plants. We consider then that where A and B are two factors between which repulsion occurs in the gametogenesis of the heterozygote formed by union of

the gametes Ab and aB , the gametes produced by the heterozygote so derived form one or other term of the series

$$AB : 3Ab : 3aB : ab,$$

$$AB : 7Ab : 7aB : ab,$$

$$AB : 15Ab : 15aB : ab, \text{ \&c.}$$

And if we take $2n$ as the number of gametes in the series we may generalise it under the expression $AB : (n-1)Ab : (n-1)aB : ab$. As the repulsion increases in intensity it is obvious that the zygotes of the form $AABB$ and $aabb$ will become relatively scarcer, for there will be only one of each of these two homozygous forms in the complete series of zygotes. At the same time the ratio of the three zygotic forms $AB : Ab : aB$ approaches more and more nearly to the ratio $2 : 1 : 1$ such as would occur if the repulsion were complete. This is brought out in the upper part of Table II where we have set out some of the gametic series in which partial repulsion is involved together with the series of resulting zygotes. The latter, as the Table shews, are covered by the general formula

$$(2n^2 + 1) AB : (n^2 - 1) Ab : (n^2 - 1) aB : ab^*.$$

TABLE II.

	Gametic series				Number of gametes in series	Number of zygotes formed	Nature of zygotic series			
	AB	Ab	aB	ab			AB	Ab	aB	ab
Partial repulsion from zygote of form $Ab \times aB$	1	$(n-1)$	$(n-1)$	1	$2n$	$4n^2$	$2n^2+1$	n^2-1	n^2-1	1
	1	31	31	1	64	4096	2049	1023	1023	1
	1	15	15	1	32	1024	513	255	255	1
	1	7	7	1	16	256	129	63	63	1
	1	3	3	1	8	64	33	15	15	1
Partial coupling from zygote of form $AB \times ab$	1	1	1	1	4	16	9	3	3	1
	3	1	1	3	8	64	41	7	7	9
	7	1	1	7	16	258	177	15	15	49
	15	1	1	15	32	1024	737	31	31	225
	31	1	1	31	64	4096	3009	63	63	961
	63	1	1	63	128	16384	12161	127	127	3969
	$(n-1)$	1	1	$(n-1)$	$2n$	$4n^2$	$3n^2-(2n-1)$	$2n-1$	$2n-1$	$n^2-(2n-1)$

Hitherto the only repulsion series which we have been able to identify with certainty is the one with which we have just dealt, i.e. $1 : 3 : 3 : 1$ series for the factors N and F .

* The general formulae made use of here and in Table II are purely empirical, and offer a convenient way of calculating the nature of the zygotic series from any series of gametes.

It is probable, however, that the case of blue and long pollen¹ is one in which the repulsion is of the 1 : 7 order. Up to the present time we have had four families of the mating $Bl \times bL$ and the 419 plants recorded in F_2 were distributed in the four possible zygotic classes as follows :

Reference Number	Blue long	Blue round	Red long	Red round
Number 61, 1910	85	33	41	1
„ F28, „	60	20	23	—
„ F31, „	9	7	5	—
„ F32, „	72	35	28	—
Total	226	95	97	1

Though the evidence for partial repulsion rests here upon the single red round plant which occurred in family 61, it is in reality very much stronger than it appears at first sight, for the following reason. All the plants in the above four families were hooded, i.e. lacking in the factor for erect standard (E). As we have already pointed out², the three factors E , B , and L constitute a series such that if any two are brought into a zygote by different gametes repulsion occurs between them. Until the present round hooded red plant appeared we had never encountered this combination in any of our experiments. It cannot therefore be regarded as due to a stray seed from another family. And it is evident that if the repulsion between any pair of these three factors were complete such a plant could never arise. For in the normal course the ebL gamete could never be formed. Only two possibilities therefore are open. Either we must look upon it as an unaccountable mutation, or we must consider that the repulsion between B and L is partial. In the light of the evidence afforded by the cretin sweet pea we prefer the latter hypothesis, and we are inclined to regard the partial repulsion between B and L as of the 1 : 7 : 7 : 1 type. On this hypothesis we should expect one red round in every 256 plants (cf. Table II) whereas experiment gave 1 in 419. At the same time we recognise that the data are not yet sufficient to preclude the 1 : 15 : 15 : 1 system. It is worthy of note that the coupling between B and L is usually on the 7 : 1 : 1 : 7 system, and it would be interesting if in such cases as these the repulsion and coupling systems for a given pair of factors were shewn to be of the same intensity. In most cases this could not be tested in practice owing to the very large

¹ Blue in the flower colour (B) is dominant to red (b), and long pollen (L) is dominant to round pollen (l).

² *Proc. Roy. Soc.* 1911, p. 7.

number of plants required. Thus the coupling between erect standard and blue is on the 127 : 1 : 1 : 127 system, and if the repulsion were of similar intensity we should expect only one hooded red in every 65,536 plants. We may, however, state that in this particular case we have grown over 4000 plants without meeting with a hooded red, so that the facts, so far as they go, point to a high intensity of repulsion for factors exhibiting a high intensity of coupling. It is obvious that the relation can only be worked out where the intensity of repulsion is low, and it is hoped that the case of the cretin may eventually throw light upon this point when the system in which *N* and *F* are coupled shall have been determined.

The question now arises how these gametic systems are formed. In each the characteristic phenomenon is that the heterozygote produces a comparatively large number of gametes representing the parental combinations of factors and comparatively few representing the other combinations. In describing the original case of coupling, namely that between the blue colour and long pollen in the sweet pea, we pointed out that no simple system of dichotomies could bring about these numbers, and also that it was scarcely possible that such a series could be constituted in the process of gametogenesis of a plant, in whatever manner the divisions took place. In saying this, regard was of course had especially to the female side, and this deduction has become even more clear in view of the fact that we now know a series consisting of 256 terms. It is practically certain that the ovules derived from one flower of the sweet pea, even if all collateral cells be included, cannot possibly be arranged in groups of this magnitude. A pod rarely contains more than nine or ten good seeds at the most, so that if we even reckon twelve potential seeds to the pod and eight potential gametic cells to the ovule, the total is still only 96, which is much too few¹. Nevertheless our series of numbers is plainly a consequence of some geometrically ordered series of divisions.

There is evidence also from other sources that segregation may occur earlier than gametogenesis. Miss Saunders' observations on *Matthiola*² and on *Petunia*³ proved that in those plants the factors for singleness are not similarly distributed to the male and female cells.

¹ From the fact that in maize the endosperm characters are the same as those of the seed itself we know moreover that segregation must have been completed before the divisions at which the male and female cells which constitute the endosperm are set apart.

² Rep. Evol. Committee R. S. IV, 1908, p. 36.

³ *Jour. Gen.* i. 1911.

The recent work of de Vries¹ on *Oenothera biennis* and *muricata* has provided other instances of dissimilarity between the factors borne by the male and female organs of the same flower. In all these examples it is almost certain that segregation cannot take place later than the formation of the rudiments of the carpels and of the stamens respectively. The only visible alternative is that in each sex the missing allelomorphs are represented by somatic parts of the sexual apparatus, which for various reasons seems improbable. There is therefore much reason for thinking that segregation can occur before gametogenesis begins, but there is no indication as to which are the critical divisions.

Now that we may regard the formation of four cells of composition AB , Ab , aB , ab , as the foundation both of the coupling- and of the repulsion-series the problem is manifestly somewhat simplified. The time, excluding gametogenesis, at which we can most readily imagine four such definite quadrants to be formed is during the delimitation of the embryonic tissues. It is then that the plant is most clearly a single geometrical system. Moreover the excess of gametes of parental composition characterising the coupling- and repulsion-series must certainly mean that the position of the planes of division by which the four quadrants are constituted is determined with regard to the gametes taking part in fertilisation. Though the relative positions of the constituents of the cells may perhaps be maintained throughout the history of the tissues, it is easier to suppose that the original planes of embryonic division are determined according to those positions than that their influence can operate after complex somatic differentiation has been brought about.

At some early stage in the embryonic development or perhaps in later apical divisions we can suppose that the $n-1$ cells of the parental constitution are formed by successive periclinal and anticlinal divisions of the original quadrants which occupy corresponding positions. The accompanying diagram gives a schematic representation of the process as we imagine it. Obviously it does not pretend to give more than a logical or symbolic presentation of the phenomena. If such a system of segregation is actually formed at the apex, it must be supposed that the axes of the system revolve with the generating spiral. Whatever hypothesis be assumed the following points remain for consideration:

1. We are as yet unable to imagine any simple system by which the four original quadrants can be formed by two *similar* divisions. Evidently there must be two cell-divisions, and if in one of them we

¹ *Biol. Centralbl.*, xxxi. 1911, p. 97.

suppose AB to separate from ab , we cannot then represent the formation of Ab and aB . Therefore we are almost compelled to suppose that the original zygotic cell forms two similar halves, each $AaBb$, and that the next division passes differently through each of these two halves, in the one half separating AB from ab , and in the other half separating Ab from aB . The formation of these four quadrants must take place

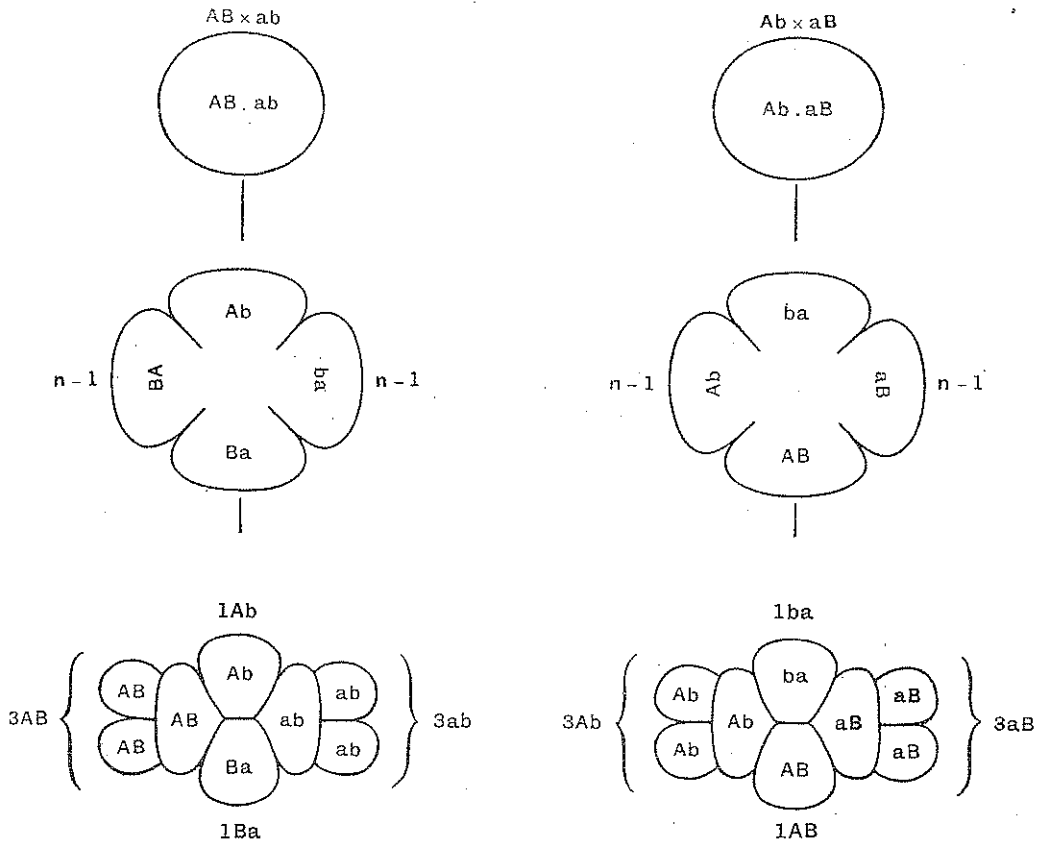


Fig. 4.

in every case in which there is segregation in respect of two pairs of factors. (For three pairs there must similarly be eight segments, and so on.) The *axes* of this system may well be determined by the position of the constituent parental gametes. Reduplication or proliferation resulting in $n-1$ gametes may then take place in either of the opposite pairs of quadrants according to the parental composition.

2. If in the gametes of any plant some factors are distributed according to one of the reduplicated series and other factors according to the normal Mendelian system—as we know they may be—the segregations by which such a system is brought about *cannot* have happened simultaneously. Moreover if various reduplications can take place very early in some individuals and not in others, we cannot imagine how the normal form of the plant remains unchanged, unless these reduplications affect tissues originally set apart as germinal.

As possibly significant we note here the fact that in the embryonic development of plants the order of the various divisions is known to be subject to great variation and it is not inconceivable that such disturbances of the order in which the planes of division occur may indicate variations in the process of segregation¹.

3. We do not yet know whether independent reduplicated systems can be formed in the same individual. In the sweet pea for instance we have not yet seen the consequences of combining blue, erect standard, and long pollen with the fertile-sterile, dark-light axil series, and much may be discovered when such families come to be examined.

ANIMALS.

The phenomena seen in animals may well be produced by the segmentations in which the parts of the ovary or testis are determined. Hitherto no case of *coupling* has been found in animals. Among the phenomena of repulsion, however, of which many examples exist, certain suspicious cases have been observed which may mean that in animals reduplicated systems exist like those of the plants. Nevertheless at present it seems not impossible that the two forms of life are really distinguished from each other in these respects.

TERMINOLOGY.

Lastly, in view of what we now know, it is obvious that the terms "coupling" and "repulsion" are misnomers. "Coupling" was first introduced to denote the association of special factors, while "repulsion" was used to describe dissociation of special factors. Now that both phenomena are seen to be caused not by any association or dissociation, but by the development of certain cells in excess, those expressions

¹ See Coulter and Chamberlain, *Morphology of Angiosperms*, 1903, p. 187.

must lapse. It is likely that terms indicative of differential multiplication or proliferation will be most appropriate. At the present stage of the inquiry we hesitate to suggest such terms, but the various systems may conveniently be referred to as examples of *reduplication*, by whatever means the numerical composition of the gametic series may be produced.

EXPLANATION OF PLATE XL.

- Fig. 1. Photograph of the flowering stalks of two cretins. The flowers are here as fully opened as they usually become in this variety, and they are represented slightly smaller than natural size.
- Fig. 2. Flower of cretin which has larger petals than usual. The standard however is not elevated and the straight stigma protrudes beyond the rest of the flower.
- Fig. 3. In the centre two flowers from a cretin in which the standards are fully elevated. On the right are two other mature flowers from the same plant shewing petals of the usual cretin form. On the left are two old buds.

PLATE XL

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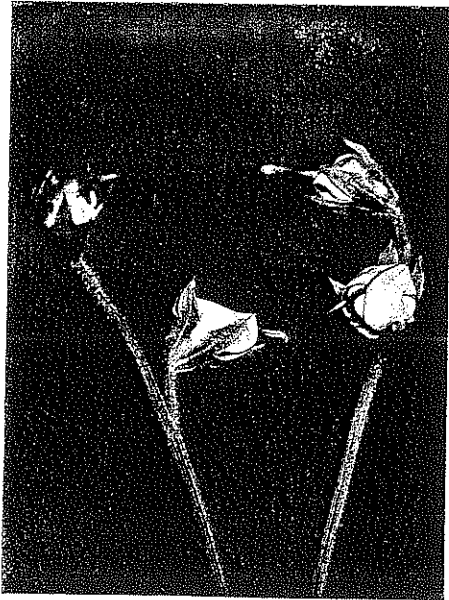


Fig. 1.



Fig. 2.

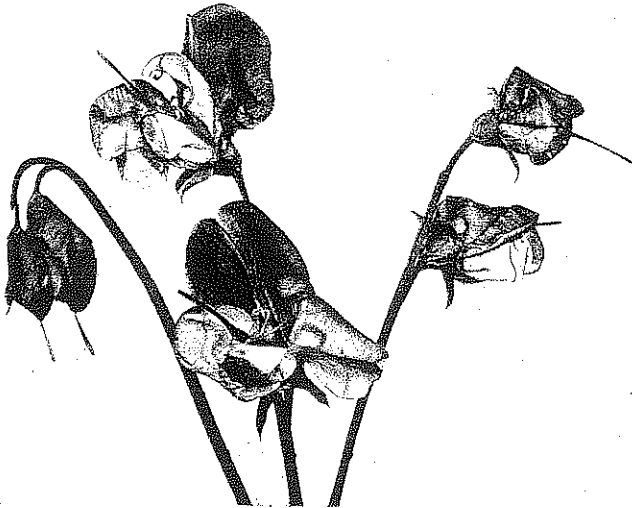


Fig. 3.