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FORMS OF REDUPLICATION:—PRIMARY AND SECONDARY.

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ACCORDING to Bateson and Punnett (*J. of Gen.* Vol. I. 4, p. 293) all forms of reduplication hitherto discovered, with one possible exception, may be grouped in two classes, the gametic series for these being represented by the empirical formulae

$$n-1 : 1 : 1 : n-1 \quad \text{and} \quad 1 : n-1 : n-1 : 1;$$

the single exception being the cases of complete repulsion, in which the end terms disappear, giving the series $n-1 : n-1$. Even this exceptional type however is now regarded by these authors as probably a special case of the series $1 : n-1 : n-1 : 1$, where n is large and therefore one of the zygotic types so scarce as not to be expected except in very extensive cultures[1].

My own studies of *Senecio vulgaris* have however revealed the existence of the ratio 2 : 1 : 1 : 2, and Baur (*Vererbungslehre*, p. 124) appears to have found the ratio 6 : 1 : 1 : 6 in an *Antirrhinum* cross. Neither of these ratios comes under the general formula given above. Such being the case, it seemed to me desirable to ascertain what the consequences of accepting the current hypothesis of reduplication would be, not simply as applied to a pair of factors AB (or two pairs of allelomorphs Aa, Bb), but to three or more factors A, B, C, D ....

The immediate problem which presented itself for solution was a comparatively simple one, yet one which has apparently been overlooked. Given three factors A, B, and C and the occurrence of reduplication between A and B in the form $n : 1 : 1 : n$ and between A and C in the form $m : 1 : 1 : m$, where n may be equal to, greater, or less than m, is there necessarily a form of reduplication between B and C,

[1] In these formulae n is a power of 2 and is equal to one-half the number of gametes in a series.

and if so, of what type must it be? We need only state now that the answer is that there is reduplication between B and C of the type

$$nm+1 : n+m : n+m : nm+1.$$

The mode by which this ratio is found is given below. We have however to note that this type of ratio also does not conform to the Bateson-Punnett formula.

Certain experimental results will, I believe, in view of these conclusions, repay further study. All the gold has not yet been extracted from the ore.

Reduplication clearly depends upon peculiarities in the mode of formation of the gametic series. As however it, so far as we know at present, affects pairs of factors only, it is convenient to ignore such possible cases of reduplication as might occur between, say, triplets or quartets. With this limitation and adopting the Bateson-Punnett hypothesis of reduplication (*Journ. of Genetics*, Vol. I. No. 4, p. 293), it is quite easy to construct the gametic series for any set of reduplications.

Let us consider first the simple case in which three factors A, B and C are involved, with reduplication between A and B only, and in the form $n : 1 : 1 : n$.

The gametic series if A and B are alone considered would be

$$n\text{AB} + 1\text{Ab} + 1\text{aB} + n\text{ab}.$$

To include the factor C, the series must consist of eight terms and be arranged so that each member of the above will be associated with C and c, without disturbing the established reduplication; thus

$$n\text{ABC} + n\text{ABc} + 1\text{AbC} + 1\text{Abc} + 1\text{aBC} + 1\text{aBc} + n\text{abC} + n\text{abc}.$$

By extracting the pairs separately from this series, we get

$$\text{AB} : \text{Ab} : \text{aB} : \text{ab} :: 2n : 2 : 2 : 2n \quad \text{or} \quad n : 1 : 1 : n.$$

$$\text{AC} : \text{Ac} : \text{aC} : \text{ac} :: n+1 : n+1 : n+1 : n+1 \quad \text{or} \quad 1 : 1 : 1 : 1.$$

$$\text{BC} : \text{Bc} : \text{bC} : \text{bc} :: n+1 : n+1 : n+1 : n+1 \quad \text{or} \quad 1 : 1 : 1 : 1.$$

Clearly a reduplication between two factors A and B does not alter the ratios for A and C and B and C.

An experimental illustration of this is furnished by Gregory's work on *Primula sinensis*, in what may be called the MSD group of experiments; where

	M = magenta	dominant over	m = red;
and	S = short style	„ „	s = long style;
and	D = single flower	„ „	d = double flower.

In these experiments there is reduplication between M and S of the form 7 : 1 : 1 : 7; but M and D and S and D show no reduplication and give each the normal ratio 1 : 1 : 1 : 1.

We may now consider the more important case, where there are three factors A, B and C and reduplication between A and B in the form $n : 1 : 1 : n$, and between A and C in the form $m : 1 : 1 : m$.

The gametic series when A and B are alone considered would be

$$n\text{ABC} + n\text{ABc} + 1\text{AbC} + 1\text{Abc} + 1\text{aBC} + 1\text{aBc} + n\text{abC} + n\text{abc}.$$

To secure reduplication between A and C as well, and of the form $m : 1 : 1 : m$, the terms involving AC and ac must be multiplied by m; the series thus becomes

$$nm\text{ABC} + n\text{ABc} + m\text{AbC} + 1\text{Abc} + 1\text{aBC} + m\text{aBc} + n\text{abC} + nm\text{abc}.$$

Extracting the three pairs separately from this series, we get

$$\text{AB} : \text{Ab} : \text{aB} : \text{ab} :: nm + n : m + 1 : 1 + m : m + nm$$
$$:: n : 1 : 1 : n.$$
$$\text{AC} : \text{Ac} : \text{aC} : \text{ac} :: nm + m : n + 1 : 1 + n : m + nm$$
$$:: m : 1 : 1 : m.$$
$$\text{BC} : \text{Bc} : \text{bC} : \text{bc} :: nm + 1 : n + m : m + n : 1 + nm.$$

From this procedure, it is clear that reduplication between A and B and between A and C involves reduplication between B and C. It is worthy of note that this derived or secondary type of reduplication has apparently been entirely overlooked, especially as there is good reason to suppose that it has already been observed experimentally. Moreover, it belongs to a fundamentally different series,—of the form $p : q : q : p$.

Gregory's interesting results on *Primula sinensis* illustrate this case. In the MSG group of experiments, where M and S have the same significance as above, G represents green stigma, dominant over g—red stigma. The best numerical results are given by the crosses in which the F_1—MSGmsg was crossed by the triple recessive msgmsg. In such cases it is clear that the ratios of the zygotic series coincide with those of the F_1 gametic series. The results may be grouped as follows:—

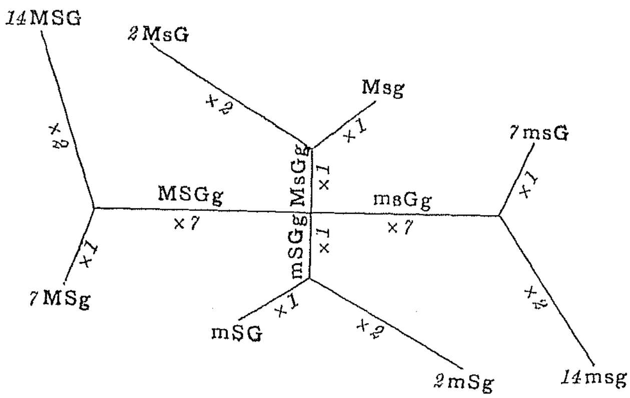
	MS	Ms	mS	ms
Nos. found	53	3	6	40
Expectation on ratio of 7 : 1 : 1 : 7	*45*	*6*	*6*	*45*

	MG	Mg	mG	mg
Nos. found	39	17	18	28
Expectation on ratio of 2 : 1 : 1 : 2	*34*	*17*	*17*	*34*

	SG	Sg	sG	sg
Nos. found	64	35	30	44
Expectation on ratio of 5 : 3 : 3 : 5 derived from {7 : 1 : 1 : 7 / 2 : 1 : 1 : 2}	*54*	*32*	*32*	*54*

The suggestion of the 2 : 1 : 1 : 2 ratio in the second case is made on my own responsibility—Gregory does not assign one. The main interest lies in the fact that the derivative ratio 5 : 3 : 3 : 5 explains fairly well the facts of the case.

The following diagram will serve to illustrate the hypothetical course of the segregations and the cell-divisions in this case.



The sign × signifies increase in the number of gametes, or gametogenic, segregating cells, and the following number the relative amount of increase along the different axes.

The primary and secondary reduplications, three in number, are notable in that each represents a case of coupling. Let us therefore consider the case in which the primary reduplications are of the form $1 : n : n : 1$ for A and B and $1 : m : m : 1$ for A and C. Under these conditions the gametic series will be

$$\mathrm{ABC} + m\mathrm{ABc} + n\mathrm{AbC} + nm\mathrm{Abc} + nm\mathrm{aBC} + n\mathrm{aBc} + m\mathrm{abC} + \mathrm{abc},$$

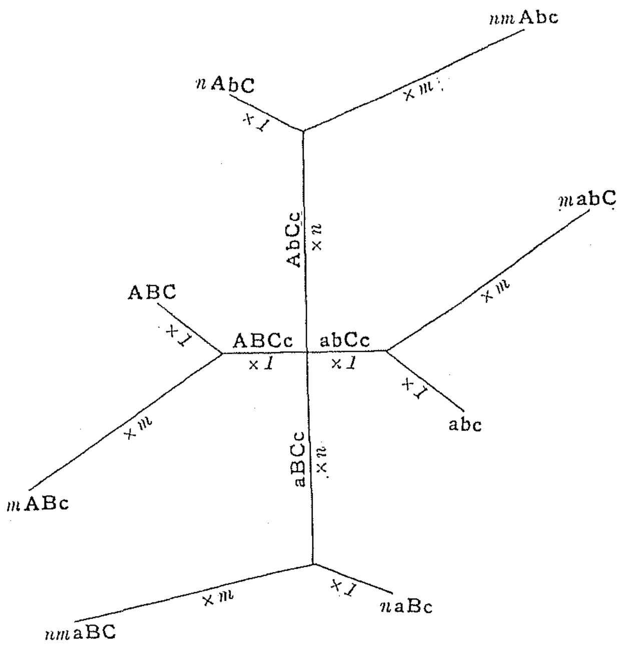
and the reduplication between B and C will be found (by extracting) to be of the form

$$\mathrm{BC} : \mathrm{Bc} : \mathrm{bC} : \mathrm{bc} :: 1 + nm : m + n : n + m : nm + 1.$$

We thus get the result that the reduplication between B and C is of the same form whether the ratios between A and B and A and C are

$$1 : n : n : 1 \text{ and } 1 : m : m : 1 \text{ or } n : 1 : 1 : n \text{ and } m : 1 : 1 : m.$$

This case may be represented diagrammatically; thus



Since n and m are each greater than one, it may be shewn that whether n is equal to, greater than or less than m, $\frac{1+nm}{m+n}$ is greater than one, and therefore that the type of reduplication between B and C is of the nature of a coupling. We have therefore established the rule that reduplications between A and B and between A and C whether of the form of couplings or of repulsions, give rise to a *secondary reduplication between* B *and* C *of the form of a coupling.*

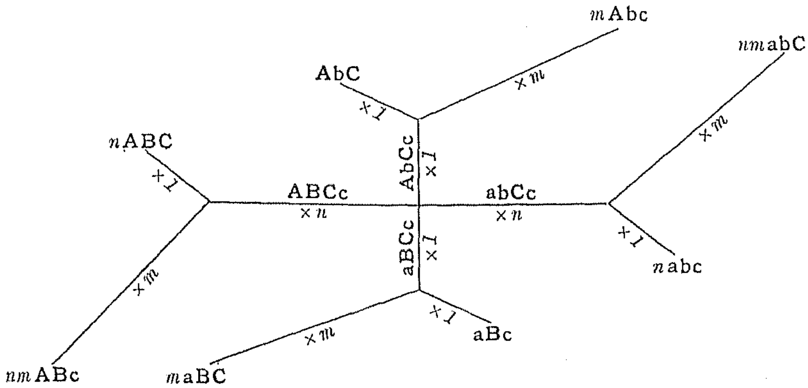
We may now consider the case in which the types of reduplication between A and B and between A and C belong to the series $n:1:1:n$ and $1:m:m:1$ respectively. The gametic series in this case will be

$$n\mathrm{ABC} + nm\mathrm{ABc} + \mathrm{AbC} + m\mathrm{Abc} + m\mathrm{aBC} + \mathrm{aBc} + nm\mathrm{abC} + n\mathrm{abc},$$

and the reduplication between B and C will be necessarily of the form

$$\mathrm{BC} : \mathrm{Bc} : \mathrm{bC} : \mathrm{bc} :: n+m : nm+1 : 1+nm : m+n,$$

and be graphically represented thus:—



Since $n+m$ is less than $nm+1$ this type of reduplication is of the nature of a repulsion.

The EBL group of experiments conducted by Bateson and Punnett and described in *Proc. Roy. Soc.* B, Vol. 84, p. 7, illustrates this case. The cross Ebl × eBL shews repulsion between E and B and coupling between B and L. It will simplify comparison to write the factors in the order BLE. It has been found that

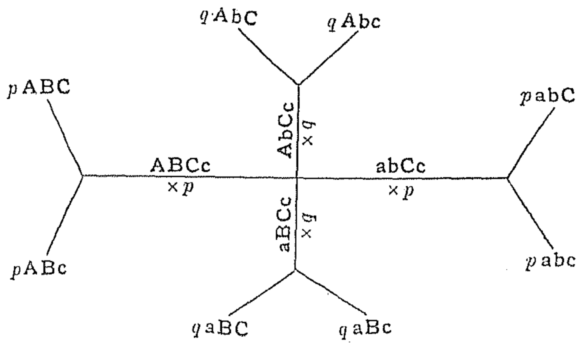
BL : Bl : bL : bl :: 7 : 1 : 1 : 7,

and BE : Be : bE : be :: 1 : m : m : 1.

Hence it may be deduced that

LE : Le : lE : le :: $7+m$: $7m+1$: $7m+1$: $7+m$,

which indicates a repulsion. This appears to have been observed, but it is not clear to me from the description of the results whether these three types of reduplication have been observed in the same cross. They should certainly be looked for.



We have found that certain derivative reduplications are of the form $p:q:q:p$. It seems probable that there may be primary reduplications also of this type. When such a reduplication is confined to one pair of factors A and B, a third factor C being unaffected, the gametic series would be

$$p\text{ABC} + p\text{ABc} + q\text{AbC} + q\text{Abc} + q\text{aBC} + q\text{aBc} + p\text{abC} + p\text{abc}.$$

The diagram would take the form shewn at the bottom of p. 318.

If $p = q$ there is no reduplication. If p is $> q$, we get coupling; if q is $> p$, we have repulsion.

But we may have reduplication between A and B of the form $p:q:q:p$ and between A and C of the form $r:s:s:r$. In this event there will be a derivative reduplication between B and C, the form of which may be ascertained as follows:—

The gametic series will be

$$pr\text{ABC} + ps\text{ABc} + qr\text{AbC} + qs\text{Abc} + qs\text{aBC} + qr\text{aBc} + ps\text{abC} + pr\text{abc},$$

and, by extracting, the derivative reduplication is found to be

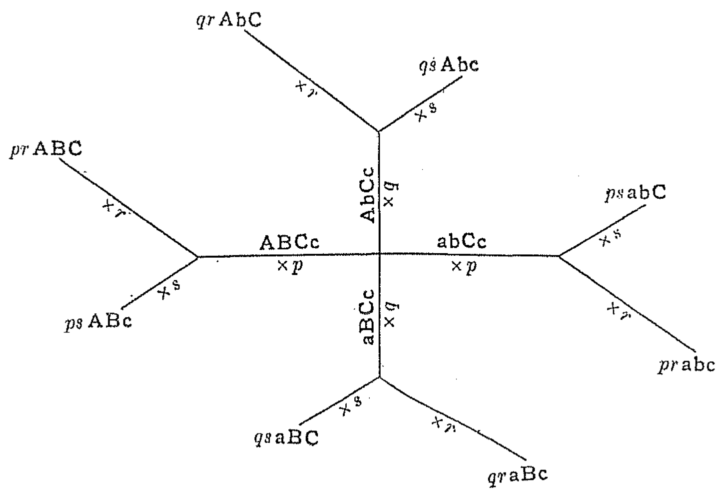
$$\text{BC} : \text{Bc} : \text{bC} : \text{bc} :: pr + qs : ps + qr : qr + ps : qs + pr;$$

or more simply

$$:: pr + qs : ps + qr : ps + qr : pr + qs.$$

This is the most general formula for a derivative reduplication and is of course applicable to all the preceding simpler cases.

The following diagram illustrates the course of the assumed segregations and cell-divisions:—



These considerations shew that the reduplication hypothesis adequately explains the occurrence of all the ratios hitherto determined. We perceive too how segregation and cell-division *may be* associated, and that these appear to be carried out symmetrically. In the complete absence of reduplication there is a typical radial symmetry of the segregation apparatus. When reduplication sets in, a bilateral structure is developed, and this may ultimately assume quite a complex form. There seems some reason, moreover, to believe that the development of cells at the two ends of the same axis may be unequal. This would produce a new form of symmetry—the structure becoming two-ended, enabling one to distinguish not only between different axes, but between the two ends of the same axis. In such a case, with a single pair of allelomorphs A, a, we should get a divergence from the gametic ratio,—1 : 1 and the normal zygotic ratio,—1 : 2 : 1. Such divergences are not infrequently met with in the literature of genetics. We may, therefore, ultimately find cases of asymmetrical types of reduplication, such as are represented by the ratios

$$(1)\quad w : x : y : w,$$
$$(2)\quad w : x : x : z,$$
$$(3)\quad w : x : y : z.$$

The experimental determination of such ratios would of course be difficult.

Finally let us consider the case of four or more factors A, B, C, D ... with reduplication between A and B, A and C, A and D ... of the form $n:1:1:n$, $m:1:1:m$, $p:1:1:p$, ... In addition to the derivative reduplication between B and C, there will be now reduplications also between B and D and C and D ....

The gametic series for four factors A, B, C and D would be

$$\begin{aligned} & nmp\mathrm{ABCD} + nm\mathrm{ABCd} + np\mathrm{ABcD} + n\mathrm{ABcd} \\ + & mp\mathrm{AbCD} + m\mathrm{AbCd} + p\mathrm{AbcD} + \mathrm{Abcd} \\ + & \mathrm{aBCD} + p\mathrm{aBCd} + m\mathrm{aBcD} + mp\mathrm{aBcd} \\ + & n\mathrm{abCD} + np\mathrm{abCd} + nm\mathrm{abcD} + nmp\mathrm{abcd} \end{aligned}$$

and it can be shewn, by extracting, that the reduplications between B and D and C and D have the form:—

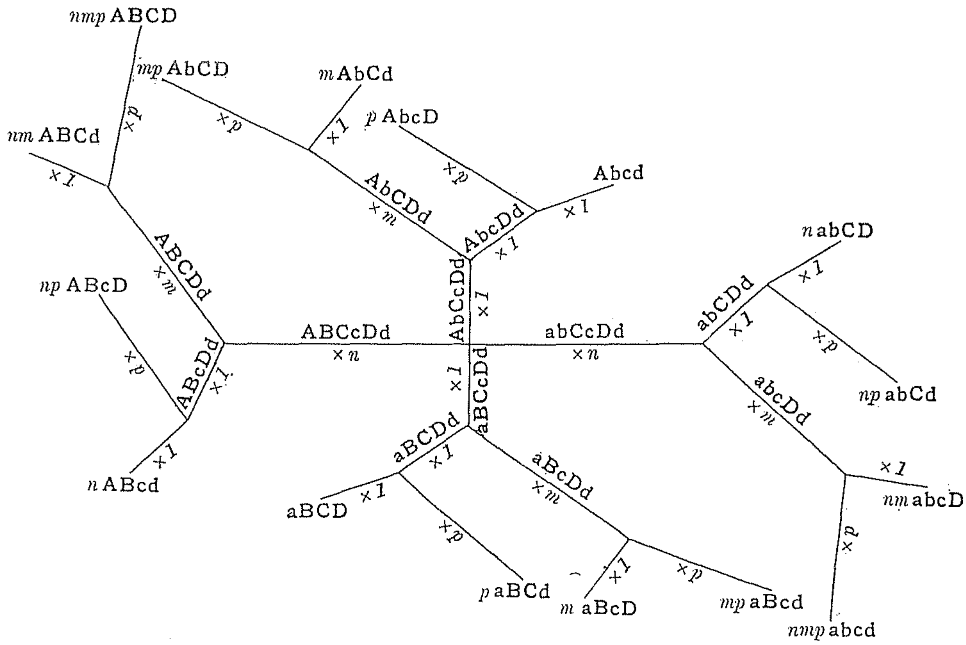
$$\mathrm{BD : Bd : bD : bd} :: np+1 : n+p : n+p : np+1,$$
$$\mathrm{CD : Cd : cD : cd} :: mp+1 : m+p : m+p : mp+1.$$

This result may be reached more easily by making use of the general formula on p. 319.

For if	AB : Ab : aB : ab ::	$n : 1 : 1 : n$,
and	AD : Ad : aD : ad ::	$p : 1 : 1 : p$,
then	BD : Bd : bD : bd ::	$np + 1 : n+p : n+p : np + 1$.

Any number of derivative ratios may be ascertained in the same way by this method.

This more complex case may be represented graphically thus:—



According to this scheme of segregation (which however must not be regarded as the only possible one), each additional factor (or pair of allelomorphs) Ee, Ff, Gg, etc. will necessitate a further dichotomy of each branch. If these additional branches are equally developed it can readily be shewn that reduplication does not take place. We have the important rule that *equal dichotomies produce normal segregation; unequal dichotomies produce reduplications.* These two types of behaviour may occur in any order or at any stage in the phylogeny, but as Bateson and Punnett have already stated, they cannot occur simultaneously.

There seems to be no reason why the most various types of reduplication should not occur together in the same plant as the result of the same cross. The hypothesis of reduplication seems adequate to explain the occurrence of any type of ratio.

The most suggestive point which emerges from the analysis is the importance of the product *nmp* ... and of its constituent factors. From these, when all the factors and all the ratios in any one cross have been ascertained, it should be possible to compute the minimum number of successive cell-divisions needed to produce the complete system of segregation. It ought to be possible to determine also, in sweet-peas for example, the *number* of successive cell-divisions which normally intervene between the first division of the zygote and the last of the gametogenic divisions, and the *distribution* of these in the ontogeny. Comparison of the two results *might* serve to fix the stage at which segregation takes place.

It is then advisable to distinguish between *primary* and *secondary* reduplications. A ratio of reduplication ascertained by experiment may belong to either series. The gametic series is based upon the primary reduplications alone. Every observed type of reduplication must be assigned to its proper position. It is comparatively easy, as we have seen, to calculate the secondary from the primary reduplications.

The schemes on p. 323 will illustrate the relationships of primary and secondary reduplications.

It is perhaps advisable to add that systems of segregation will probably be seldom found in which all the primary reduplications take place between one factor A and a number of others B, C, D, E, etc. Primary reduplications may occur between any pair of factors, and the consequent secondary reduplications will undergo corresponding modifications.

The construction of the gametic series, when the ratios of primary reduplication are known, is easy, and from these any secondary reduplication is ascertainable. The following scheme illustrates such a system of reduplications:—

Primary reduplications	Secondary reduplications	
A and B $= n : 1$		
B and C $= m : 1$	A and C $= nm+1 : n+m$	
C and D $= p : 1$	A and D $= nmp+n+m+p : nm+np+mp+1$	B and D $= mp+1 : m+p$

Factors A, B, C, D, E, F, etc. The ratios are halved for the sake of brevity.

Primary reduplications	Secondary reduplications			
A and B $=n:1$				
A and C $=m:1$	B and C $=nm+1:n+m$			
A and D $=p:1$	B and D $=np+1:n+p$	C and D $=mp+1:m+p$		
A and E $=q:1$	B and E $=nq+1:n+q$	C and E $=mq+1:m+q$	D and E $=pq+1:p+q$	
A and F $=r:1$	B and F $=nr+1:n+r$	C and F $=mr+1:m+r$	D and F $=pr+1:p+r$	E and F $=qr+1:q+r$
etc.				

or more generally,

Primary reduplications	Secondary reduplications			
A and B $=n:m$				
A and C $=p:q$	B and C $=np+mq:nq+mp$			
A and D $=r:s$	B and D $=nr+ms:ns+mr$	C and D $=pr+qs:ps+qr$		
A and E $=v:w$	B and E $=nv+mw:nw+mv$	C and E $=pv+qw:pw+qv$	D and E $=rv+sw:rw+sv$	
A and F $=x:y$	B and F $=nx+my:ny+mx$	C and F $=px+qy:py+qx$	D and F $=rx+sy:ry+sx$	E and F $=vx+wy:vy+wx$

Two numerical examples may be added:

Primary	Secondary			
A and B $=2:1$				
A and C $=3:1$	B and C $=7:5$			
A and D $=4:1$	B and D $=3:2$	C and D $=13:7$		
A and E $=5:1$	B and E $=11:7$	C and E $=2:1$	D and E $=7:3$	
A and F $=6:1$	B and F $=13:8$	C and F $=19:9$	D and F $=5:2$	E and F $=31:11$

Primary	Secondary			
A and B $=2:1$				
A and C $=1:2$	B and C $=4:5$			
A and D $=2:3$	B and D $=7:8$	C and D $=8:7$		
A and E $=1:1$	B and E $=1:1$	C and E $=1:1$	D and E $=1:1$	
A and F $=3:1$	B and F $=7:5$	C and F $=5:7$	D and F $=9:11$	E and F $=1:1$

It is also noteworthy, that complex reduplications may arise owing to the combination of a primary and a secondary reduplication in the same gametic series; e.g. the primary reduplications may be of the following types:

$$\text{A and B} = n : 1 : 1 : n$$
$$\text{A and C} = m : 1 : 1 : m,$$
$$\text{B and C} = p : 1 : 1 : p.$$

The first two alone involve a secondary reduplication between B and C of the type

$$nm + 1 : n + m : n + m : nm + 1,$$

and this combined with the primary reduplication between B and C gives the complex reduplication for B and C of

$$\text{BC} : \text{Bc} : \text{bC} : \text{bc} :: p\,(nm + 1) : n + m : n + m : p\,(nm + 1).$$

A careful study of systems of segregation will therefore, as soon as two or more reduplications have been discovered, furnish the student of genetics with data which will enable him on the one hand to test his hypotheses by further experiment, and on the other hand to extend and facilitate his researches.

It must be borne in mind however that cell-divisions, if they do really set up the phenomena of reduplication, must themselves depend upon the structure of the protoplasm. It may be that the systems of segregation will prove of some value in the analysis of this structure.

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