

ON A CASE OF PATCHING IN THE FLOWER COLOUR OF THE SWEET PEA (*LATHYRUS* *ODORATUS*).

By R. C. PUNNETT, F.R.S.

(With three Text-figures and Plate XXI.)

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THE publication of Baur's striking researches on variegated *Pelargoniums* and other plants, and his enunciation of the chimaera hypothesis, have led to a growing interest in the genetics of variegated plants in general. Not only do the anomalies in their hereditary behaviour offer a standing challenge to the geneticist, but it is difficult for those who work with them to resist the conviction that they hold the clue to much that is puzzling in connection with the process of segregation. No excuse therefore is offered for adding to the literature an account

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of a fresh case, even though it cannot at present be satisfactorily related to the existing corpus of genetical knowledge. Since it is one of some complexity, a description of the material will be followed by a brief outline of what appear to be the main genetical features before passing on to consider it in detail.

Material.

The wild purple type of flower, once met with among cultivated forms as "Purple Invincible," is closely related to the deep purple¹, and to the hooded forms of purple known as "Duke of Westminster" and "Duke of Sutherland." Earlier experiments on the genetics of these four forms shewed that their interrelations could be expressed in terms of two factors, viz. a factor for light wing (L) in the absence of which the wing is dark (l), and a factor for the notched erect standard (E) in the absence of which the standard is hooded (e). The experiments further shewed that, where the standard is erect, its colour is deeper and brighter than in the corresponding hooded form. Flowers with the erect standard are more markedly bicolor than the corresponding hooded forms. The four forms will be found illustrated on Pl. V, figs. 4, 5, 7 and 8 of Bateson's *Mendel's Principles of Heredity*².

Corresponding to each of these four normal purple forms is a recessive "red-purple" form. The difference between the normal and the red-purple is perhaps best appreciated in the case of the light-winged varieties, where there is a striking contrast between the blue wing of the normal, and the pink wings, slightly tinged with purple, of the corresponding red-purple. This is well shewn on Figs. 4 and 6 of the plate accompanying this paper, from which a good idea may be obtained of the difference in colour between a normal Duke of Westminster flower and its corresponding red-purple form. The red-purple forms of the deep purple (Ppw.) and Duke of Sutherland have the characteristic coppery appearance shewn on Pl. XXI, fig. 1. We may attribute the appearance of the red-purple colour to the lack of a factor J which is present in the normal purple. And here it should be stated that this factor brings about a change in the general appearance of the plant as well as in the colour of the flower. Red-purples are always smaller plants than normals, reaching on the average to

¹ Known as Ppw. (=purple with purple wings) in our earlier experiments. See *Rep. to Evol. Comm. Roy. Soc.* III. 1906, p. 31.

² Though this plate brings out the relative difference in the four forms, the actual colours are not well rendered. A better representation of "Duke of Westminster" is that shewn on Fig. 4 of the Plate at the end of this paper.

about two-thirds of the height of the latter. This diminution in height is accompanied by a corresponding diminution in the parts of the plant; the stems are thinner, the leaves are smaller, and flower stems shorter. The vegetative parts of the red-purple also present a different appearance to the eye, for the foliage is of a deeper green, and there is a greater development of anthocyan pigment, especially in the flower stems and pedicels, which give to the plant a characteristic "dusky" appearance.

Corresponding to the series of normal purples there is also a recessive "blue" series in the sweet pea. Lord Nelson, for example (Pl. XXI, fig. 3), is the blue form of Ppw., and there are blue forms corresponding to the other three members of the normal purple series. We may suppose that these blue forms each lack a factor D which is found in the normal purple. Corresponding to each of these "blue" forms there is a "red-blue" which bears the same relation to the blue that the red-purple bears to its equivalent normal purple form. In the blue series the colour assumed by the "red" form is a peculiar dusky violet, such as is shewn on Pl. XXI, fig. 2. We have therefore the following 16 colour varieties which, at one time or another, have figured in the present series of experiments.

Normal Series				Red Series			
Purple Invincible (P. I.)	...	ELDJ		Red P. I.	ELDj
Deep Purple (Ppw.)	...	EIDJ		Red Ppw.	EIDj
Duke of Westminster (D. W.)	...	eLDJ		Red D. W. ¹	eLDj
Duke of Sutherland (D. S.)	...	eIDJ		Red D. S.	eIDj
Blue bicolor	...	ELdJ		Violet bicolor	ELdj
Deep blue	...	EIdJ		Deep Violet bicolor	EIdj
Blue hood	...	eLdJ		Violet Duke	{eLdj
Lord Nelson (L. N.)	...	eIdJ	}				

It should at once be stated that the "Red" series has nothing to do with red sweet peas in the accepted sense. They are all true purples in that they contain the factor B, upon the presence or absence of which depends the difference between a purple sweet pea and its corresponding true red, e.g. between Purple Invincible and Painted Lady, or between Picotee and Tinged White². Thus a cross between Red Duke and Painted Lady gives Purple Invincible. Where the colour is deep, a visible difference may be exhibited among true reds between those containing and those lacking J. There is a "red" series also among true reds, but ordinarily it is not possible to differentiate the true

¹ The term "Red Duke" includes Red D. W. and Red D. S.

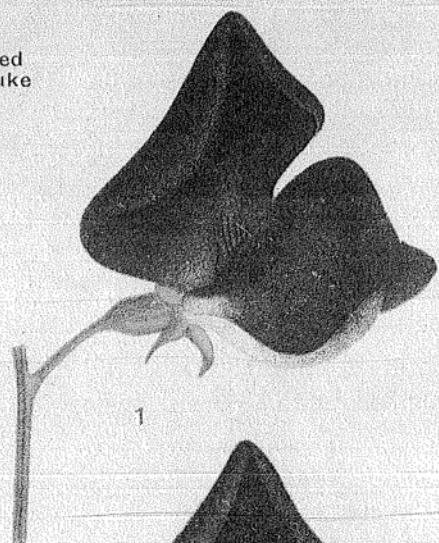
² *Reports to the Evolution Committee of the Royal Society*, III, 1906, p. 4; cf. also Bateson's *Mendel's Principles of Heredity*, 1909, Pl. III.

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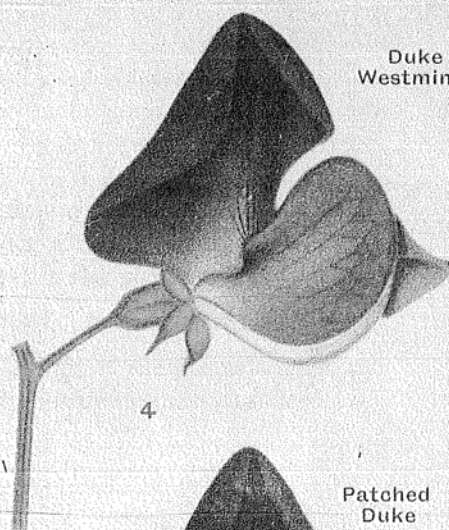
reds (J) from the red reds (j) by the colour of the flowers. The point, however, is not of importance in the present series of experiments since, with the exception of a couple of crosses, the material used was homozygous in B throughout.

Though, as will appear later, there is ample evidence for regarding the relation between the normal purple or blue, and its homologue in the red-purple series, as a simple Mendelian one, yet in certain families this relation does not obtain, but is complicated by the appearance of another form. These are plants in which the flowers are characterised by shewing a mosaic of the normal and the corresponding "red" shade of colour. A typical flower from one of these "patched" plants is shewn on Pl. XXI, fig. 5. In this instance the general colour of the flower is that of a normal D. W., but on one of the wings is a patch of the purplish pink characteristic of the Red D. W. The extent of the patching on a plant exhibits great variability among the individual flowers borne on a given plant. Usually most of the flowers shew but small patches of normal colour, such as the one figured on Pl. XXI, fig. 6. But there are nearly always flowers, more on some plants, fewer on others, which shew a greater amount of normal colour. One may be predominantly normal, as that figured on Pl. XXI, fig. 5, another may be red except for a blue wing, while another again may be patched all over, but with much more normal colour than the flower figured on Pl. XXI, fig. 6. Or the normal colour may be reduced to a minute speck which is only evident when looked for. Besides these various grades of patched flowers, a patched plant may bear normal and fully red flowers. Sometimes these are isolated, so that a flowering stem may bear two patched flowers and one normal one; at other times the plant may put up a shoot which bears only normal flowers, or again, one that has only red flowers. After examining hundreds of these patched plants, one gets the impression that in some the nature of the mosaic is finer than in others. In the former the great majority of the flowers are predominantly red, and the normal colour is present as small flecks, often very numerous, scattered about over the surface. In the latter the normal colour is present as blotches, fewer in number but of larger size, and it is in these that completely normal flowers are perhaps more common. No sharp line, however, can be drawn between the finer and the coarser mosaics. Moreover either can put up a shoot which is wholly normal, or wholly red, as the case may be. I have the impression however that the normal shoot is more often to be found in plants of the coarser mosaic type.

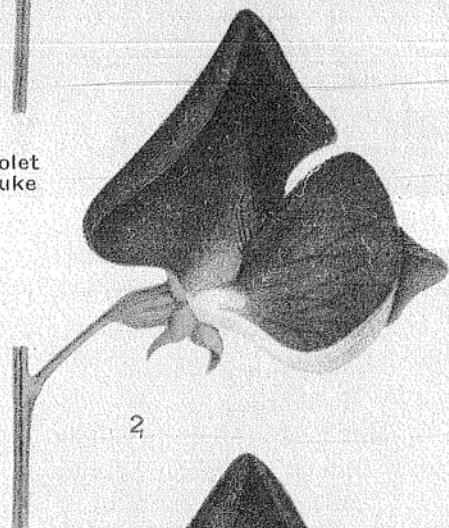
Red
Duke



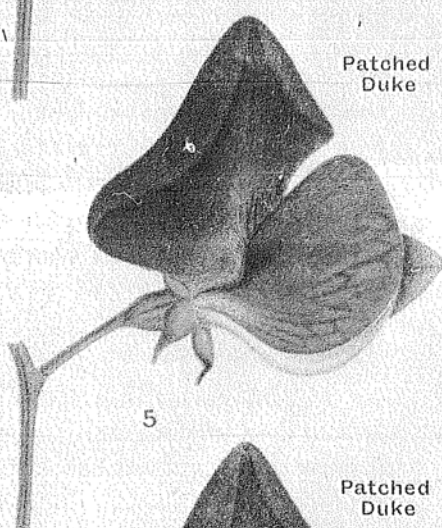
Duke of
Westminste



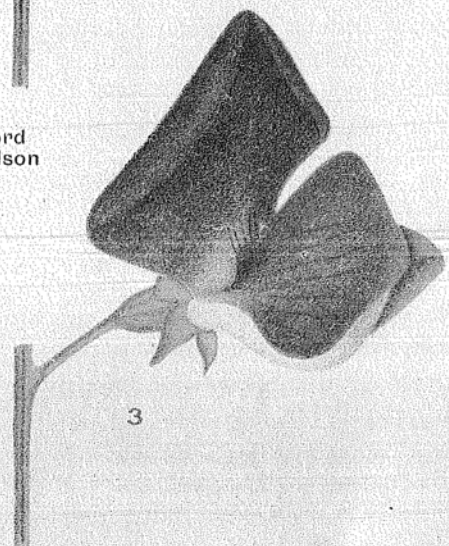
Violet
Duke



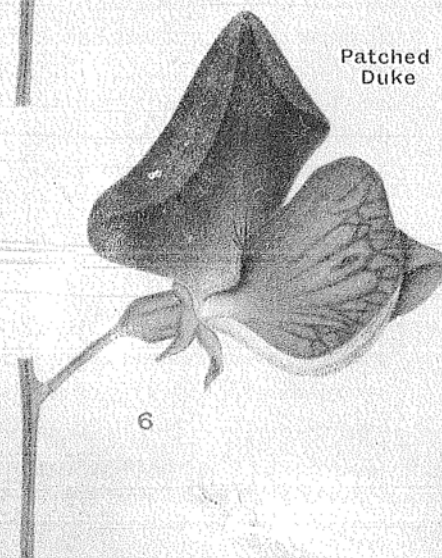
Patched
Duke



Lord
Nelson



Patched
Duke



In general habit of growth the patched plant is intermediate between the red and the normal, tending however more towards the red, a point easily noted in families where all three kinds appear. When, however, a shoot bearing only normal flowers arises on a patched plant, the habit of that shoot is the habit of the normal flowered plant. With its normal purple flowers, more luxuriant habit, and brighter green colour, such a shoot offers a striking contrast to the rest of the plant.

Brief outline of the case.

In its main features the genetic behaviour of the normals, reds, and patched arising from patched plants may be summarized as follows:

(1) *Normals* give either

(a) Normals only.

(b) Normals and reds in the ratio 3:1.

(c) Normals, reds, and patched. In such families the proportions are irregular, but there is almost always a considerable excess of normals over the other two classes taken together.

(2) *Patched* give all three kinds in irregular proportions¹, but the reds and patched together are almost always considerably in excess of the normals.

(3) *Reds* give either

(a) Reds only².

(b) All three kinds. When this is the case the proportions are similar to those arising from patched plants, and I regard such reds as, in all probability, patched plants in which the patching is so reduced as to have escaped notice.

Such, in its barest outline, is the nature of the case. It will be found substantiated by the data given below, and is introduced here to enable the reader to grasp more clearly the fuller account that follows. Since the mode of origin of the red and of the patched forms has a bearing upon their interpretation, we may commence our analysis with what is known of it.

Earlier History.

In 1903 a cross was made between the two whites Emily Henderson (round pollen) and Blanche Burpee (long pollen). The F_1 plants, grown in 1904, were normal P. I. in appearance. In one of the F_2 families raised

¹ With one exception in which only reds occurred (cf. p. 272).

² Occasional normals or patched may appear in families which are almost entirely composed of reds. I am inclined to regard these as rogues due to insect agency.

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in 1905 it was recorded that several of the purples had a reddish tinge, but beyond noting the fact no further attention was paid to it at the time. From a normal P. I. sister plant, 309⁹/05, was raised the family 305/06 (see Pedigree, p. 261). It consisted of purples, reds and whites. Of the 59 purples, 54 were normal, while the remaining 5 were patched. From one of the latter came Fam. 66/07 which consisted of 7 plants only. One of these is recorded as a red purple with a normal branch, and another as a Red Duke. No note was made of the rest. The Red Duke may have been a patched plant with a small amount of patching, for at that time so few red plants had been seen that we were not conversant with the material. The Red Duke, 66¹/17, was used as pollen parent in a cross with 93³/07, a plant belonging to a pure Ppw. strain, and the three F_1 plants raised in the following year (40¹⁻³/08) were recorded as being "reddish P. I."¹

Here the matter rested for three years. At that period Mr Bateson and I were busy working at the problem of repulsion and coupling, and had neither time nor space to spare for other material. It was for this reason that nothing had been done with the Red P. I. story beyond the few observations recorded above. When, in 1911, it fell to my lot to continue the sweet pea work alone, I decided, among other things, to look into the case more fully. The only material existing consisted of the seeds of the 2 F_1 plants from the cross with Ppw. above mentioned. From these were reared the 2 F_2 families, 63/11 and 64/11, forming the starting point of the series of experiments tabulated in Tables I—IV and the accompanying pedigree.

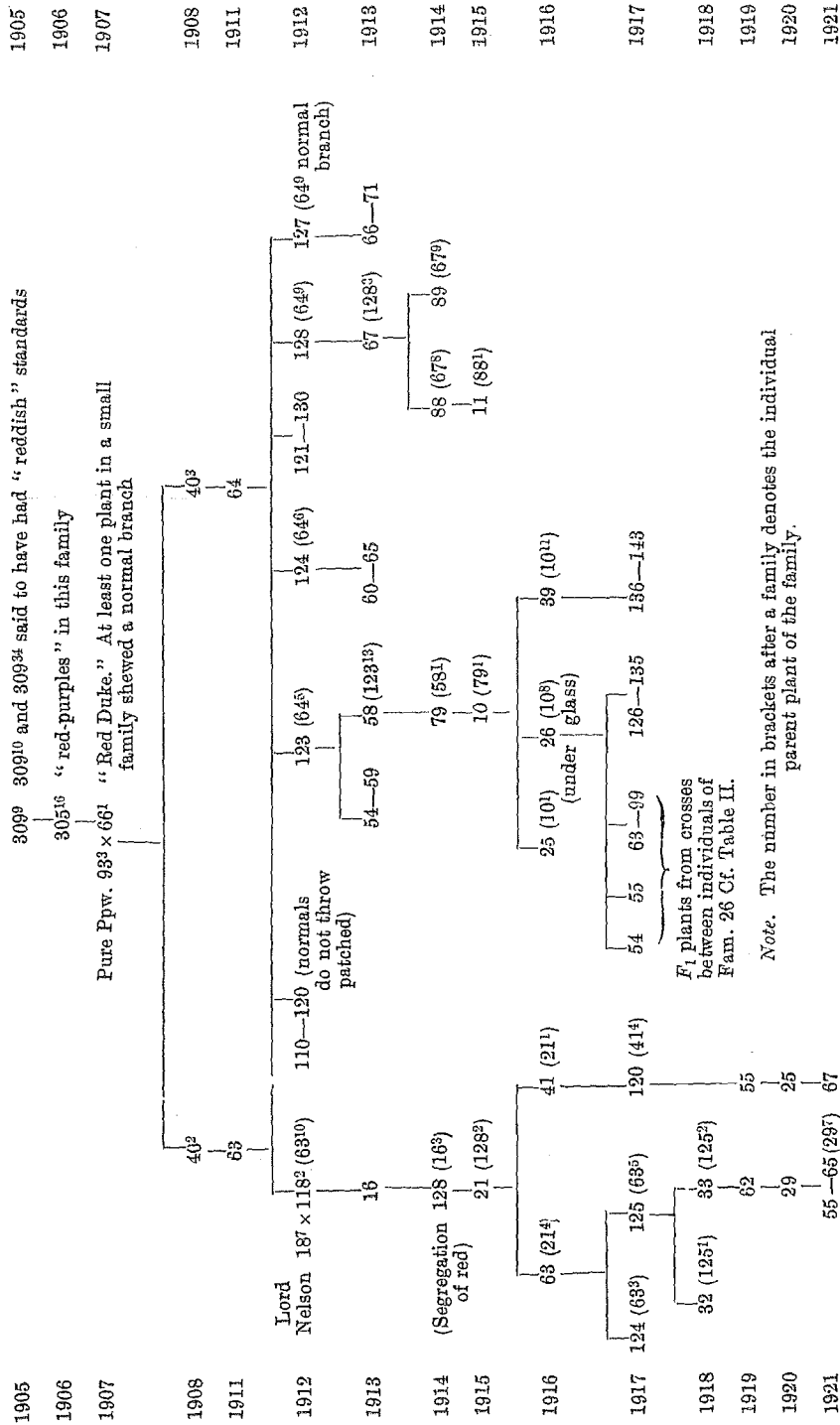
ACCOUNT OF THE EXPERIMENTS.

A. *The main series.*

The two F_2 families proved to be not dissimilar. In each there was an excess of normals accompanied by a small proportion of plants recorded as "patched" and "red." The numbers for 63 were 76 normal, 3 patched and 4 red: for 64, 40 normal, 4 patched and 3 red. In 1912 an F_3 generation was raised from 20 of these F_2 plants (cf. Table I)². Of the 9 normals tested 7 bred true, while 2 gave only normals and reds in the ratio 3:1. This clearly pointed to the existence of a pure red

¹ My recollection of the meaning attached to this term is that it denoted a purple in which the wings were not so blue as in the normal. They were far removed however from the "red P. I." itself.

² These families will be found set out in tabular form on p. 273.

Pedigree.

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behaving as a simple recessive to the normal. Of the five patched plants tested all gave normals, patched, and reds. In 4 families the patched and reds, taken together, were in excess of the normals, a relation which later experiments shewed to be generally true. In one family (124/12) the normals were considerably in excess, an aberrant result which is referred to later on p. 271. Of the six plants classed as reds, five behaved similarly to patched plants, giving all three classes with the reds and patched in excess. Genetically these reds were evidently of the same nature as the patched. One of them, viz. 64⁹/11, was a red bearing a normal branch, and for this reason should perhaps have been more appropriately classed as a patched. The seeds of the normal branch were harvested separately from those of the rest of the plant, and in 1912 were sown as No. 127, the remainder as No. 128. Each sowing gave a similar result. This point will however be gone into in more detail later on. One red plant (63¹⁰/11) gave a family consisting only of reds viz. 118/12. Of these one plant, 118²/12, was used for crossing with Lord Nelson and provided the basis of a set of experiments which will be dealt with below (p. 263). From individuals of the F_2 family, 64/11, the main series of experiments was carried on until the F_8 generation was reached in 1917, when it was brought to an end with families 126–143. The details can be readily gathered from a study of Table I in conjunction with the pedigree. The data so obtained serve to demonstrate the existence of the six different kinds of plants already set out on p. 259.

B. *Data from crosses inside the "red" families.*

In 1916 the seeds of a patched plant, 10⁸/15, were sown and raised in pots under glass. They gave a small family 26/16 consisting of 2 normals, 8 patched, and one red. During their flowering period in the greenhouse various crosses were made between these different plants. Of the successful fertilisations the nature and results are set out on Table II. Where patched plants were concerned note was made as to whether the particular flower used in each instance was normal, patched or red. The results will be discussed below (p. 266) in considering the question whether the different kinds of flower on a patched plant differ in their genetic behaviour.

In 1917 the seeds of 10 of the 11 plants of Family 26 were sown in the open. Neither of the two normals proved to breed true. There was however a marked difference in the proportion of normals that they produced. This proportion was very much higher in the case of 26⁴

(cf. 129/17) than of 26¹ (cf. 126/17). To this point we shall return later. The patched plants behaved as expected, while the red (26²/16), though giving but six plants, bred true (127/17). That 26² was a true-breeding red is confirmed by the results of the F_2 generation raised from it when crossed by its two normal sister plants. Ten families of this breeding were grown in 1918, and, as Table I shews, nine of them exhibited a clean segregation between normal and red. The appearance of patched plants in the remaining family, 47/18, is doubtless to be traced to the normal parent, 26¹/16, which had been shewn to throw all three classes.

In 1918 and 1919, the seeds of a number of the F_1 plants were sown, and the results are recorded in Table II. We need only say here that they are consistent with the data obtained in the main series of experiments.

C. Data from crosses with unrelated normals.

The Red Duke, devoid of patches, made an undoubted appearance in 1911. One such plant in the F_2 family, 63/11, was grown on in the following year to produce a small family consisting only of reds (118/2). A cross was made between one of these reds (a red D. S.) and Lord Nelson. From the F_1 D. S. plants was raised an F_2 generation shewing clean segregation of the red from the normal purples. Corresponding to D. S. were deep red Dukes such as that figured on Pl. XXI, fig. 1, while among the blues the red class was represented by the Violet Duke (Pl. XXI, fig. 2), a distinct colour hitherto unrecorded in the sweet pea. The close approximation to a 3:1 ratio indicated a case of simple segregation, red behaving as recessive to normal (cf. Table III, p. 281). No patching was seen on any plant belonging to the red class. A Red Duke (128²/14) saved from one of these F_2 families (cf. Pedigree) subsequently gave rise to the stock used in further crossing experiments. The details of these may be readily gathered from Table III in conjunction with the pedigree. The results in most cases indicate simple segregation as in the Nelson cross, but in three cases there is a record of a single patched plant, while in another cross (Red D. \times E. H. round) no less than 12 patched plants appeared among 104 purples. This last case is certainly aberrant, but it is doubtful whether much stress can be laid on it. For the white parent (43¹/16) was a lineal descendant of the Emily Henderson strain used in the original cross of 1903, and it is not impossible that the patched character may have been introduced similarly in the two instances. Certainly we are not entitled to make

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use of it as evidence of the failure of the purity of the Red Duke parent. And this is also the case for the 1918 cross, R. White \times Helen Pierce¹, where a single patched plant occurred in a small family. There remain the two other exceptions. Ought we to regard them as real exceptions involving some process of segregation different from what we are accustomed to regard as normal, or should we look upon them as due to an accidental cross-fertilisation due to insect agency? For patched plants were growing in the garden alongside of these F_1 plants, and *Megachile* is always with us. It is not impossible that the single patched plant arising in F_2 from the cross Red Duke \times M. H. hood may owe its origin to this cause. Fortunately, however, the circumstances are such as to allow of our arriving at a definite decision in the case of the last remaining exception, viz. that from the cross Red Duke \times Helen Pierce. The F_1 plants were D. S., and in F_2 appeared the four colour varieties D. S., Nelson, Red Duke, and Violet Duke, together with their respective marbled forms. Now the single patched plant that made its appearance was *marbled*. The only marbled plants growing in the garden where these F_1 plants were setting seed were Helen Pierce: the only plants carrying marbling were certain F_1 plants derived from crosses with Helen Pierce. Helen Pierce has never produced a patched or a red plant; nor has such a thing occurred in the F_2 of any of the crosses with Helen Pierce. Hence the single patched plant in F_2 cannot be attributed to what we may term a red patched marbled gamete brought by *Megachile* from some other plant. We are forced to regard it as having arisen through some process of imperfect segregation in the parent plant. Moreover the strong evidence that exists for this particular plant must render us willing to admit that something of the nature of imperfect segregation may also underlie the other exception dealt with above.

Apart from these exceptional patched plants the result of the out-crosses with Red Duke clearly suggests a single factor difference between the red-purple and the normal purple classes. In a total of over 2000 F_2 plants a 3:1 ratio is closely approximated to.

D. *The Red Duke line.*

The Red strain isolated in family 118/12 was accidentally allowed to die out. Another strain was however established from an F_2 plant,

¹ A blue hooded marbled form. Marbling is recessive to self colour, and Helen Pierce behaves as a recessive to Lord Nelson.

128²/14, which arose from the 1912 cross between Lord Nelson and 118². The subsequent history of this strain, which is shewn in the pedigree, presents a point of interest, in spite of the fact that all of the plants in it proved to be shy seeders. In 1916 the line was duplicated. Of the one branch (Ex. 21¹/15) five generations have been grown to date. The total number of individuals only amounts to 35, but all have been clear reds with no indication of any patching. In the other branch however (Ex. 21⁴/15), which has been grown on for six generations, patched plants have occurred. Family 124 of 1917 consisted of 9 plants. On a single flower of one of these plants occurred a patch of purple which covered about one third of one of the wings. Unfortunately it was not found possible to save seed from any member of this family. No further indication of patching occurred in the line until 1920 when two patched plants made their appearance in a small family of seven (No. 29). Here the parent (62/19) was a Violet Duke, a fact of importance in helping us to decide upon the origin of these two patched plants. In 1919 there were numbers of patched plants growing in the garden. But all of these belonged to what we have termed the main series of experiments, all of the plants of which were homozygous in D. Had the two patched plants from 62/19 been due to insect agency they must have been red-purples—not violet. The evidence clearly points to their spontaneous origin from 62/19. It may be added that the patching in these two plants was pronounced and of a coarse type. One of them bore a full blue branch of which further mention will be made below.

SPECIAL POINTS.

A. *The genetical behaviour of the different kinds of flowers on patched plants.*

In any attempt to formulate views as to the nature of the patched plant, one is at once met with the question whether the mosaic arrangement of the colours indicates an irregular distribution of the corresponding genetic factors in the germinal tissue. Do normal flowers on patched plants tend to produce a higher proportion of normals than do patched flowers? The facts that may contribute to a decision fall into two groups, and are as follows:—

(1) In four cases where a patched plant has put up a normal branch, the seeds of that branch have been harvested separately from those of the rest of the plant. These plants are:

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		N.	P.	R.	N.	P.	R.
64 ⁰ /11	{normal branch ...	2	9	10	—	—	—
	{red branches ...	—	—	—	13	19	36
66 ² /17	{normal branch ...	6	1	3	—	—	—
	{patched branches...	—	—	—	6	4	25
97 ¹ /17	{normal branch ...	1	4	4	—	—	—
	{patched branches...	—	—	—	—	3	2
297 ⁷ /20	{normal branch ...	3	10	15	—	—	—
	{patched branches...	—	—	—	1	8	3
Totals ...		12	56		20	100	

I.e. normal branches give ... 17·6 % normals
red and patched branches give 16·6 % „

The data afford no ground for supposing that normal branches of a patched plant exhibits any constant genetical difference from the rest of the plant.

(2) Crosses were made in 1916 between normal and patched members of the same family (26), in which the nature of the flower used from the patched plant was recorded. The two sister normal plants used, viz. 26¹/16 and 26⁴/16, were subsequently shewn to give a markedly different result on selfing, and must therefore be considered separately. The data, which are given in full in Table II, may, for our present purpose, be summarized as follows:

(a) Crosses between 26¹ (a normal which gave 10 N.: 6 R. + P.) and different sorts of flowers from various sister patched plants.

		N.	P.+R.
Normal flowers gave	...	10	7
Patched „ „	...	28	14
Red „ „	...	5	6

(β) Crosses between 26⁴ (a normal which gave 17 N.: 1 P.) and different sorts of flowers from various sister patched plants.

		N.	P.+R.
Normal flowers gave	...	2	1
Patched „ „	...	13	5
Red „ „	...	7	0

These figures shew that the three sorts of flowers tend to behave in the same way. In spite of irregularities there is no indication of any excess of normals when normal flowers were used as compared with patched; nor again when patched flowers were used as compared with red. In other words, there are no grounds for supposing that the normal, patched, and red flowers on a patched plant differ genetically from one another.

B. *The genetical behaviour of earlier and later ripened seed.*

It is conceivable that in the cell divisions of a mosaic plant a process may occur whereby the more distal parts of the germinal layer may come to differ genetically from the more proximal. The possibility was tested in the case of one plant, 29⁷/20, by saving separately the seed of each flowering stem on the normal branch (cf. p. 265). The pods set well, but the final result is meagre owing to the numerous casualties from the drought of 1921. Such as it is, it is set out in Fig. 1, and offers no suggestion of any regular genetical differentiation with the age of the stem.

Some further observations bearing on the point are given in Table I. From three large normals in Fam. 40/20 the ripe seeds were taken at intervals, the first gathering being made some three weeks earlier than the second. In the case of one plant (40⁹) five gatherings were made, the last being in October. Only fully ripe seeds were taken, some of those ripening between the successive gatherings being naturally shed and

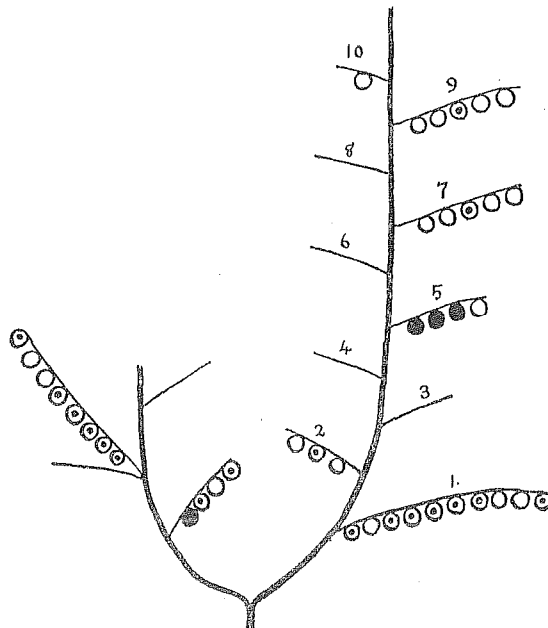


Fig. 1. Diagram of 29⁷/20. On the left a patched branch; on the right a normal-flowered branch. Seeds giving rise to normal flowered plants shewn black; seeds giving rise to patched plants shewn as ○; seeds giving rise to red plants shewn ○. The order in which the seeds are shewn on the flowering stem is imaginary.

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lost. The data may be regarded as rough samples indicating the nature of the germ plasm at different stages in the history of the plant. It cannot however be said that they reveal any indication of definite change in the nature of the germ plasm in the later, as compared with the earlier stages of its growth.

C. On the proportions of red, patched, and normal plants produced by individuals of the three kinds.

Although the data are too scanty for adequate statistical treatment they offer nevertheless some interesting points for discussion. The first question which it is natural to ask is whether there is any evidence of regularity in the proportions of the three kinds of plants, reds, patched, and normals, when they occur together in mixed families. This may be attempted on the data given in Table I. Not all of these data are suitable for treatment in this connection, for many of the families are unfortunately too small to allow of our attaching much meaning to the proportions in which the three sorts occur. For this reason we shall consider only families containing 20 or more plants. Again, the records refer in large measure to plants which were small and imperfectly developed owing to adverse conditions. In extreme cases the individual had to be classified on a single flower, and often on but a few. Though there is no mistaking a normal, it is, under these circumstances not possible to be certain that a plant classified as a red should not more properly have been placed in the patched class. For the history of some plants that were kept under critical observation shewed that an individual may sometimes start as a red, and later on come to have a fair proportion of patched flowers, or even a normal branch. Moreover, as is evident from Table I, a plant classified as a red may, in its breeding behaviour, be indistinguishable from a patched. Doubtless many plants classified as reds ought really to be regarded as patched plants in which the flecks of normal colour are very much reduced. No parallel difficulty arises in the case of the normals, for I have never seen a normal with flecks of red. While red and patched grade insensibly into one another, the distinction between patched and normal is always unmistakeable. In the following paragraphs therefore I have taken account only of two groups of plants, viz. reds and patched taken together, and normals.

For the construction of Fig. 2 there were available 56 parents which arose in mixed families and gave all three kinds among their progeny¹. Of these 20 were normals (Fig. 2, A), 20 were patched

¹ These families are all marked by an asterisk in Table I.

(Fig. 2, B), and the remaining 16 were reds (Fig. 2, C). In each of these 56 families the percentage of reds and patched taken together was calculated, and these percentages are plotted in Fig. 2. Here the percentage in each family is shewn separately, and grouped according as the parent was (A) normal, (B) patched, or (C) red. With the exception of one aberrant family (No. 111/19), all the families produced by

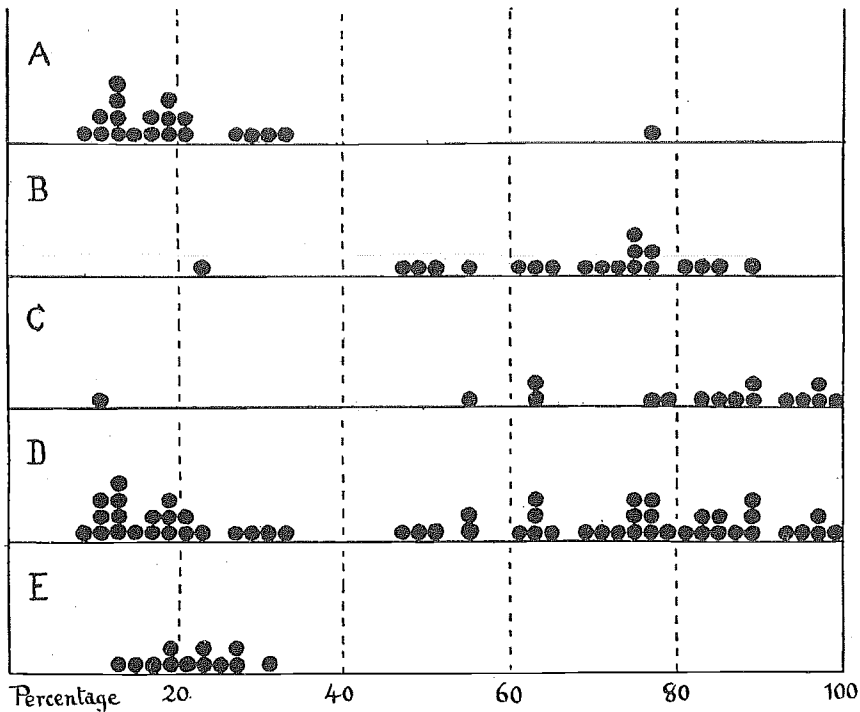


Fig. 2. Shewing percentage of reds and red-patched, as opposed to normals, in families from (A) normals, (B) red-patched, and (C) red parents. D is combined from A, B, and C, and shews families in which the three kinds of plants appeared, irrespective of their parentage. E shews percentage of reds where only normals and reds occurred. The data are derived from Table I. Only families containing 20 or more plants have been made use of.

normals agree in having a low percentage of reds and patched, varying from 10–33 %. The total number of reds and patched in the 20 families was 199, and of normals 876; so that the average percentage of normals is 18.5 %. This is distinctly below the 25 % characteristic of a simple recessive relation, such as occurs in families where normals and reds alone are found. Sixteen such families are shewn in Table IV, and the percentage of reds in those with 20 or more individuals is also plotted

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in Fig. 2, E. Though the proportion of reds and patched in A is lower than that of reds in E, the range of variation is not widely dissimilar in the two cases.

When however we turn to families derived from patched we find a very much wider range of variation (Fig. 2, B). But except for one aberrant family (124/12) the proportion of reds and patched hardly drops below 50 %, while it may rise to almost 90 %. Out of a total of 855 plants in these 20 families 574 are red or patched, i.e. 67 %. The range of variation is here very considerable.

There remain the 16 families from red parents. Some of these may be closely matched by families derived from patched plants. In others however the proportion of patched and normals is very low, and it is not impossible that in such cases we may be dealing with rogues, due to *Megachile*, in families of pure reds. Taken as they stand however the families from reds (Fig. 2, C) resemble those from patched in their wide range of variation, though, on the whole, the proportion of reds and patched is higher. The 16 families comprised 708 plants, among which were 109 normals, giving an average of 77 % of reds and patched.

A point which seems to emerge from this necessarily inadequate analysis is that the patched plants can hardly be regarded as all constituted alike genetically. The proportion of normals produced even by sister plants (cf. 57 and 58 of 1913) differs too widely, and to these differences attach even greater weight when it is remembered that there is no evidence of a genetical difference being associated with a preponderance of normal coloration in the mosaic (cf. p. 266). On the other hand we must not lose sight of the possibility that the germinal layer may also be constituted as a mosaic, and that the germinal mosaic may be independent of the epidermal mosaic which is rendered visible through colour difference. An unusually high proportion of normals from a patched might conceivably be due to the higher prolificness of a branch in the germinal mosaic in which the factors making for normal were preponderant. A difference in the proportion of normals produced by two plants might depend upon the manner in which this mosaic happened to develop. In some plants a "normal" germinal covering of the flowering shoots might, through accidents of growth, preponderate more than in others. Such patched plants would throw a higher, and even a considerably higher proportion of normal offspring, than other patched plants in which, through accidents of growth, the greater part of the germinal layer consisted of the portion lacking in the factors for normal. Yet all may have started as similar zygotes. The point might

be tested by harvesting separately the separate branches of a number of patched plants. The data on p. 266 are obviously too few for testing the point.

The great range of variation for the patched and red plants, as brought out in Fig. 2, B and C, obviously points to a gametic output which differs quantitatively in different plants. For the normals the range of variation (Fig. 2, A) is much smaller, and not very markedly different from that shewn by plants where the relation between normal and red is that of ordinary dominant and recessive (Fig. 2, E). Nevertheless there is other evidence to shew that the normals which give rise to normals, patched, and reds, must often differ quantitatively in their gametic output.

In the series of crosses made between the various members of Fam. 26/16 (see Table II, p. 280) two different normals were made use of, viz. 26¹ and 26⁴. The selfing of these two plants (see Table I) resulted in a very much higher proportion of normals from the latter. The inference that the normal output of gametes was higher in 26⁴ is borne out by the behaviour of these two normals on crossing. Crossed with 26², a pure red, 26¹ gave 16 normals, 2 patched, and 6 reds, while 26⁴ gave 9 normals and 2 reds. Crossed with various patched plants in the same family 26¹ produced 43 normals, 24 patched, and 3 reds, while 26⁴ gave 22 normals, 4 patched and 2 reds. Whether selfed, crossed with red, or crossed with patched, 26⁴ consistently gave a much higher proportion of normals than did 26¹.

There remains, in connection with the data represented on Fig. 2, the question of the three aberrant plants, one of which occurred in each of the three groups A, B, and C. The exception in A is a family with an unusually high proportion of reds and patched (111/19) from a normal parent. A conceivable explanation is that the parent was genetically a patched. Patched plants often throw up one, or even more, normal branches. It is not impossible that a small plant, such as the parent of this family was, may shew only normal flowers. Such a plant would be genetically a patched, putting up one or more normal branches, as any patched may do, but failing to develop flowering stems from the non-normal part of the mosaic. On the other hand the exception in B, where a patched plant (64⁸/11) produced a family (124/12) with a great excess of normals, is harder to account for. I can only suggest that it may be an extreme instance of preponderance on the part of the normal portion of the germinal mosaic in the region of the flowering stems. Of the authenticity of the last exception (139/17) in which a red gave a high

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proportion of normals I am doubtful. For in 1916 the seeds of some plants were collected by my gardener, and among them was 39¹⁸, the parent of the family in question. I detected one certain error of labelling among the seed so taken, and for this reason I have never been satisfied that the present aberrant result may not also be due to some mistake.

D. *The formation of "pure" gametes by plants giving mixed families.*

That the patched plant must be regarded as producing some "pure" normal, and some "pure" red gametes is evident from a study of Table I. For example 39/16 contained 7 normals out of a total of 32 plants. Of these 7 normals 5 were grown on in the following year. Two of them, viz. 39³ and 39¹⁰, gave families consisting respectively of 29 (137/17) and 61 (138/17) normals. The numbers are in each case sufficiently large to make it fairly certain that we are dealing with true-breeding normals in each case. Other examples of the origin of such normals are to be found among the crosses undertaken in 1916 among the members of Fam. 26. Thus Fam. 90/19 arose from a normal (63⁶) that was produced by fertilising a patched plant with a normal (cf. Table II). Since it produced only normals to the number of 84 we are justified in regarding it as a true-breeding normal, and in supposing that the gamete from the patched parent (26⁶) was a normal one. So also a patched plant gives rise to "pure" red gametes, for from such plants may be derived true breeding recessive reds such as 26²/16. From patched plants too may come normals which give normals and recessive reds only. 60/13 and 65/13 are examples of this. Moreover, there is the peculiar case of 41 + 42/18. The parent of this family was a patched plant (96²/17) derived from the fertilisation of a purple flower on a patched plant (26¹¹/16) by the pollen of a pure red (26⁴/16). It was a patched plant with a pure red branch. The seed from the red branch was sown separately and gave 25 reds; that from the patched portion gave 5 reds. All of the plants were unfortunately small and failed to set seed satisfactorily, so that the matter could not be followed up. Nevertheless we have here an undoubted case of a patched plant from which only reds were recorded. It is conceivable that some of these reds, under more favourable conditions of growth, would have developed into patched plants to give a family similar to 34/13. Still we can hardly help inferring that 96²/17 was producing a high proportion of "pure" red gametes.

In connection with the proportion of normal gametes produced by normals occurring in families with a large excess of normals, the F_2

families from the 1908 cross between Ppw. and Red Duke are of interest. The details are set out separately in tabular form below:

Fam. 63/11, Ex. 40²/08, a normal which on selfing gave

N., 76 : P., 3 : R., 4.

11 F_2 plants tested by growing on to F_3 , viz.:

	Normals							Patched		Reds	
1911 nos.	63 ²	63 ³	63 ⁴	63 ⁵	63 ⁶	63 ¹¹	63 ¹²	63 ⁷	63 ⁹	63 ⁸	63 ¹⁰
1912 nos.	110	111	112	113	114	119	120	115	117	116	118
Result N.	15	25	10	30	23	40	32	7	4	3	—
P.	—	—	—	—	—	—	—	5	2	2	—
R.	—	—	2	—	—	—	12	12	6	19	12

In this family out of 7 F_2 normals tested, 5 bred true, while 2 gave only normals and reds. None of the normals tested produced a patched plant. This may have been an accident, but in any case it is evident that we must suppose such plants to have been producing a high proportion of normal gametes.

Fam. 64/11 Ex. 40³/08, a normal which on selfing gave

N., 40 : P., 3 : R., 4.

9 F_2 plants tested by growing on to F_3 , viz.:

	Normals		Patched				Reds		
1911 nos.	64 ²	64 ³	64 ⁶	64 ⁷	64 ⁹	64 ¹¹	64 ⁵	64 ⁸	64 ¹⁰
1912 nos.	121	122	124	125	{127} {128}	130	123	126	129
Result N.	30	39	32	6	15	5	8	3	8
P.	—	—	4	11	28	13	18	6	13
R.	—	—	6	8	46	3	13	12	1

The interesting point is that of the 9 F_2 normals tested in these 2 F_2 families where patched occurred, 7 bred true, while 2 gave only normals and reds. None of these normals produced a patched plant. This may have been an accident, but in any case it is evident that we must suppose such plants to have been producing a high proportion of normal "gametes." As shewn in Table V some of the normals arising in mixed families breed true, but the proportion here indicated—viz. 4 out of 20—is very much smaller than in the case of the 2 F_2 families referred to above. The facts suggest that true breeding normals are much more likely to occur in mixed families where the proportion of normals is unusually high, than in families where it is markedly lower.

DISCUSSION.

The case of the patched sweet pea naturally challenges comparison with the other cases in which the genetics of mosaic flower colour have been investigated, notably in *Antirrhinum*, *Primula*, and *Mirabilis*. In maize, too, a case of somewhat similar nature was described some years ago by Emerson, where the patch-work affected the colour of the pericarp. As these various cases all present peculiar features it will be convenient to consider them separately.

Gregory's¹ work suggests that the flaked *Primula* breeds true, but this is based more upon the behaviour of the flaked forms on crossing, than upon the offspring of flaked plants themselves. He does not, however, give any records of self-coloured flowers arising from flaked plants. Certainly a close parallel cannot be instituted between the *Primula* and the sweet pea, and Gregory was able to symbolise his results on a simple factorial scheme.

Emerson² shewed that in maize the variegated throws some reds, but no non-reds, while the proportion of reds thrown by the variegated depends upon the amount of red in the variegated grains. The reds so formed behaved as heterozygotes between self-red (dominant) and variegated (recessive), and in later generations homozygous self-reds were established. Though the amount of colour in some of the variegateds was much less than in others, no completely uncoloured head was produced.

The much discussed case of de Vries' striped *Antirrhinums*³ presents many features in common with Emerson's maize. Here again the striped throw a variable, though relatively small proportion of self-red, while the self-reds so produced behave as heterozygotes between self and striped. It is true that de Vries did not obtain a homozygous red, but this was evidently due to his not having tested the offspring of the self-reds which sprang from the striped⁴. As with the maize, no

¹ *Journal of Genetics*, Vol. I. 1911, p. 121.

² *Amer. Nat.* Vol. XLVIII. p. 191.

³ *Die Mutationstheorie*, Vol. I. 1901, p. 494; Vol. II. 1903, p. 351. *Species and Varieties*, 1905, p. 315.

⁴ In some experiments with a striped strain of *Antirrhinum* I have recently produced homozygous reds in a manner analogous to that in which Emerson produced his homozygous red maize. Some reds arising from a self-fertilised red branch on a striped plant proved to be heterozygous, striped being recessive to self-colour. On self-fertilisation such reds produced striped, heterozygous reds, and homozygous reds in the expected proportions. I hope later to publish a fuller account of these and other experiments with the striped *Antirrhinum*.

completely uncoloured individual appeared during the course of the experiments. A further point of resemblance between these two cases is that the variegated maize appears to behave as a simple dominant to white, and, except for the production of a few reds, the striped *Antirrhinum* appears to behave similarly towards the colourless form¹. The schemes of inheritance for *Antirrhinum* and for maize appear to be similar, though presenting points of difference from that for *Lathyrus*.

There remains the case of *Mirabilis*. Miss Marryat came to the conclusion that "though flaked forms occasionally throw self-coloured individuals, this phenomenon is so irregular that its significance is quite uncertain²." In the following year Correns³ published his interesting account of the behaviour of the striped forms in this species. He found that *striata* plants did not, as a rule, breed true, but gave a small percentage ("0 bis 10 und mehr") of *rosea* plants with self-coloured flowers. When, as at times happened, *rosea* branches appeared on *striata* plants, such branches, on self-fertilisation, behaved as *striata* branches, though the proportion of *rosea* plants produced tended to be rather higher⁴. The *rosea* plants, which sprang from seed, turned out on testing, to be of 3 kinds, viz.

- (a) those which bred true,
- (b) those giving *striata* as recessive,
- (c) those giving *gilva*⁵ as recessive.

¹ Cf. *Die Mutationstheorie*, Vol. II. p. 352.

² *Reports to the Evolution Committee of the Royal Society*, v. 1909, p. 49.

³ *Ber. d. Deut. Bot. Gesell.* Vol. XXVIII. 1910.

⁴ There appears to be some misconception of this case in the accounts given by Bateson and by Baur, for both of these authors state that the majority of the plants raised by selfing the red branches are reds.

"When a plant bears both striped branches and unstriped branches, each type produces offspring which in the great majority resemble itself." *Mendel's Principles of Heredity*, 3rd Imp. 1913, p. 312.

"Alle gestreiften Pflanzen bilden einzelne rotblühende Äste, die weiterhin bei Selbstbefruchtung aufmenden in 3/4 rot : 1/4 gestreift....." *Einführung in die Experimentelle Vererbungslehre*, 3 u. 4 Aufl. 1919, p. 302.

Correns however is explicit in his statement as to the genetical similarity between striped and red branches on the same plant.

"Die *rosea*-Äste geben (als F_1) eine Nachkommenschaft, die ebenfalls aus *striata*- und *rosea*-Pflanzen besteht. Auch das Zahlenverhältnis ist oft annähernd das gleiche wie bei den *striata*-Ästen. Zuweilen kommen aber doch relativ mehr *rosea*-Pflanzen vor, gelegentlich entschieden mehr als bei der Nachkommenschaft der *striata*-Äste desselben Individuums." (*Loc. cit.* p. 426.)

Moreover the scheme he gives on p. 427 is in accordance with his statement.

⁵ I.e. the pale yellow form without any red flaking.

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According to Correns class (c) was very rare. Further, Correns states that occasional *gilva* plants were produced from self-fertilised *striata* (*loc. cit.* p. 426), and that these bred true to *gilva* (*loc. cit.* p. 429). Owing probably to their rarity, Correns lays no stress upon these *gilva* plants, and omits them in the scheme of inheritance that he has drawn up on p. 427. Nevertheless the recognition of their existence allows us to institute a close parallel between the *Mirabilis* and the *Lathyrus* cases. In either case the general scheme of inheritance is the same. In either case we must suppose the variegated plants to be giving off three kinds of gamete, viz. *rosea*, *striata*, and *gilva* in *Mirabilis*; purple, patched, and red in *Lathyrus*. In *Lathyrus* the patched gametes are more numerous than the purple, and much more numerous than the red gametes: in *Mirabilis* the *striata* gametes are much more numerous than the *rosea* gametes, and very much more numerous than the *gilva* gametes. The most noticeable difference between the two cases would appear to be the higher proportion of "flaked" gametes, as opposed to the "pure" ones, that is produced by the flaked *Mirabilis*¹. But in either case the flaked plant produces also two kinds of "pure" gametes, and the relation between these two is the simple Mendelian relation with which we are so familiar.

Although some stress has been laid upon the points of difference between the *Primula*, *Antirrhinum* and maize cases on the one hand, and those of *Mirabilis* and *Lathyrus* on the other, it is yet possible that they may be all fundamentally of the same nature. For as we pass through the series *Lathyrus*, *Mirabilis*, *Antirrhinum*, maize, *Primula*, translating it, so far as we can, into terms of "pure" and "mosaic" gametes, we cannot but notice the gradual increase in the proportion of "mosaic" gametes, with its accompanying diminution in that of the "pure" ones. Further, those of the "pure" gametes corresponding to the recessive form are not only fewer to begin with, but decrease more rapidly than those corresponding to the dominant form. In a crude way the idea of such a conjectural series is illustrated in Fig. 3. Whether *Primula* properly belongs here must depend upon future work with flaked

¹ The statement that in *Mirabilis* one of the classes of *rosea* throws *striata* as a recessive would at first sight appear to constitute a difference from the *Lathyrus* case. For the purple sweet pea that throws patched, throws also a small proportion of reds. I am inclined to regard the difference as more apparent than real, and to suppose that, if a considerable number of offspring were bred from such *rosea* plants, a very small proportion of *gilva* would appear. At present we have no means of testing the probability of this conjecture since Correns does not give the actual numbers of plants bred in his experiments.

forms. If it is rightly placed in the series we should look for occasional self-coloured forms from self-fertilisation of the "flakes"; also, very rarely, for a white.

But whether *Primula*, *Antirrhinum*, and maize fall into such a series or not, it is clear that in *Lathyrus* and *Mirabilis* we have two cases where, in a given strain, a pair of colour characters may either shew a simple Mendelian relation, or else form a mosaic. The most interesting thing about such a mosaic is the nature of its germ cells. Must we suppose that "mosaic" germ cells are formed besides "pure" ones that give ordinary Mendelian phenomena? Or is it possible that only "pure" gametes are formed, and that the "mosaic" is a special manifestation of the heterozygous condition. On this latter view it is

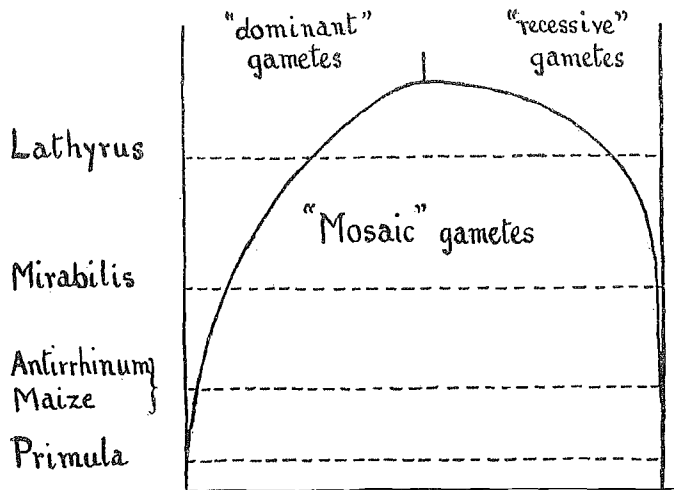


Fig. 3.

clear that the case is one of great complexity. For if we are to interpret it in terms of factors which are located in chromosomes, and segregate at the reduction division, we must explain, not only the difference between the normal and the mosaic heterozygotes, and the fact that either can throw all three kinds, but also the widely variable proportions in which the three kinds appear in different families. Though an interpretation must probably be sought along some such lines if this case is to be reconciled with the widely accepted chromosome theory of heredity, it seems unlikely that this reconciliation will prove to be a simple task.

On the other hand one cannot help being struck by a general similarity between these cases of flaking in flower colour, and certain

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cases where the leaf is variegated¹. Here, as has been pointed out by Baur and others, we must suppose that the hereditary factors, whether in the form of plastids, or of some other cytoplasmic enclosure, are extra-nuclear, and distributed in segregation independently of the reduction division. Indeed, while considering these cases of variegation, Bateson has suggested that even in normal Mendelian heredity, segregation may possibly be regarded as brought about on similar lines, i.e. as "a phenomenon capable of occurring at *any* cell-division, and not merely in gameto-genesis²." The nature of the resultant mosaic, whether coarse or fine, regular or irregular, would depend upon the number of cytoplasmic enclosures which go to make up the "factor," upon the way in which the surrounding protoplasmic medium affected their separation during cell-division, and upon various other circumstances. Ordinary Mendelian heredity would on this view be but a special case, due to the regularity and fineness of the heterozygous mosaic. Whether such a view will prove to be more than a suggestion, and whether it could be extended from plants to animals, further work alone can decide.

EXPLANATION OF PLATE XXI.

Fig. 1. Red D. S.

Fig. 2. Violet D. S.

Fig. 3. Blue (Lord Nelson).

Fig. 4. Normal D. W.

Fig. 5. Patched D. W.

Fig. 6. Red D. W., with a few small flecks of purple on wing (i.e. lightly patched).

For the coloured drawings of the flowers from which the Plate was made I am greatly indebted to the skill and kindness of the Hon. Mrs H. Onslow.

¹ For a recent discussion of such cases, see Winge, Ö., "On the Non-Mendelian Inheritance in Variegated Plants." *Comptes Rendus des Travaux du Laboratoire Carlsberg*, Vol. xiv. 1919.

² *Mendel's Principles of Heredity*, 3rd Imp. 1913, p. 313.

TABLE I.

Parent normal						Parent patched						Parent red					
			N.	P.	R.			N.	P.	R.			N.	P.	R.		
1912	110	63 ²	15 +	—	—	115*	63 ⁷	7	5	12	116*	63 ⁸	3	2	19		
	111	63 ³	25 +	—	—	117	63 ⁹	4	2	6	118	63 ¹⁰	—	—	12		
	112	63 ⁴	10	—	2	124*	64 ⁶	32	4	6	123*	64 ⁶	8	18	13		
	113	63 ⁵	30 +	—	—	125*	64 ⁷	6	11	8	126*	64 ⁸	3	6	12		
	114	63 ⁶	23 +	—	—	{127}* {128}	64 ⁹	15	28	46	129*	64 ¹⁰	8	13	1		
	119	63 ¹¹	40 +	—	—	130*	64 ¹¹	5	13	3							
	120	63 ¹²	32	—	12												
	121	64 ²	30 +	—	—												
	122	64 ³	39 +	—	—												
1913	59*	123 ¹⁴	17	4	3	57*	123 ⁵	36	25	8	54*	123 ¹	13	32	11		
	60	124 ⁴	16	—	4	58*	123 ¹³	6	22	9	68*	123 ⁴	4	9	13		
	62	124 ⁷	12	—	—	67*	128 ³	9	15	13	70*	128 ¹⁰	9	13	3		
	63*	124 ⁹	35	2	7	71*	128 ¹¹	9	20	6	34*	118	—	10	27		
	64*	124 ¹⁰	47	6	7												
	65	124 ¹¹	17	—	3												
	66	128 ²	50 +	—	—												
	69*	128 ⁹	18	4	3												
1914	76	57 ¹	3	—	1	78	57 ³	1	1	2	84	67 ³	6	2	5		
	86	67 ⁶	10	—	2	79*	58 ¹	10	4	6	88	67 ⁸	7	6	5		
						81	67 ¹	4	—	1	90	67 ¹⁰	1	—	5		
						82	67 ²	2	—	2							
						85	67 ⁵	3	2	2							
						87	67 ⁷	1	1	6							
						89	67 ⁹	7	—	3							
1915						10	79 ¹	7	7	1							
						11	88 ¹	—	3	3							
1916						25	10 ¹	—	4	—							
						26	10 ⁸	2	8	1							
						39*	10 ¹¹	7	21	4							
1917	126	26 ¹	10	2	4	128	26 ³	11	1	4	127	26 ²	—	—	6		
	129	26 ⁴	17	1	—	130	26 ⁶	4	(?)	7	139*	39 ¹⁸	32	—	4		
	136*	39 ²	42	3	3	131	26 ⁷	2	6	11	140*	39 ²¹	9	6	5		
	137	39 ³	29	—	—	132	26 ⁸	2	3	—	142*	39 ²⁶	1	5	41		
	138	39 ¹⁰	61	—	—	133	26 ⁹	4	3	3							
	141*	39 ²³	43	3	4	134*	26 ¹⁰	10	10	9							
	143	39 ³¹	6	—	1	135*	26 ¹¹	20	20	6							
1918	35	54 ¹	20	—	4	{39}* {40}	66 ²	13	38	7	46*	72 ¹	2	—	119		
	36	54 ²	21	—	6	{41} {42}	96 ²	—	—	30	50*	81 ¹	3	1	46		
	37	54 ⁴	37	—	11	{43} {44}	97 ¹	1	6	7	51*	81 ²	6	—	55		
	38	55 ²	15	—	7	49*	92 ⁵	24	38	2							
	45	70 ²	19	—	6												
	47*	72 ³	40	12	6												
	48	74 ²	66	—	26												
	52	78 ²	19	—	3												
	53	79 ³	66	—	22												
	54	79 ⁵	40	—	10												

(continued over page)

* Families used in compilation of Fig. 2.

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	Parent normal				Parent patched				Parent red						
			N.	P.	R.			N.	P.	R.			N.	P.	R.
1919	88*	63 ³	16	2	2	83	39 ⁶	9	1	4	92	65 ⁴	—	—	27
	89	63 ⁵	8	—	—	84	39 ¹⁷	3	1	1	95*	66 ⁴	3	5	66
	90	63 ⁶	84	—	—	85	39 ¹⁹	1	1	—	100*	82 ⁶	5	27	17
	91	64 ¹	7	1	—	96	67 ²	—	1	1	102	89 ³	—	—	5
	93*	65 ⁵	25	5	2						103	90 ³	—	—	4
	94*	66 ³	27	2	2										
	97	68 ²	6	1	1										
	98*	76 ³	47	10	2										
	99*	82 ¹	57	8	—										
	101*	82 ³	25	13	—										
	104	91 ¹	13	5	—										
	106*	94 ¹	59	9	—										
	107	94 ³	24	—	—										
	108	94 ⁴	11	2	1										
	109	94 ⁵	20	—	—										
	110	94 ⁷	6	—	—										
	111*	98 ⁴	5	15	2										
112*	98 ¹	25	3	2											
113*	98 ⁵	30	3	2											
114	99 ¹	8	4	—											
115*	99 ⁴	25	3	—											
<hr/>															
1920						40*	106 ¹	31	32	2					
						41*	111 ⁵	32	45	11					
						86*	111 ¹	5	22	8					
<hr/>															
1921	101*	40 ² (a)	47	1	6	55-65*	29 ⁷	4	18	18					
	102*	„ (b)	30	1	8										
	103*	40 ⁵ (a)	12	2	1										
	104*	„ (b)	12	—	2										
	105*	40 ⁹ (a)	48	3	6										
	106*	„ (b)	47	—	7										
	107*	„ (c)	57	—	4										
	108*	„ (d)	26	1	2										
	109*	„ (e)	14	1	—										

* Families used in compilation of Fig. 2.

TABLE II.

1917 No.	Cross (1916 plants)	Nature of Cross	Result			1917 No.	Cross (1916 plants)	Nature of Cross	Result		
			Normal	Patched	Red				Normal	Patched	Red
63	26 ⁶ × 26 ¹	P × N	5	1	—	64	26 ¹ × 26 ⁶	N × P (r)	1	3	—
65	„	P (p)* × N	2	2	1	68	26 ⁴ × 26 ⁶	N × P (p)	2	1	—
66	„	P (p) × N	2	2	1	76	26 ⁴ × 26 ⁷	N × P	5	1	—
67	„	P (r) × N	—	3	—	77	„	„	3	1	—
69	26 ¹⁰ × 26 ¹	P × N	1	—	—						
75	26 ³ × 26 ¹	„	1	—	—	54	26 ¹ × 26 ²	N × R	5	—	—
80	26 ⁷ × 26 ¹	„	7	3	—	55	„	„	1	1	2
82	26 ⁷ × 26 ⁴	„	5	1	2	70	„	„	2	—	1
84	26 ⁹ × 26 ¹	„	1	—	—	71	„	„	3	1	2
85	„	„	2	1	—	78	26 ⁴ × 26 ³	„	3	—	2
86	„	„	1	—	—	79	„	„	6	—	—
87	26 ¹⁰ × 26 ¹	„	1	1	—	72	26 ² × 26 ¹	R × N	2	—	1
91	„	„	3	1	—	74	„	„	3	—	—
92	„	„	2	3	—						
93	„	„	2	1	1	81	26 ⁷ × 26 ³	P × R	3	—	4
94	26 ¹¹ × 26 ⁴	P (r) × N	7	—	—	89	„	P (r) × R	—	—	3
95	26 ¹¹ × 26 ¹	P × N	2	1	—	90	„	„	—	—	3
98	„	P (p) × N	6	2	—	96	26 ¹¹ × 26 ³	P (p) × R	—	2	1
99	„	P (r) × N	4	—	—	97	„	„	—	1	—

* (p) denotes a normal purple flower, and (r) a red flower on a patched plant. In other cases the flower used was a patched one.

TABLE III.

Nature of Cross	Parents	No. of F_1 plants	F_2 Results			Remarks
			Normal	Red. Pur.	Patched	
Lord Nelson \times Red Duke ...	18 ⁷ /12 \times 118 ² /12	4	248	74	—	—
Red Duke \times D. W. Cupid ...	26 ² /16 \times 24 ¹ /16	3	57	27	—	—
Red Duke \times M. H. hood ...	26 ² /16 \times 22 ⁵ /16	5	60	15	1	+ 18 reds
Red Duke \times Ppw. rd. ...	41 ⁴ /16 \times 50 ¹ /16 } 41 ³ /16 \times 50 ¹ /16 }	3	21	9	—	—
Red Duke \times E. H. rd. ...	41 ³ /16 \times 43 ¹ /16 } 41 ³ /16 \times 43 ¹ /16 }	3	74	18	12	+ reds and whites
Red Duke \times Robert Sydenham	63 ³ /16 \times R. S.	7	111	41	—	—
Red Duke \times Helen Pierce ...	120 ¹ /17 \times 100 ⁴ /17 } 120 ⁶ /17 \times 100 ⁴ /17 } 120 ⁶ /17 \times 100 ¹ /17 }	7	433	134	1	—
Helen Pierce \times Red Duke } (Cupid) }	29 ⁴ /18 \times 78 ¹ /18	1	86	16	—	78 ¹ /18 was F_2 plant ex Red D. \times D. W. cupid. (See above.)
R. White \times Helen Pierce } (ex Red Duke) }	27 ³ /18 \times 29 ⁵ /18	1	22	5	1	27 ³ /18 was F_2 plant ex Red D. \times E. H. rd. (See above.)
119/13* + 5 offspring ...	—	34 6	1112 457	339 163	15 —	—
Totals	40	1569	502	15	—
Expectation	1564.5	521.5	...	—

* An F_2 family which doubtless arose from the union of a normal purple cretin gamete with a Red P. I. gamete through insect agency in 1911.

TABLE IV

*Normals giving normals and
reds only.*

		N.	R.
1912	112	10	2
	120	32	12
1913	60	16	4
	65	17	3
1914	76	3	1
	86	10	2
1917	143	6	1
1918	35	20	4
	36	21	6
	37	37	11
	38	15	7
	45	19	6
	48	66	26
	52	19	3
	53	66	22
	54	40	10
Totals ...	397	120	
Expectation	388	129	

TABLE V.

*Families produced by normals
arising in mixed families.*

		N.	P.	R.
1913	59	17	4	3
	60	16	—	4
	62	12	—	—
	63	35	2	7
	64	47	6	7
	65	17	—	3
	66	50+	—	—
	69	18	4	3
1914	76	3	—	1
	86	10	—	2
1917	126	10	2	4
	129	17	1	—
	136	42	3	3
	137	29	—	—
	138	61	—	—
	141	43	3	4
	143	6	—	1
1921	101+	77	2	14
	103+	24	2	3
	105+	192	5	19

Hence out of 20 normals arising in mixed families 4 produced only normals. (Numbers however too small for certainty in 62/13.)
Therefore patched plants must produce a fair proportion of normal gametes.