THE FLAKED SWEET PEA

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(With Plate V and One Text-figure)

Introductory

The flaked variety of sweet pea is well known in horticulture, and certain forms of it, such as the purple "Senator" and the red "America", were regularly offered in seedsmen's catalogues some twenty years ago. Hence when searching for characters with which to test out linkage groups it was natural to choose so distinct a form for purposes of experiment. When crossed with a self-coloured form it gave rise to a self-coloured F_1, and flakes reappeared in F_2. Moreover, in certain crosses there was evident linkage between the flaked forms and the tendril-acacia pair of characters. This led me in 1927 to postulate the existence of a self-flaked pair of characters dependent upon a factor located in chromosome **D**.[1] In this I was mistaken, for, as I pointed out later,[2] the matter was in reality more complex. Further experience revealed three features incompatible with the simple recessive interpretation, viz. (1) a consistent deficit in the 25 per cent. of recessive flakes expected in F_2, (2) a wide range in the grading of the extracted flakes, from the normal light type (Pl. V, fig. 1) up to an almost self-coloured form (Pl. V, fig. 4), and (3) the fact that certain forms of flake gave rise to some self-coloured individuals which thereafter bred true.

It was not until 1931 that I was led to frame the hypothesis now given concerning the genetical nature of the flaked flower, but since it presented certain features without close parallel in the genetics of such things I withheld publication until the matter had been thoroughly tested out. More recently I have made many further experiments which have all served to confirm the hypothesis. In what follows I shall begin with an outline of the hypothesis and then support it by selected data from the contents of my note-books.

Hypothesis

Flaking in the sweet pea depends upon a factor belonging to a series of multiple allelomorphs. The series is self-colour (G_1), flaking (G_1') and white (g_1), the white being the so-called *C*-white of earlier papers.

[1] *Proc. roy. Soc.* B, **102**, 237.

[2] *J. Genet.* **26**, 1932, p. 98.

The flaked character is recessive to self-colour but dominant to white.[1] In its expression the flaked character is influenced by a modifying factor, $\mathbf{D}_3$. A flaked plant ($\mathbf{G}_1'\mathbf{G}_1'$) becomes much darker (*i.e.* nearer to self-colour) when heterozygous for $\mathbf{D}_3$ (Pl. V, fig. 4). When homozygous for $\mathbf{D}_3$ it develops self-coloured flowers indistinguishable from those of a normal self-coloured plant (cf. Pl. V, fig. 5). When the flaked plant carries white, and is at the same time heterozygous for $\mathbf{D}_3$, the flower is darker than that of the normal flake, but not so dark as in the $\mathbf{G}_1'\mathbf{G}_1'\mathbf{D}_3\mathbf{d}_3$ plant. Such $\mathbf{G}_1\mathbf{g}_1\mathbf{D}_3\mathbf{d}_3$ plants have been termed "medium" flakes (cf. Pl. V, fig. 3). Finally $\mathbf{D}_3$, the flake modifier, is linked with the tendril-acacia pair ($\mathbf{D}_1$–$\mathbf{d}_1$), with the bright-dull flower-colour pair ($\mathbf{D}_2$–$\mathbf{d}_2$), and presumably also with the other factors located in the **D** chromosome (cf. *J. Genet.* 1932, p. 101). The various flower forms connected with the flake series may be tabulated as follows.

TABLE I

No.	Genetical constitution	Phenotype	Offspring on selfing
1	$\mathbf{G}_1\mathbf{G}_1$	Self	Selfs only, whatever the constitution in respect of the $\mathbf{D}_3$–$\mathbf{d}_3$ pair
2	$\mathbf{G}_1\mathbf{G}_1'\mathbf{d}_3\mathbf{d}_3$	Self	Selfs and light flakes in the ratio 3 : 1
3	$\mathbf{G}_1\mathbf{G}_1'\mathbf{D}_3\mathbf{D}_3$	Self	Selfs only
4	$\mathbf{G}_1\mathbf{G}_1'\mathbf{D}_3\mathbf{d}_3$	Self	Selfs, dark flakes and light flakes in the ratio 13 : 2 : 1
5	$\mathbf{G}_1\mathbf{g}_1$	Self	Selfs and whites in the ratio 3 : 1, whatever the constitution in respect of the $\mathbf{D}_3$–$\mathbf{d}_3$ pair
6	$\mathbf{G}_1'\mathbf{G}_1'\mathbf{D}_3\mathbf{D}_3$	Self	Selfs only
7	$\mathbf{G}_1'\mathbf{g}_1\mathbf{D}_3\mathbf{D}_3$	Self	Selfs + whites in ratio 3 : 1
8	$\mathbf{G}_1'\mathbf{G}_1'\mathbf{D}_3\mathbf{d}_3$	Dark flake	Selfs, dark flake + light flake in ratio 1 : 2 : 1
9	$\mathbf{G}_1'\mathbf{g}_1\mathbf{D}_3\mathbf{d}_3$	Medium flake	Selfs, dark flakes, medium flakes, light flakes + whites in the ratio 3 : 2 : 4 : 3 : 4
10	$\mathbf{G}_1'\mathbf{G}_1'\mathbf{d}_3\mathbf{d}_3$	Light flake	Light flakes only
11	$\mathbf{G}_1'\mathbf{g}_1\mathbf{d}_3\mathbf{d}_3$	Light flake	Light flakes + whites in ratio 3 : 1
12	$\mathbf{g}_1\mathbf{g}_1$	White	Whites only—whatever the constitution in respect of the $\mathbf{D}_3$–$\mathbf{d}_3$ pair

Experimental

We may now turn to a set of experiments illustrating the manner in which the facts accord with the hypothesis. Since the set chosen extends over four generations it will be convenient to consider it under each of these heads.

F_1. In 1926 a purple light flake was crossed with two self-coloured picotee plants of different origin. One of these ($60^2/26$) came from a family in which whites occurred, the other ($30^7/26$) from a family in

[1] Dominance is here not quite complete, flakes carrying white being on the whole somewhat lighter than homozygous ones. The difference is most easily seen on comparing a row of flakes derived from crossing flake by white with a row of true breeding flakes.

which there were no whites. The F_1 plants from the former comprised 7 self-coloured and 9 flakes; from the latter 16 self-coloured only. This is normal expectation on the assumption that 60^2 (G_1g_1) carried white, and that 30^7 (G_1G_1) did not.

F_2. In the following year (1928) an F_2 family (22/28) was grown from a self-coloured F_1, and an F_2 family (21/28) from a flaked F_1.

On hypothesis the flaked F_1 should be $G_1'g_1D_3d_3$ and should on selfing behave as No. 9 in Table I.[1] At that time the distinction between the grades of flaking was not appreciated, notes on this head being made only on plants from which seed was saved. The flakes must therefore be taken together, in which case expectation becomes 3 self : 9 flake : 4 white. Actual numbers were 15 self, 72 flake and 28 white. The selfs are somewhat below expectation but qualitatively the results accord with hypothesis.

The self-coloured F_1 should be constitutionally $G_1G_1'D_3d_3$ and should on selfing behave as No. 4 in Table I. Actually it gave 119 self-coloured and 26 flakes, expectation being 118 : 27. Although the grade of the flakes was not recorded a note was made to the effect that both dark and light were present, the former being the more numerous. This also accords with hypothesis.

F_3. In 1929 families were raised from four plants of each of the above F_2 families. These F_2 plants with their hypothetical constitution and progeny may be set out as below.

1929 No.	F_2 plant	Constitution	Progeny: Self	Flake	White	Type of family
Ex 21/28:						
6	Picotee flake	$G_1'g_1D_3d_3$	6	19	4	No. 9
7	Purple flake	$G_1'g_1d_3d_3$	—	20	4	No. 11
8	Purple self	$G_1'g_1D_3D_3$	22	—	10	No. 7
9	Purple flake	$G_1'g_1D_3d_3$	5	18	6	No. 9
Ex 22/28:						
10	Picotee self	G_1G_1 or $G_1G_1'D_3D_3$	23	—	—	No. 1 or No. 3
11	Purple self	G_1G_1 or $G_1G_1'D_3D_3$	36	—	—	No. 1 or No. 3
12	Purple self	$G_1G_1'D_3d_3$	22	4	—	No. 4
13	Purple self	$G_1G_1'D_3d_3$	19	4	—	No. 4

All of these families are such as might be expected to appear on hypothesis, as also are the proportions in which the various types make their appearance.

F_4. In 1930 a number of F_4 families were grown on from the two F_3 families 6/29 and 9/29. In both cases the F_2 parent was presumably

[1] Assuming the original picotee parent to have carried D_3, which became evident as the experiment proceeded.

$\mathbf{G_1'g_1D_3d_3}$ in constitution, and in both cases the F_3 family conformed to the type of No. 9 in Table I. By this time a more careful distinction was being made between the grades of flaking, and indeed it was with the idea of ascertaining the extent to which these grades might be genetically different that the F_4 families were raised. The results are given in Table II. In all there are 35 families of which 6 were from F_3 self-coloured and 29 from various flakes. On the assumption that the F_2 parent was in each case $\mathbf{G_1'g_1D_3d_3}$ it should be producing the 4 types of gamete $\mathbf{G_1'D_3}$, $\mathbf{G_1'd_3}$, $\mathbf{g_1D_3}$, $\mathbf{g_1d_3}$ in equal numbers, and the various types of progeny expected are given in Fig. 1.

$\mathbf{G_1'D_3}$ $\mathbf{G_1'D_3}$ Self	$\mathbf{G_1'D_3}$ $\mathbf{G_1'd_3}$ Dark flake	$\mathbf{G_1'D_3}$ $\mathbf{g_1D_3}$ Self	$\mathbf{G_1'D_3}$ $\mathbf{g_1d_3}$ Medium flake
$\mathbf{G_1'd_3}$ $\mathbf{G_1'D_3}$ Dark flake	$\mathbf{G_1'd_3}$ $\mathbf{G_1'd_3}$ Light flake	$\mathbf{G_1'd_3}$ $\mathbf{g_1D_3}$ Medium flake	$\mathbf{G_1'd_3}$ $\mathbf{g_1d_3}$ Light flake
$\mathbf{g_1D_3}$ $\mathbf{G_1'D_3}$ Self	$\mathbf{g_1D_3}$ $\mathbf{G_1'd_3}$ Medium flake	$\mathbf{g_1D_3}$ $\mathbf{g_1D_3}$ White	$\mathbf{g_1D_3}$ $\mathbf{g_1d_3}$ White
$\mathbf{g_1d_3}$ $\mathbf{G_1'D_3}$ Medium flake	$\mathbf{g_1d_3}$ $\mathbf{G_1'd_3}$ Light flake	$\mathbf{g_1d_3}$ $\mathbf{g_1D_3}$ White	$\mathbf{g_1d_3}$ $\mathbf{g_1d_3}$ White

Fig. 1. The type of family corresponding to No. 9 of Table I.

We may now compare expectation on this scheme with the results given in Table II.

(1) *Self-coloured* should either breed true or give self-coloured and white in the ratio 3 : 1. Actually 4 bred true and 2 threw whites.

(2) *Dark flakes* should always throw self-coloured, dark flakes and light flakes in the ratio 1 : 2 : 1. Five dark flakes gave the expected result.

(3) *Medium flakes*. These also should all be of one genetical type, throwing self-coloured, dark flakes, medium flakes, light flakes and whites in the ratio 3 : 2 : 4 : 3 : 2. My experience at that time was not sufficient to make a sharp distinction between the grades of flaking, particularly between the dark and medium grades. Nevertheless in throwing selfs, whites, and various grades of flakes these 12 medium flakes all conformed to hypothesis.

(4) *Light flakes* should either breed true or give light flakes and whites in the ratio 3 : 1, the latter class being twice as numerous as the former. Of the 12 plants tested 10 gave light flakes and whites while 2 bred true.

TABLE II

<table>
<tr><th rowspan="2">Nature of F_3 plant</th><th rowspan="2">No. of F_3 plant</th><th rowspan="2">No. of F_4 family</th><th colspan="5">Composition of F_4 family</th></tr>
<tr><th>Self</th><th>Dark flake</th><th>Medium flake</th><th>Light flake</th><th>White</th></tr>
<tr><td>Self-coloured</td><td>6^1</td><td>32</td><td>30 +</td><td>—</td><td>—</td><td>—</td><td>—</td></tr>
<tr><td>,,</td><td>6^8</td><td>33</td><td>20 +</td><td>—</td><td>—</td><td>—</td><td>—</td></tr>
<tr><td>,,</td><td>6^9</td><td>34</td><td>20 +</td><td>—</td><td>—</td><td>—</td><td>—</td></tr>
<tr><td>,,</td><td>6^{18}</td><td>35</td><td>11</td><td>2*</td><td>—</td><td>—</td><td>3</td></tr>
<tr><td>,,</td><td>6^{20}</td><td>36</td><td>27</td><td>—</td><td>—</td><td>—</td><td>7</td></tr>
<tr><td>,,</td><td>9^1</td><td>53</td><td>32</td><td>—</td><td>—</td><td>—</td><td>—</td></tr>
<tr><td>Dark flake</td><td>6^6</td><td>41</td><td>2</td><td>6</td><td>—</td><td>3</td><td>—</td></tr>
<tr><td>,,</td><td>6^7</td><td>42</td><td>1</td><td>20</td><td>—</td><td>3</td><td>—</td></tr>
<tr><td>,,</td><td>9^9</td><td>58</td><td>7</td><td>26</td><td>—</td><td>10</td><td>—</td></tr>
<tr><td>,,</td><td>9^{13}</td><td>61</td><td>6</td><td>9</td><td>—</td><td>3</td><td>—</td></tr>
<tr><td>,,</td><td>9^{19}</td><td>65</td><td>2</td><td>6</td><td>—</td><td>4</td><td>—</td></tr>
<tr><td>Medium flake</td><td>6^{11}</td><td>43</td><td>3</td><td>6</td><td colspan="2">6</td><td>6</td></tr>
<tr><td>,,</td><td>6^{12}</td><td>44</td><td>4</td><td>12</td><td colspan="2">15</td><td>7</td></tr>
<tr><td>,,</td><td>6^{13}</td><td>45</td><td>5</td><td>2</td><td colspan="2">3</td><td>3</td></tr>
<tr><td>,,</td><td>6^{16}</td><td>48</td><td>2</td><td>—</td><td>1</td><td>—</td><td>3</td></tr>
<tr><td>,,</td><td>6^{22}</td><td>52</td><td>3</td><td>3</td><td colspan="2">8</td><td>4</td></tr>
<tr><td>,,</td><td>9^2</td><td>54</td><td>6</td><td colspan="2">14 —</td><td>9</td><td>11</td></tr>
<tr><td>,,</td><td>9^8</td><td>57</td><td>7</td><td colspan="2">11</td><td>3</td><td>5</td></tr>
<tr><td>,,</td><td>9^{11}</td><td>59</td><td>12</td><td colspan="2">15</td><td>7</td><td>7</td></tr>
<tr><td>,,</td><td>9^{12}</td><td>60</td><td>12</td><td colspan="2">21</td><td>6</td><td>8</td></tr>
<tr><td>,,</td><td>9^{16}</td><td>62</td><td>4</td><td colspan="2">4</td><td>3</td><td>1</td></tr>
<tr><td>,,</td><td>9^{17}</td><td>63</td><td>7</td><td colspan="2">12</td><td>3</td><td>9</td></tr>
<tr><td>,,</td><td>9^{20}</td><td>66</td><td>4</td><td>4</td><td colspan="2">5</td><td>3</td></tr>
<tr><td>Light flake</td><td>6^2</td><td>37</td><td>—</td><td>—</td><td>—</td><td>6</td><td>1</td></tr>
<tr><td>,,</td><td>6^3</td><td>38</td><td>2*</td><td>—</td><td>—</td><td>21</td><td>8</td></tr>
<tr><td>,,</td><td>6^4</td><td>39</td><td>—</td><td>2*</td><td>—</td><td>18</td><td>6</td></tr>
<tr><td>,,</td><td>6^5</td><td>40</td><td>—</td><td>1*</td><td>—</td><td>18</td><td>—</td></tr>
<tr><td>,,</td><td>6^{14}</td><td>46</td><td>—</td><td>—</td><td>—</td><td>+</td><td>+</td></tr>
<tr><td>,,</td><td>6^{15}</td><td>47</td><td>1*</td><td>1*</td><td>—</td><td>27</td><td>9</td></tr>
<tr><td>,,</td><td>6^{17}</td><td>49</td><td>—</td><td>—</td><td>—</td><td>+</td><td>+</td></tr>
<tr><td>,,</td><td>6^{19}</td><td>50</td><td>—</td><td>3*</td><td>—</td><td>30</td><td>13</td></tr>
<tr><td>,,</td><td>6^{21}</td><td>51</td><td>1*</td><td>—</td><td>—</td><td>22</td><td>—</td></tr>
<tr><td>,,</td><td>9^3</td><td>55</td><td>—</td><td>—</td><td>—</td><td>+</td><td>+</td></tr>
<tr><td>,,</td><td>9^5</td><td>56</td><td>1*</td><td>—</td><td>—</td><td>+</td><td>+</td></tr>
<tr><td>,,</td><td>9^{18}</td><td>64</td><td>—</td><td>1*</td><td>—</td><td>10</td><td>6</td></tr>
</table>

Notes to Table II. Plants marked with an asterisk are almost certainly due to rogueing through *Megachile*. In the original records the F_3 plant $9^2/29$ which gave rise to the F_4 family 54/30 was recorded as a dark flake. From its breeding behaviour I have classed it among the medium flakes, and regard the original record as an error due to my lack of experience. In the original records $9^5/29$ was recorded merely as a flake. From its breeding behaviour I have placed it in the table as a light flake. In families 46, 55, and 56 the actual numbers of flakes and whites were not recorded. But my notes state that in each case there was a fair row (probably 30 or more plants) with only light flakes and whites.

Allowing for the few errors in grading noted in connection with Table II, the general result of this set of experiments clearly bears out the hypothesis which was framed a year after its completion. Much more evidence of a similar nature has since accumulated but this I shall spare the reader, confining myself to a brief account of three further crosses which may be conveniently denoted as *A*, *B*, and *C*.

Cross A. Light flake ($\mathbf{G_1'G_1'd_3d_3}$) × white ex self-coloured ($\mathbf{g_1g_1D_3D_3}$).[1] The F_1 plants were all medium flaked purples. From 5 such F_1 plants was raised an F_2 generation consisting of 960 plants. Since the F_1 plants must be genetically $\mathbf{G_1'g_1D_3d_3}$ the expectation in F_2 is 5 classes of plants, viz. self-coloured, dark flakes, medium flakes, light flakes and whites in the ratio 3 : 2 : 4 : 3 : 4. The actual figures, recorded in 1931 when I had become more experienced in grading flakes, together with the expectation on hypothesis are given below:

	Actual	Expected
Self-coloured	202	180
Dark flakes	115	120
Medium flakes	240	240
Light flakes	165	180
Whites	238	240

Cross B. White ex light flake ($\mathbf{g_1g_1d_3d_3}$) × self-coloured ($\mathbf{G_1G_1D_3D_3}$). The F_1 plants were all self-coloured purples. From 4 such F_1 plants was raised an F_2 generation consisting of 752 plants. Since the F_1 plants must be genetically $\mathbf{G_1g_1D_3d_3}$ the expectation in F_2 is self-coloureds and whites in the ratio 3 : 1. Actually there were 545 self-coloured and 207 whites. In spite of the fact that the white was derived from a light flake no flakes were to be expected, and none appeared.

Cross C. Self-coloured ($\mathbf{G_1'G_1'D_3D_3}$) × self-coloured ($\mathbf{G_1G_1d_3d_3}$). This cross is a critical one for the hypothesis. The difficulty in making it lies in obtaining the plant which is at once homozygous in $\mathbf{G_1}$ and $\mathbf{d_3}$. By a rather elaborate and tedious process I have now succeeded in producing such a self-coloured strain. Fortunately, however, a cross made for another purpose turned out to be of this nature. This was one made in 1932 between a purple from a self-coloured strain derived from flakes (*i.e.* $\mathbf{G_1'G_1'D_3D_3}$) and Lord Nelson, a blue self. Both of these were proved true breeding self-coloured strains. F_1 plants were purple self-coloured, and from two of these an F_2 generation was raised. Since the F_1 plant is genetically $\mathbf{G_1G_1'D_3d_3}$ the F_2 should consist of

[1] Such a plant may of course have any constitution in respect of the $\mathbf{D_3}$–$\mathbf{d_3}$ pair. In view of the results it must be supposed to have been homozygous in $\mathbf{D_3}$.

PLATE V

1

2

3

4

5

self-coloured dark flakes and light flakes in the ratio 13 : 2 : 1 (cf. Table I, No. 4). Actually it consisted of 146 self-coloured, 15 dark flakes, and 10 light flakes, both qualitatively and quantitatively a reasonably close approximation to hypothesis.

In conclusion I may remark that the evidence for the postulated existence and behaviour of the modifying factor $\mathbf{D}_3$ is greatly strengthened by the fact that it shows linkage both with the tendril-acacia ($\mathbf{D}_1$–$\mathbf{d}_1$) pair and with the bright-dull flower colour ($\mathbf{D}_2$–$\mathbf{d}_2$) pair. Experiments are now in progress on the linkage relations of the five factors in the **D** chromosome, and of these I hope to give an account on some later occasion.

SUMMARY

The gist of this paper is conveniently summarised in the first few sentences of the section under the heading *Hypothesis*.

EXPLANATION OF PLATE V

Fig. 1. Light flake purple ($\mathbf{G}_1'\mathbf{G}_1'\mathbf{d}_3\mathbf{d}_3$).
Fig. 2. Light flake blue ($\mathbf{G}_1'\mathbf{G}_1'\mathbf{d}_3\mathbf{d}_3$).
Fig. 3. Medium flake purple ($\mathbf{G}_1'\mathbf{g}_1\mathbf{D}_3\mathbf{d}_3$).
Fig. 4. Dark flake purple ($\mathbf{G}_1'\mathbf{G}_1'\mathbf{D}_3\mathbf{d}_3$).
Fig. 5. Self-coloured ($\mathbf{G}_1'\mathbf{G}_1'\mathbf{D}_3\mathbf{D}_3$).