SOMATIC CONVERSION IN THE HEREDITY OF THE CRUCIATA CHARACTER IN *ÆNOTHERA*

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1. INTRODUCTION

IN the genera *Epilobium* and *Ænothera*, types with sepaloid petals are known and these are called *cruciata* forms. The sepaloidy expresses itself in the form, colour, anatomical structure and mode of development of the petals. The character shows single factor Mendelian segregation in crosses of *E. hirsutum* var. *cruciata* with the normal types of *E. hirsutum* and *E. parviflorum*. The normal is dominant.

In *Ænothera*, likewise, normal (*Cr*) can be clearly dominant to *cruciata* (*cr*). Usually, however, dominance is variable and the form of the corolla fluctuates between *Cr* and *cr* on different individuals or even on the same individual. This variability has a genotypic basis for the extreme flower forms commonly breed more or less true with selfing. The cause of the variability is certainly not somatic crossing-over. Mutation must therefore be taking place.

2. SOME EXPERIMENTS

The most exact study has been made of the cross between the following :—

- (i) Normal-flowered *Æ. biennis* L. (heterogamous : *albicans . rubens*) ;
- (ii) The strictly cruciate *Æ. atrovirens* Shull et Bartl. (heterogamous : *pingens . flectens*).

The hybrid *Æ. (atrovirens × biennis) pingens . rubens*, which is known as *pictirubata*, forms only pure *pingens* eggs and pure *rubens* pollen. In meiosis there are two rings : (10) + (4). Combinations of five *pingens* and two *rubens* chromosomes and vice versa might therefore be expected. They are, however, eliminated and do not appear in the progeny. Indeed they appear in the pollen as dead and empty grains additional to the active *rubens* and inactive *pingens*, which are both full grains.

F₁ plants with normal petals give almost all their selfed progeny normal ; *cruciata* plants give almost all *cruciata*. The results of selfing from 1949 to 1954 are shown in table 1.

For analysis of the gametes of hybrids, *cruciata* types were selected whose *cr* alleles showed themselves entirely recessive in crosses with *Cr*. Such were a small-flowered *Æ. Lamarckiana cruciata* (with flowers

no larger than *biennis*) of unknown origin and *cr sp-blandina*. Thus :—

Cr-pictirubata × *cr-Lamarckiana* gives

{ normal (*Cr*) : *pingens . gaudens* (*pictilata*)
 { normal (*Cr*) : *pingens . velans* (*pictivelutina*).

Reciprocal cross gives

{ normal (*Cr*) : *velans . rubens*
 { [dies] *gaudens . rubens*.

Thus all *rubens* pollen has *Cr* and all *pingens* eggs likewise have *Cr* (instead of *cr* as expected).

Taking another experiment, the two reciprocal crosses of *Cr pictirubata* with *cr-Lamarckiana* or with *cr sp-blandina* (plate 1) show us (i) that almost all *pingens* eggs still carry *cr* and (ii) that all *rubens* pollen carries *cr* instead of *Cr*.

TABLE 1

Progenies from *Æ. biennis* × *Æ. atrovirens cruciata*

Parent	F ₂		F ₃		F ₂ +F ₃	
	<i>Cr</i>	<i>cr</i>	<i>Cr</i>	<i>cr</i>	<i>Cr</i>	<i>cr</i>
<i>Cr</i>	309	2	159	0	468	2
<i>cr</i>	15	243	4	145	19	388

The *cr-Cr* heterozygotes have therefore become homozygotes : partly *Cr-Cr* and partly *cr-cr*. Such transformation of one gene under the influence of its allele Winkler (1930) described as *conversion*. In our case it is a question of a monogenic conversion ; moreover it is a somatic conversion while Winkler was considering the possibility of a reciprocal transformation occurring at meiosis.

The *Cr* homozygotes, as we saw, breed true on selfing. If the *cr* homozygotes "segregate" *Cr* plants we have to assume that it is the result, not of recombination by way of crossing-over, but of mutation or conversion. In later generations the *cr* condition can be almost as constant as the *Cr*.

If *cr-pictirubata* is back-crossed with *Cr-biennis* pollen the result is most surprising : the whole progeny is *Cr-pictirubata*. The *cr* allele in *pingens*, which showed itself as *active* in conversion, or capable of causing conversion, when it first made contact with *Cr-rubens*, is thus altered in its condition. It is weakened, shocked or "shaken" as it were, and goes under on another encounter with a fresh *Cr*.

Similarly the cross *cr-atrovirens* × *Cr-pictirubata* has mostly *cruciata* progeny. The *Cr* in *rubens* is thus also shaken by contact with *cr pingens*—although at first it has the upper hand. Corresponding results, showing the weakening of one allele by contact with the other, have come from several other combinations.

Back-crossing *Cr-pictirubata* with *cr-atrovirens* pollen we should now expect to give only *cr-pingens . flectens* (*pictiflexa*). According to its complexes *pictiflexa* is no other than *atrovirens*. The progenies of 1953 had in fact mostly sepaloid petals :

205 *cr* : 33 intermediate : 55 *Cr*.

But in the first experiment of 1926 all *pictiflexa* had been normal. So were all *pictirubata* from the cross *Cr-pictirubata* $F_1 \times biennis$, v. *cruciata*. At that time, therefore, the *pingens* complex was much more inclined to be converted from *cr* to stable *Cr* than it was thirty years later. Such shifts have been repeatedly observed in the "strength" in the activity relations with the conflicting allele.

Crossing of normal *Æ. biennis* with the same small-flowered *cr-Lamarckiana* yields :

{ normal, *albicans . gaudens* (*albilata*)
 { normal, *albicans . velans* (*albivelutina*)

If these two twin hybrids are crossed with one another reciprocally the combinations produced, *gaudens . velans* or *velans . gaudens* (which reconstitute *Lamarckiana*), are mostly *Cr*. But both complexes were originally *cr*.

Thus through living together with *Cr-albicans* the *cr* allele is in both complexes converted to *Cr*. The conversion may be complete (59 *Cr* ; 18 *Cr*) or not quite complete (113 *Cr*, 4 intermediate, 1 *cr*), or slight (38 *Cr*, 16 *cr*).

The individuals of *Cr-albilata* and *Cr-albivelutina*, from whose crossing the last family arose, must have therefore still been partly *Cr . cr*, not yet wholly converted to *Cr . Cr*. Such wobbling in behaviour is to be found in the most various combinations. Conversion is always a potentiality. It does not show the regularity of Mendelian recombinations.

Owing to the occurrence of conversion the position of the *cr* gene in the genome is difficult to determine. Crosses of *Æ. biennis* ♂ with the homozygous taxa *Æ. Hookeri* and *Æ. Lamarckiana* mut. *blandina* as ♀ have indicated, however, that *cr* lies in chromosome 5·6 of *rubens*. This also contains the blunt calyx factor *sp*. Where 5·6 is missing as in *albicans* and *pingens* we can only say that *cr* is in the 5 or the 6 arm. It is not certain whether crossing-over in respect of *Cr-cr* takes place. A decision would be useful because it would indicate if the locus was far from the ends, perhaps on the borders of euchromatin and heterochromatin.

The cross of *biennis cruciata* by *Lamarckiana* normal is especially interesting because here the influence of flower size on the expression of the *cruciata* character is particularly clear. The main gene for flower size, *Co* (small) and *co* (large) lies in the 13 or 14 segment. It is so far distal that in all complex combinations *Co-co* recombine freely.

In the progeny of *cr-albileta* $F_1 \times albivelutina$ F_1 , there are three kinds of *Lamarckiana* (besides *albivelutina*) :

(i) Small-flowered individuals which have the *Co* of *albicans* in double dose. They are stable *cruciata*.

(ii) Intermediate-flowered *Co.co*. They are mostly *cruciata* but can also be normal.

(iii) Large-flowered *co.co*. They are mostly normal, sometimes with slight defects in the petals, rarely *cruciata*. These last, large-flowered *cruciata*, have almost solely *Cr*, i.e. normal offspring.

The stabilisation of the *cr* gene which has arisen from *Cr* by conversion is thus encouraged by the *Co* gene for small flowers which comes from *biennis*.

In the genomes of the homozygous *Æ. Hookeri* and *Æ. blandina* the *cr* allele behaves as though it were located in chromosome 5·6. Small-flowered and large-flowered *sp sp cr cr blandina* are fairly constant stable *cruciata*. The similar *sp sp cr cr Hookeri*, however, is stable when small-flowered. When large-flowered it remained *cruciata* only when it had received the red-nerve factor R in heterozygous state ; this came from *rubens* of *biennis* in the 1·2 chromosome which is lethal when homozygous. With homozygous *rr*, *cr* mutated to *Cr*.

Thus, it seems, the total genotype can condition the re-conversion of *cr* which has come from *Cr* (of *gaudens velans*) back to *Cr*. And it can also condition the mutation of *cr* to *Cr* in the 5 *cr sp* 6 chromosome (of *Hookeri* and *blandina*).

3. DISCUSSION

The *Cr* and *cr* genes are both entirely stable in the original forms. They become labile through crossing. In one case they remain virtually unchanged ; that is in the hybrid :

Æ. (biennis cruciata × Hookeri) albicans. ^h*Hookeri*.*

In one case the dominant allele remains unchanged while the recessive becomes changed to the dominant ; that is in the twin hybrids :

Æ. (biennis × Lamarckiana cruciata) albileta and *albivelutina*.

In this *cr-Lamarckiana* it is remarkable that the *cr* gene was very inconstant thirty-eight years ago and often gave more *Cr* than *cr* offspring. Only after a time did it become stable. And in crossing with *Cr* types it always showed itself recessive.

Apart from these exceptions the common behaviour is that both alleles become labile on crossing. And in the same F_1 , even in the same individual, partly *Cr* is converted to *cr* and partly *cr* to *Cr*. Not only the dominant but also (in other cells) the recessive allele can be active in conversion or *prepotent* and the dominant allele can be passive in

* haplo-*Hookeri*.

Plate

- A. (*Lamarckiana cruciata* small-flowered $\times$ *pictirubata* F₁ normal) *velans* . *rubens* normal. 1953/38.
- B. (*Lamarckiana cruciata* small-flowered $\times$ *pictirubata* F₁ *cruciata*) *velans* . *rubens cruciata*. 1953/34.
- C. (*Pictirubata* F₁ normal $\times$ *sp-blandina cruciata*) *pingens* . *hblandina* normal. 1953/67.
- D. (*Pictirubata* F₁ *cruciata* $\times$ *sp-blandina cruciata*) *pingens* . *hblandina cruciata*. 1953/44.

conversion or *succumbent*. The struggle between the antagonists for prepotency lies at the genotypic level. It is often finished early in development as shown by the uniformity of many F_1 individuals.

The relation of valencies is of importance only when the conversion from heterozygous to homozygous condition does not take place. Prevalency or dominance belongs to the phenotypic level of activity.

What the intermediate forms of the petals mean is not clear. It is not even clear whether they are expressions of equivalence or of equipotence : (that is to say of physiological activity or of conversion activity). Mosaics of definitive *Cr* or *cr* zones can, however, arise. These show how late the conversion may occur.

Many observations suggest that the *Cr* and *cr* alleles may each be composed of a large number of units. Oehlkers has even proposed that the two may differ only in the number of their constituent units. The strongest *Cr* allele would then have the most, and the strongest *cr* the fewest, units.

Attempts to influence conversion by treatment of soaked seeds with high temperatures have not succeeded. How one allele acts on the other in conversion is quite unknown. It is not even known whether homologous segments lie together during the preparation of mitosis or whether the heterochromatin which extends on both sides of the centromere is concerned. Thus, although conversion itself can be regularly demonstrated in *Ænothera*, we still await its explanation.

It is hard to say whether conversion in *Ænothera* might happen in meiosis as well as in mitosis. But it is doubtful whether it has any connection with the irregular or partial and purely meiotic "conversion" recently discussed elsewhere, e.g. in *Saccharomyces* by Lindegren and Winge ; in *Neurospora* by Mitchell and Beadle ; in *Aspergillus* by Strickland ; in *Drosophila* by Goldschmidt.

4. SUMMARY

1. In crosses between normal and cruciate types of *Ænothera*, both of them stable, normal (*Cr*) can dominate over cruciate (*cr*).

2. Commonly the F_1 is variable in petal form. The normal individuals or parts of individuals then breed as *Cr Cr*, the cruciate as *cr cr*.

3. The mutational change from hetero- to homo-zygote is described as *Somatic Conversion*.

4. The dominant allele is more often active or *prepotent* in conversion than the recessive. But the recessive can also be prepotent.

5. Thus the process of conversion happens at the genotypic level. It has nothing to do with the phenotypic valency relation of dominant to recessive.

6. In the complex *rubens* of *Æ. biennis*, *cr* is linked with *sp* : *cr* thus belongs to the 5.6 chromosome, either to the 5 or the 6 arm.

7. The stability of the *cr* allele is influenced by the genotype as a

whole but the empirical observations do not reveal how somatic conversion takes place.

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