THE GENETICS OF COTTON.

PART IX. FURTHER EXPERIMENTS ON THE INHERITANCE OF THE CRINKLED DWARF MUTANT OF *G. BARBADENSE* L. IN INTERSPECIFIC CROSSES AND THEIR BEARING ON THE FISHER THEORY OF DOMINANCE.

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(With Plate XI.)

CONTENTS.

Introduction.

In a previous paper (1932 *a*) the writer presented the results of experiments on the mode of inheritance of the Crinkled Dwarf mutant of *G. barbadense* L. when crossed with *G. hirsutum* L. It was shown that the F_1 of such a cross, instead of exhibiting complete dominance of normal, showed distinct crinkling, and the crinkling persisted in successive back-crosses of heterozygote to normal *G. hirsutum* L.

These experiments were carried to the fourth back-cross, in which (*a*) the ratio of 1 crinkled (intermediate) : 1 normal was obtained, (*b*) the crinkled class was practically uniform, (*c*) the normals were completely *hirsutum* in type, with no trace of *barbadense* genes.

For the purpose of the Fisher theory it was important to observe the characters of both homozygous and heterozygous crinkled when trans-

ference to *hirsutum* was complete. Comparison was therefore made of the selfed offspring of both fourth and sixth back-cross heterozygotes. It was also important to study the behaviour of crinkled when transferred to other types of *hirsutum*.

The experimental results.

The fourth back-cross selfed.

The *hirsutum* to which the heterozygote was continuously back-crossed was a variety of Upland known as Meade, and in our records as Type 9. It has been selfed for at least seven generations and is probably almost a pure line.

Selfing of the heterozygous fourth back-cross plants resulted in segregation into the three expected classes, normal, intermediate crinkled, and extreme crinkled. The results are presented in Table I below.

TABLE I.

Results of selfing fourth back-cross heterozygotes of cross barbadense *crinkled* × hirsutum *normal.*

Family	Normal	Intermediate	Crinkled	Total	Seeds sown
351	2	4	3	9	13
352	6	17	15	38	44
353	0	9	4	13	21
356	1	5	2	8	19
357	5	4	5	14	21
358	4	10	5	19	27
359	9	14	8	31	36
Total	27	63	42	132	181
Expected	*33*	*66*	*33*		
Expected on No. seeds sown	*45*	*90*	*45*		

Here it will be seen that a close approximation to a 1 : 2 : 1 ratio is obtained. There is, however, a deficiency of normals and heterozygotes as compared with crinkled, since crinkleds show nearly perfect agreement with expectation on number of seeds sown (93 per cent.), the heterozygote class coming next (70 per cent.), and the normal last (60 per cent.).

General characters of homozygous and heterozygous hirsutum *crinkled.*

The crinkled class was uniform. Under field conditions they grew to a height of about 9 in. compared with 2–3 ft. in the intermediate and normal classes. Comparison with *barbadense* crinkled in respect of vigour showed that on the whole they were much less vigorous and less able to survive under unfavourable field conditions. No plant produced more

than two bolls, whereas *barbadense* crinkled has been observed to produce three or four times this number. Nevertheless, when given careful culture in the greenhouse, there is much less difference in the vigour of the two types, and *hirsutum* crinkled is not noticeably at a disadvantage. The phenotypic characters of *barbadense* crinkled, *hirsutum* crinkled, and *hirsutum* heterozygote are illustrated in Plate XI.

Productivity of hirsutum *heterozygotes compared with normals (fourth back-cross selfed).*

In view of Fisher's assumption (1928)—necessary to his hypothesis of the origin of dominance—that on the initial appearance of a mutant in a species the heterozygote would be at a disadvantage compared with the wild type, observations were made on the productivity of *hirsutum* heterozygotes compared with normals. The results of the examination for number of bolls per plant are placed below in Table II.

TABLE II.

Number of bolls per plant of hirsutum *heterozygotes and normals.*

Family		5	10	15	20	25	30	35	40	Mean	Condition
G 351	N.	.	.	1	1	.	.	.	.	17·5	Good
	Cr.	.	.	2	1	.	1	.	.	20·0	
G 352	N.	.	.	1	2	1	2	.	.	23·3	Good
	Cr.	.	.	2	4	5	4	.	2	25·6	
G 353	N.	No normals									Bad
	Cr.	5	4	.	.	.	.	.	.	7·2	
G 356	N.	.	.	1	.	.	.	.	.	15·0	Good
	Cr.	.	1	.	2	1	1	.	.	21·0	
G 357	N.	3	2	.	.	.	.	.	.	7·0	Bad
	Cr.	1	3	.	.	.	.	.	.	8·8	
G 358	N.	2	2	.	.	.	.	.	.	7·5	Bad
	Cr.	7	2	1	.	.	.	.	.	7·0	
G 359	N.	4	3	1	1	.	.	.	.	9·4	Medium
	Cr.	7	5	2	.	.	.	.	.	8·2	
Total	N.	9	7	4	4	1	2	.	.	12·6	
	Cr.	20	15	7	7	6	6	.	2	14·4	

It may be noted that:

(1) In the most productive families (G 351 and G 352) there is a slight but definite *increase* in number of bolls per plant in the heterozygous class as compared with the normal.

(2) In families where the yield is low, through bad conditions, there is practically no difference in the yields of the two classes. Bad soil conditions, however, tend to emphasise the crinkledness and to reduce the size of the leaves.

(3) The summarised results show that on a *hirsutum* (Type 9) genotype background, heterozygous crinkled is not appreciably at a disadvantage compared with normal even under bad conditions, while under good conditions it may actually be at some advantage.

Second generation from fourth back-cross selfed.

Normals—twelve families from normals gave normals only.

Intermediate crinkled—ten families from intermediate crinkleds were grown, and all segregated into the expected three classes, viz.: normal, intermediate crinkled, and crinkled. The results follow in Table III.

TABLE III.

Second generation from fourth back-cross selfed.

	Progeny of intermediates			
Family	Normal	Intermediate	Crinkled	No. of seeds sown
302	4	4	2	104
332	1	2	1	83
341	2	7	5	45
349	7	16	7	78
353	3	6	3	20
361	6	7	2	56
363	5	15	7	92
375	18	30	10	153
376	13	30	10	170
377	12	31	12	261
Total	71	148	59	
Expected	*69·5*	*139·0*	*69·5*	

It will be seen that the ratio of the three phenotypes is not appreciably different from the expected 1 : 2 : 1 ratio. It was hoped that the results might throw some light on the excess of crinkled reported in Table II, but the germination of the seed was very bad, and it was not possible to examine the plants in the field till they were several weeks old. The results cannot therefore provide any indication of the proportions of the three types present in the original seed.

The productivity of the three types was not recorded, though the intermediates seemed to be fully as productive as the normals.

Crinkled. Three families were grown and all bred true to crinkled of uniform type.

The sixth back-cross selfed.

In order to see whether any change in *hirsutum* crinkled would result from further back-crossing to Type 9, several sixth back-cross heterozygotes were selfed. The results follow in Table IV.

TABLE IV.

Results from selfing heterozygotes of sixth back-cross.

Family	Normal	Inter-mediate	Crinkled	Total	Seeds sown
G 1823	10	21	9	40	48
G 1824	6	13	9	28	31
G 1825	10	25	11	46	48
G 1826	18	17	17	52	52
G 1827	5	14	12	31	36
G 1828	4	13	14	31	38
Total	53	103	72	228	258
Expected on 1 : 2 : 1 basis	*57*	*114*	*57*		
Expected on seeds sown	*64·5*	*129·0*	*64·5*		

As in the progeny of the fourth back-cross there is a deficiency of normal as compared with crinkled, and although it is clear that under field conditions crinkled is at considerable disadvantage, it is possible that during the period of inter-ovular competition crinkled may be at an advantage.

It was again observed that the degree of crinkledness varied considerably with environmental conditions. Family 1826, which was kept in the greenhouse in 6 in. pots under optimum cultural conditions, showed little difference between normal and heterozygote until about 5 weeks old when separation became practicable. Other families planted at the same time in the field showed early development of crinkling in heterozygotes.

Comparison of height of normals and heterozygotes of sixth back-cross selfed.

Family 1826 (see above) was grown in 6 in. pots under good cultural conditions, and the height of the normal and intermediate groups measured at 5 weeks old. The results follow in Table V.

TABLE V.

Frequency array of height of normals and intermediates of sixth back-cross selfed. Plants 5 weeks old.

	Height in cm.									
	18	19	20	21	22	23	24	25	26	Mean
Normal	.	.	3	1	1	4	.	.	.	21·7
Intermediate	1	1	3	1	3	1	5	.	1	22·1

Here it will be seen that the heterozygotes are slightly taller though more variable than the normals. On the whole the results confirm those previously put forward in connection with the selfed fourth back-cross,

viz. that the heterozygote under good conditions may be at an advantage compared with normal.

Counts were made of the number of bolls per plant of the remaining families planted in the field. The results are presented in Table VI.

TABLE VI.

Frequency arrays of No. of bolls per plant of normal, intermediate and crinkled in selfed sixth back-cross.

		No. of bolls per plant																					
Family		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	Mean
G 1823 S.	N.	.	.	.	.	1	.	.	.	.	2	1	2	2	1	.	.	.	1	.	.	.	.	10·8
	Int.	.	.	.	.	.	.	1	1	.	.	1	2	4	1	3	2	2	.	1	.	.	1	13·1
	Cr.	.	.	7	1	2	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2·7
G 1824 S.	N.	.	.	.	.	.	.	.	.	.	2	.	1	.	.	.	1	1	1	.	.	.		12·8
	Int.	.	.	.	.	.	1	1	1	2	1	2	.	.	3	.	.	1	.	1	.	.	.	10·4
	Cr.	.	.	2	.	4	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4·1
G 1825 S.	N.	.	.	.	.	.	.	.	.	1	1	3	.	1	.	.	2	2	.	.	.	.	.	12·1
	Int.	.	.	1	.	.	.	1	.	1	6	2	3	.	1	2	3	2	.	2	.	1	.	11·9
	Cr.	3	4	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1·3
G 1827 S.	N.	.	1	.	.	.	.	.	1	1	.	.	1	.	.	.	1	.	.	.	.	.	.	8·4
	Int.	.	.	.	1	.	.	1	2	1	1	1	1	.	1	.	.	3	1	1	1	.	.	11·7
	Cr.	.	.	1	.	5	3	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	5·6
G 1828 S.	N.	.	.	.	.	.	.	.	.	.	.	.	1	1	1	1	.	.	.	.	.	.	.	12·5
	Int.	.	.	.	3	.	2	.	.	1	.	1	.	1	2	1	.	2	.	.	.	1	.	10·1
	Cr.	1	3	7	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2·0
Total	N.	.	1	.	.	1	.	.	1	2	5	4	5	4	2	1	4	3	2	.	.	.	.	11·4
	Int.	.	.	1	4	.	3	4	4	5	8	7	6	5	8	6	5	10	1	5	1	2	1	11·6
	Cr.	4	7	19	4	13	5	3	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2·9

The above results again go to show that the yield of the heterozygote is slightly above that of the normal. The yield of the crinkled plants is very low and is in accordance with the great reduction which they exhibit in height and in the size of all the vegetative parts of the plant. To sum up: The transference of a texonomically restricted mutant, (crinkled) from a species, *G. barbadense* L. in which it is common, to a variety (Type 9) of another, *G. hirsutum* L. in which it is unknown, results in a change in ratio in the progeny of heterozygotes from 3 normal : 1 crinkled, to a ratio of 1 normal : 2 intermediate : 1 crinkled. Further, there is evidence that the heterozygote when so transferred is somewhat more productive than the normal under good conditions.

Transference of *hirsutum* crinkled to two other varieties of *G. hirsutum*.

It was recognised that the results of the experiments just described could be recognised as valid only for the particular variety of *G. hirsutum* grown, and that in order to obtain general confirmation of the conclusion

it was necessary to transfer crinkled to the genetic background characteristic of other types of *G. hirsutum*. Experiments were accordingly initiated with this object in view.

(1) *To* G. hirsutum (*variety Virescent Yellow*).

A heterozygous crinkled of the fourth back-cross was crossed with the Upland variety Virescent Yellow. This variety differs somewhat from T 9, but only in such minor characters as length of lint, boll size, etc. In the fifth back-cross seven plants were obtained, four normal and three crinkled. The development of the crinkled character was rather less intense than in the corresponding T 9 heterozygote, and one of the plants was so slightly crinkled that there was at first some doubt respecting its classification.

To obtain the sixth back-cross all three heterozygotes were used and three families obtained. *It proved impossible to classify the plants into normal and heterozygous crinkled. Most of the plants were typically normal, but a few showed faint crinkling of the young leaves.* Selfed families were grown from nine plants, and the results are set out in Table VII.

TABLE VII.

Results of selfing sixth back-cross heterozygotes of cross barbadense *crinkled* × hirsutum *normal* (*variety Virescent Yellow*).

	Normal	Intermediate	Crinkled	Remarks
G 1161 × G 1145				
G 2168	14	–	–	True to normal
G 2169	15	–	–	True to normal
G 2172	3	2	3	Intermediates phenotypically near to normal
G 2173	11	–	4	Clear segregation into 3 normal : 1 crinkled
G 1163 × G 1145				
G 2124	10	2	5	1 intermediate similar to T 9 intermediate
G 2125	7	–	4	Clear segregation into normal and crinkled
G 1158 × G 1145				
G 2178	16	–	–	True to normal
G 2179	17	–	–	True to normal
G 2180	2	1?	2	1 very doubtful intermediate crinkled

In segregating families even the slightly crinkled class is seen to be rare and crinkling of the degree found in the T 9 heterozygote is only found in one plant out of five. Two families show a clear segregation into 3 normal : 1 crinkled.

These results show unequivocally that in at least one typical member of the *hirsutum* group there may be *complete* dominance of normal over crinkled.

(2) *To* G. hirsutum (*variety Triumph T* 57).

An extracted crinkled from fourth back-cross selfed was crossed with a single plant of T 57. Six F_1 plants were grown and it was observed that none of the plants was as crinkled as the T 9 heterozygote. Faint traces of crinkling were seen in two plants which were selfed, giving the following results:

Family	Normal	Slightly crinkled	Crinkled	Remarks
G 1584	22	10	6	Most intermediates were very near normal
G 1585	10	4	2	Most intermediates were very near normal

The slightly crinkled group contained no plants as crinkled as the T 9 heterozygotes, and many on a cursory examination would be classified as normal. As in the previous experiment there can be no doubt that the normal group contains a mixture of normals and heterozygotes, and that T 57 contains a modifier complex which may also confer dominance upon normal.

Plant G 1584 (heterozygote) was crossed again with T 57 and gave 20 plants. All these were normal except two, which exhibited faint traces of crinkling. Definite proof is thus provided that the *hirsutum* variety T 57 is as dominant over its own particular crinkled as the corresponding *barbadense* normal is over the *barbadense* crinkled.

Discussion.

In the writer's previous paper (1932 *a*) on the mode of inheritance of crinkled in the interspecific cross *barbadense* × *hirsutum*, it was stated that the experimental evidence was fully in accordance with expectation on Fisher's theory (*loc. cit.*) that dominance of the wild type is due to the reaction of the heterozygote to modifying factors which ultimately cause it to be indistinguishable from the wild type. It was, however, considered an improbable assumption that normals descended from heterozygotes had replaced the original normal population.

In the first part of this paper it is shown that after four back-crosses of heterozygous crinkled to *hirsutum* (T 9) two sharply demarcated classes are produced, intermediate crinkled heterozygotes and normals. The normals breed true while the heterozygotes segregate in the ratio 1

normal : 2 intermediate : 1 crinkled. Two further back-crosses of heterozygote to normal Upland resulted in no change in the phenotypic appearance of the heterozygote, and the behaviour of the sixth back-cross on selfing differed in no respect from that of the fourth back-cross.

So far the experimental evidence is fully in accordance with the Fisher theory of dominance.

The theory, however, in its original form breaks down completely in the light of new evidence obtained through experiments to transfer crinkled to other strains of *G. hirsutum*. It is shown that there is *complete dominance* of normal over crinkled in the genotypic background of the variety *Virescent Yellow*, and also in that of a pure line derived from the well-known commercial Upland variety *Triumph*. It is possible that the relation 3 normal : 1 crinkled holds good generally throughout the species *G. hirsutum*, and that the ratio 1 normal : 2 intermediate : 1 crinkled found in T 9 is exceptional.

The variety which exhibits the 1 : 2 : 1 ratio (Type 9) is a pure line extracted from the commercial variety Meade, which in most morphological characters differs very little from ordinary standard varieties of Upland. It possesses much longer and finer staple than Upland and is alleged to be descended from a cross between Sea Island (*barbadense*) and Upland, and to derive the long lint from a Sea Island progenitor. Since according to our experiments long lint is not simply inherited but is the result of multiple factors, it is likely that Meade may have a certain number of *barbadense* genes, which two back-crosses with the varieties Virescent Yellow or T 57 are adequate almost completely to displace, but which nevertheless show their presence by a genotypic effect on the normal dominance reaction system of *G. hirsutum*.

It was noted from the results of the first back-cross, (*barbadense* crinkled × *hirsutum* normal) × *hirsutum* normal (*loc. cit.*), that it was possible to obtain a heterozygous crinkled much nearer to the homozygous form than the ultimate *hirsutum* crinkled obtained after several back-crosses.

It is clear that *hirsutum* and *barbadense* have a markedly different make-up of the association of genes which constitutes the character "normal" as opposed to the character "crinkled."

This is shown best by the fact of blending inheritance between *barbadense* crinkled and *hirsutum* normal. This has been demonstrated to occur in the F_2 of crosses between *hirsutum* T 57 and *barbadense* crinkled, as well as in several other crosses in which different *hirsutum* parents were used.

When the two sets of dominance modifiers are brought into contact, there will occur an inability to preserve the characteristic species dominance mechanism, since each species will presumably contain allelomorphs of the dominance modifiers of the other.

It cannot now be assumed that the occurrence of a mutant in a species is necessary for the acquisition of dominance by the wild type, and the fact that *hirsutum* in two types at least is protected against mutation in the crinkled locus, coupled with the further observation that the crinkled mutant does not occur at all in this species, renders necessary some modification of the Fisher theory.

The view arrived at as a result of these experiments may be briefly stated.

Though the point of view emphasised by Fisher that dominance is a function of the genotype as a whole is thoroughly substantiated, the attainment in a species of dominance over a deleterious mutation may be quite unconnected with modification of the reaction of the species to the mutant through the occurrence of initially disadvantageous heterozygotes. It is apparently attained by the species, in this particular instance at least, irrespective of the occurrence of the mutant, and it must be assumed that protection against deleterious recessives is arrived at because the modifiers of dominance are of advantage to the wild type, and are thus selected on their own account.

The suggestion has been put forward by Haldane (1930) that one possible explanation of the behaviour of crinkled dwarf in interspecific crosses is that the New World cottons are tetraploids, and that failures of Mendelian inheritance are to be expected on crossing them.

A survey of the genetic data presented by the writer (1932 *b* and previous papers) indicates that all the complications encountered are explicable on the basis of differences in modifier complexes characteristic of the different species which yield to straightforward analysis by studying the behaviour of a gene on a constant genetic background—obtained by back-crossing to the requisite genotype and then selfing. Granted that the New World cottons are polyploids, they exhibit no signs of this in their genetic behaviour, with the exception that cases of duplicate genes exhibiting normal 15 : 1 F_2 ratios have been several times encountered.

SUMMARY.

1. Further experiments are described on the mode of inheritance of the crinkled dwarf mutant of *G. barbadense* Linn. when crossed with normal *G. hirsutum* Linn.

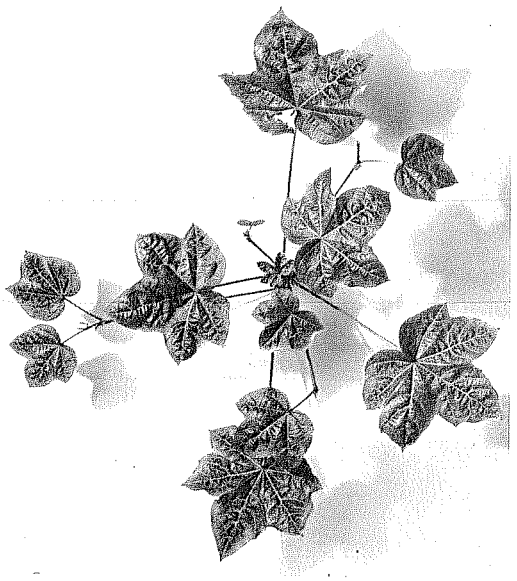

Fig. 1.

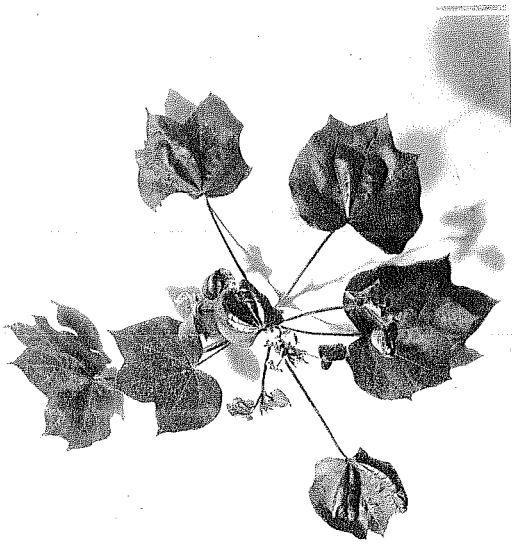

Fig. 2.

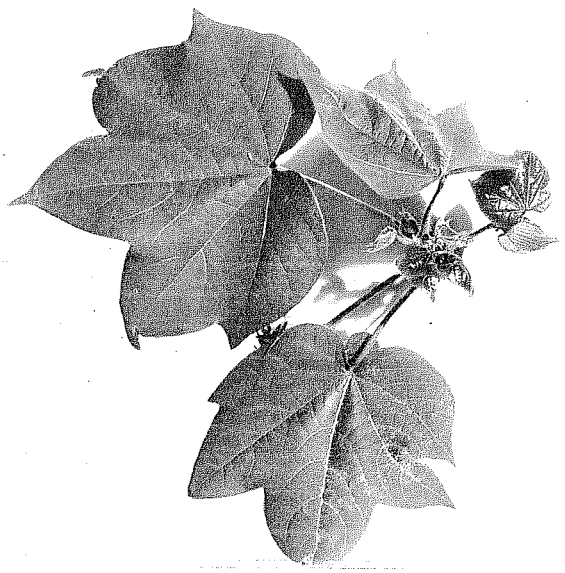

Fig. 3.

2. Observations were made on the characters of crinkled when transferred by repeated back-crossing to *G. hirsutum* (T 9). Selfing of the heterozygotes of the fourth back-cross plants produced normal, intermediate crinkled, and extreme crinkled in a 1 : 2 : 1 ratio, and the results from selfing six back-cross heterozygotes showed that no change had taken place through further back-crossing.

3. The new type of *hirsutum* crinkled was apparently slightly less vigorous and productive than the original *barbadense* mutant, though under good conditions little difference was observable.

4. *Hirsutum* heterozygous for the crinkled factor was shown to have a slight advantage over normal under good conditions and was not at any considerable disadvantage under bad conditions.

5. Transference of crinkled to two further types of *hirsutum* revealed complete or nearly complete dominance of *hirsutum* to the crinkled type.

6. The bearing of the experiments on Fisher's theory of dominance is discussed and it is concluded that modification of the theory is necessary. Complete dominance of normal over crinkled exists in two types of *G. hirsutum* although the crinkled mutant does not occur in that species. It is concluded that modifiers of dominance are of advantage to the wild type and are thus selected on their own account.

EXPLANATION OF PLATE XI.

Fig. 1. Crinkled from Sea Island variety of *G. barbadense* L.

Fig. 2. Extracted homozygous crinkled from back-cross of (*barbadense* crinkled × *hirsutum* T 9 normal) × *hirsutum* T 9 normal. Sixth back-cross selfed.

Fig. 3. Heterozygous crinkled showing intermediate type of crinkling in a seventh back-cross heterozygote (*G. hirsutum* T 9).

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