Parental Generation.  

F₁ Generation.  

F₂ Generation  

Wool Inheritance in Hampshire-Rambouillet Crossbreds

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†In cooperation with U. S. Dept. of Agriculture.
Wool Inheritance in Hampshire-Rambouillet Crossbreds

By Robert H. Burns

INTRODUCTION—THE ART OF SHEEP BREEDING

Sheep breeding is at least 6,000 years old as we find it mentioned in Biblical times when Jacob proved his skill in this line of endeavor. The use of selection has been a most powerful instrument in the hands of skillful sheep breeders, and the change a breeder can make in a flock within a comparatively short time by changing the standard used for selection is most startling. This constant change of type, which necessitates strict culling, shows most effectively the constant variability of expression of the large number of multiple factors responsible in their combination and manifestation for the utility characters of the sheep.

Robert Bakewell (1725-1795) was the first breeder to effect a marked change in the methods used for the improvement of livestock. He set up very rigid standards in his selection of breeding stock and paid particular attention to the propensity of his sheep to fatten, and was not particular as to their size. These quick maturing sheep invariably gave a high dressing percentage when butchered. He was the first to practice ram leasing with the privilege of recalling those whose progeny showed them to be outstanding sires. Thus he was able to retain a larger number of his best rams and give them a chance to prove their breeding ability or potenciy, when such a procedure would have been very difficult in an individual flock. Bakewell is most often associated with the system of in-and-in breeding which he introduced with marked success.

The art of sheep breeding, with a wealth of accumulated experience and skill handed down from generation to generation over a period of at least six thousand years, has given the sheep breeder of the present time a heritage of unlimited value. It owes its success to the correct selection by skillful breeders of those individuals best suited to a specific purpose. The use of this system of selection, and the fact that the blood of sires is handed down to more
individuals than that of any individual dam, has led to the use of the so-called progeny test. By a process of “trial and error” the prepotent sires’ sons of one generation have become the sires of the next generation and the progenitors of a satisfactory type of sheep.

THE SCIENCE OF SHEEP BREEDING

The use of the progeny test is of necessity slow and expensive. Hence, if science could offer a means of analysis whereby the potentialities of an individual could be recognized with considerable accuracy, a new era in sheep breeding would result.

The first step is to develop suitable methods for an accurate analysis of the utility characters of the animals under investigation. In sheep breeding excellence in mutton conformation, fleece quality, hardiness, fertility, and early maturity are the factors which determine the usefulness of the sheep. The emphasis placed on these factors, individually and collectively, varies in different localities and environments and is largely dependent on the economic balance between the relative prices obtained for wool on the one hand and mutton on the other. Hardiness, fertility, and early maturity are closely associated with economic and environmental conditions and are indispensable when efficient dual-purpose sheep are required for the production of both mutton and wool.

CROSSBREEDING OF SHEEP

The crossbreeding of sheep has always been a difficult, yet fascinating problem, for the sheep breeder, who is intrigued with the uniformly excellent individuals of the first cross, only to be very much disappointed with the results obtained should he attempt to establish the excellent type of the first crossbred generation by interbreeding the individuals of this cross. The first crossbred generation seems to show all of the good characters of both parents with none of their weak points, but when interbred the characters due to segregation and recombination show all degrees of variability and undesirable recessives.

Genetically speaking, the closer the parental individuals approach a homozygous condition in regard to the utility characters which they display, the less variability there will be in the crossbred generations to follow. The most striking results which have
been obtained in recent years in the development of new types and breeds of sheep from crossing other types have been obtained when the parental breeds were very strictly selected for type and breeding performance, and when the breeds selected were not so widely divergent in wool type. For instance, there is the experience of the breeders of the various breeds and types which have been developed in recent times.

The Corriedale developed in New Zealand and the Columbia developed in the United States have a similar origin in that they are the result of crossing long wool and fine wool sheep, the extremes of wool types as found in the improved breeds of sheep. In both of these breeds there has been a long period of strict selection in order to cull out all of the undesirable extreme variations of wool type which occur in all gradations from even wider ranges than the difference between the two parental types.

The Polwarth developed in Australia is the same original cross as the Corriedale, but in this case a back-cross was made to the fine wool type, giving a three-quarter blood Merino wool which was known commercially as “come-back.” The predominance of fine wool blood seemed to aid in setting the type, and as a consequence this breed has had less trouble in setting its type than the Corriedale, which has more widely divergent parental types.

The so-called Romeldale developed in California from very carefully selected parentage of the Romney and Rambouillet breeds is another illustration of the excellent results obtained when the variation between the parental types is not too great.

The Mele developed at Neunkirchen in northern Germany is one of the outstanding examples of recent times. The dual-purpose sheep produced at Neunkirchen show excellent performance and prepotency, and possess to a marked degree most of the desirable characters of fleece and body conformation required for successful commercial production. Careful selection of the parental stock of Border Leicester and German Merino, together with a comparatively small difference in wool type between the parental breeds, has given a crossbred product which is remarkably efficient in commercial production and prepotent in passing on these desirable characters.
WOOL INHERITANCE STUDIES
A CONCISE REVIEW OF THE LITERATURE

A number of research workers in various parts of the world have reported results in wool inheritance, but the great variety of results has been in many cases contradictory. During recent years there has been considerable controversy concerning the wool inheritance of the Mele sheep, some maintaining that it showed typical blended inheritance while others found a marked variation and segregation. Those investigators who used unimproved native breeds or mixed wool breeds as one of the parental breeds had much more variation in the crossbred generations than when improved breeds were used for both parental generations. The whole question of blended wool inheritance is quite controversial. However, in looking over the data of the various investigators one cannot help noticing that the crossbred generations were affected noticeably by the standard of selection used, both in the crossbred generations and in the original parental generations. One investigator (Kronacher), who reports on the Mele wool, suggests that there is no more variation in the Mele wool than in any of a number of the pure blooded breeds which have been established for a long time. One investigator with animals most of which were homozygous would get less variation in the crossbred generations than would another investigator who had more animals which were heterozygous in fleece character. This is strikingly illustrated in the Mele and in the Rambouillet x Karakule cross reported by Adametz. The mixed wool (heterozygous) type of the Karakule gave a marked variation in the succeeding crossbred generations, with types varying from one parental type to the other and even beyond. On the other hand, the Meles, which have originated from parental types more homozygous in character, have not shown any such amount of variability. The results reported by Spoettel (1925) bring out the fact that a more variable type of inheritance in wool fineness occurs with mixed or primitive wool type parentage than with sheep whose progenitors had a similar or more stable wool type.
THE WOOL INHERITANCE EXPERIMENT
AT WYOMING

In 1921 a project was started at the Wyoming Experiment Station to study the inheritance of fleece fineness and density (number of fibers per skin area measuring one-half inch square) using the Hampshire and Rambouillet breeds. Two purebred, registered rams and sixteen purebred, registered ewes of each breed were used in the parental generations. Owing to unforeseen and unavoidable circumstances the actual number of crossbreds produced was smaller than had been planned. Wool samples were taken from seven body regions shown in Figure No. 1. These

**FIGURE 1.**

samples were taken with a pair of engineer's calipers which separated the wool growing on a skin surface measuring one-half inch square. One of these calipers is shown in Figure No. 2. The calipers as shown in the figure were altered somewhat for use in wool sampling. The points were tapered to a sharp tip and the inside measuring points on the back of the calipers were removed.

In taking the samples the wool was folded back and a caliper with the jaws set one-half inch apart was pushed into the wool perpendicular to the fold (line of opening), and the fibers inside of the jaws were carefully separated from the surrounding wool. Then another caliper with the same width of opening between its jaws was pushed through the wool at a right angle to the jaws of the first caliper, and again the fibers inside of the jaws were carefully separated from the surrounding wool. When the sample inside of the jaws was separated, it was grasped with the fingers, the calipers were withdrawn, and the sample was cut off close to the skin with a pair of curved scissors. Thus the sample contained the wool fibers growing on a skin surface measuring one-half inch square, or one-quarter of a square inch in area, and could be used for the determination of fleece fineness and fleece density (i.e. the number of fibers growing on a skin surface measuring one-half inch square).

One hundred fibers from each sample, which had been thoroughly cleaned, were measured for fineness, using the machinists' micrometer caliper described by Burns and Koehler (1925). Each fiber was measured in three places along its middle and the
average of the three readings in ten thousandths of an inch was recorded as the fineness (thickness) of that fiber. The bundle of 100 fibers measured for fineness was weighed and the weight compared with the weight of the entire sample, and by a simple proportion the number of fibers in the entire sample was calculated. The following specific case illustrates the method of calculating density:

Weight of weighing bottle \((W_b)\) \(\cdots\cdots\) 38.2537 grams.

Gross weight including both the wool sample and the 100-fiber bundle \((W_g)\) \(\cdots\cdots\) 38.5960 grams.

Weight with the 100-fiber bundle removed \((W_r)\) \(\cdots\cdots\cdots\) 38.5908 grams.

Weight of the 100-fiber bundle \(W_{100} = W_g - W_r\) \(\cdots\cdots\cdots\cdots\cdots\) .0052 grams.

Weight of the entire sample including the 100-fiber bundle \(W_t = W_g - W_b\) \(\cdots\cdots\cdots\cdots\cdots\) .3423 grams.

Calculated density, or number of fibers per skin surface measuring one-half inch square, \(100W_t\)

\[
D = \frac{100W_t}{W_{100}} \cdots \cdots \cdots \cdots 6,583
\]

**EXPERIMENTAL RESULTS**

*The Inheritance of Fineness.*

The figures given in the following table are the means of all seven body areas of the first fleece of each sheep, using the mean fineness of each body area sample as a unit for the purpose of calculating the means, probable errors, and coefficients of variability (per cent standard deviation), which were calculated by means of standard formulas of statistical methods as adapted to machine calculation. The number of fleeces of each individual available for study varied, and, in order to have each individual exert an equal influence on the measurement data for each generation, the first fleece was used to furnish the wool samples for these wool studies.
The F₁ (first crossbred generation) sheep were intermediate in wool fineness between their Rambouillet and Hampshire parents. The two F₁ rams used as the sires of the F₂ (second crossbred generation) were both intermediate in wool fineness and were quite close to the average figure for all of the sheep of this generation. The F₂ sheep were very similar in wool fineness to their Rambouillet parentage. A statistical treatment of the data shows the F₁ generation to be very definitely intermediate in wool fineness with significant differences from both parental generation, the differences being four to seven times the maximum allowable error (three times the probable error of mean fineness for the F₁ generation). A similar treatment of the data for the F₂ generation shows it to be very close in wool fineness to its Rambouillet grandparents, the difference being only twice the maximum allowable error, and far removed from its Hampshire grandparents, the difference in this instance being nine times the maximum allowable error. There would seem to be a strong tendency for the Rambouillet wool type to predominate in the F₂ generation, for each individual sheep of this generation was fine wooled rather than intermediate in wool fineness. Both of the crossbred generations were more uniform in wool fineness than their purebred parental generations, as shown by the smaller coefficients of variability. The difference between the coefficients are significant, as they are larger than the maximum allowable error. The F₁ generation was an excellent type of sheep, being large in size and carrying a high yielding, combing length of fleece of half-blood grade. The F₂ generation tended to be smaller than the F₁ generation and had finer wool, in fact almost as fine as the Rambouillet grandparents.

<table>
<thead>
<tr>
<th></th>
<th>Mean Fineness .0001 Inch</th>
<th>Coefficient of Variability. Per cent</th>
</tr>
</thead>
<tbody>
<tr>
<td>15 Rambouillet Sheep</td>
<td>6.815 ± .079</td>
<td>17.23 ± .828</td>
</tr>
<tr>
<td>14 F₁ Sheep (first crossbred generation)</td>
<td>8.250 ± .069</td>
<td>12.22 ± .598</td>
</tr>
<tr>
<td>11 F₂ Sheep (second crossbred generation)</td>
<td>7.274 ± .072</td>
<td>12.85 ± .710</td>
</tr>
<tr>
<td>14 Hampshire Sheep</td>
<td>9.212 ± .121</td>
<td>18.06 ± .959</td>
</tr>
</tbody>
</table>
The Inheritance of Fleece Density. The Number of Fibers on a Skin Surface Measuring One-half Inch Square.

The figures given in the following table have been calculated in a similar way to those on fineness:

<table>
<thead>
<tr>
<th>Breed</th>
<th>Average Density</th>
<th>Coefficient of Variability</th>
</tr>
</thead>
<tbody>
<tr>
<td>15 Rambouillet Sheep</td>
<td>6148 ± 153</td>
<td>37.61 ± 1.993</td>
</tr>
<tr>
<td>14 F₁ Sheep (first crossbred generation)</td>
<td>4003 ± 97</td>
<td>23.91 ± 1.217</td>
</tr>
<tr>
<td>11 F₂ Sheep (second crossbred generation)</td>
<td>3736 ± 92</td>
<td>32.12 ± 1.916</td>
</tr>
<tr>
<td>14 Hampshire Sheep</td>
<td>2254 ± 83</td>
<td>37.71 ± 2.224</td>
</tr>
</tbody>
</table>

Both of the crossbred generations were intermediate in density as compared with their purebred parental generations, showing a blended inheritance. There was no significant difference between the two crossbred generations. A statistical treatment of the data for the F₁ generation showed it to be definitely intermediate to its purebred parents, for the difference in fleece density was from five to seven times the maximum allowable error. A similar treatment of the data for the F₂ generation showed the differences from the grandparental generations to be from four to twelve times the maximum allowable error, again showing distinctive differences from both grandparental generations and denoting a uniformly blended inheritance of density. The figures for the coefficients of variability showed that the F₁ generation did not have as great a variation in density among the different individuals of the generation as did the purebred or F₂ generations, which bears out the same relationship as found in fineness. The differences in variability were not significant between the purebred and F₂ generations, but both of these were significantly different from the F₁ generation.
The Effect of the Breed of the Sire on the Fleece Fineness of the \( F_1 \) Generation.

<table>
<thead>
<tr>
<th>Breed Type</th>
<th>Mean Fineness .0001 Inch</th>
<th>Coefficient of Variability Per cent.</th>
</tr>
</thead>
<tbody>
<tr>
<td>2 Rambouillet Sires</td>
<td>8.076 ± .091</td>
<td>6.22 ± .797</td>
</tr>
<tr>
<td>5 ( F_1 ) Sheep</td>
<td>8.072 ± .114</td>
<td>12.41 ± 1.015</td>
</tr>
<tr>
<td>4 Hampshire Dams</td>
<td>10.092 ± .278</td>
<td>19.15 ± 2.018</td>
</tr>
<tr>
<td>2 Hampshire Sires</td>
<td>10.188 ± .181</td>
<td>7.45 ± 1.264</td>
</tr>
<tr>
<td>9 ( F_1 ) Sheep</td>
<td>8.349 ± .085</td>
<td>11.94 ± 0.727</td>
</tr>
<tr>
<td>7 Rambouillet Dams</td>
<td>6.676 ± .101</td>
<td>15.61 ± 1.090</td>
</tr>
</tbody>
</table>

Although the \( F_1 \) sheep were intermediate in fineness, still the Rambouillet wool type predominated. The differences were much smaller between \( F_1 \) sheep and their Rambouillet sires or dams than they were between the \( F_1 \) generation and their Hampshire sires or dams. The \( F_2 \) sheep were almost as fine in the fleece as their Rambouillet grandparents, as shown by the following figures:

<table>
<thead>
<tr>
<th>Breed Type</th>
<th>Mean Fineness .0001 Inch</th>
</tr>
</thead>
<tbody>
<tr>
<td>15 Rambouillet Sheep</td>
<td>6.815 ± .070</td>
</tr>
<tr>
<td>14 ( F_1 ) Sheep</td>
<td>8.250 ± .069</td>
</tr>
<tr>
<td>11 ( F_2 ) Sheep</td>
<td>7.272 ± .072</td>
</tr>
<tr>
<td>14 Hampshire Sheep</td>
<td>9.212 ± .121</td>
</tr>
</tbody>
</table>

If one arranges the data so that male and female individuals of the \( F_1 \) generation are segregated a very interesting relationship shows up in the following figures:

<table>
<thead>
<tr>
<th>Breed Type</th>
<th>Mean Fineness .0001 Inch</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Hampshire Sire</td>
<td>10.188 ± .181</td>
</tr>
<tr>
<td>2 ( F_1 ) Rams</td>
<td>9.086 ± .128</td>
</tr>
<tr>
<td>9 ( F_1 ) Sheep</td>
<td>8.349 ± .085</td>
</tr>
<tr>
<td>7 ( F_1 ) Ewes</td>
<td>8.138 ± .003</td>
</tr>
<tr>
<td>7 Rambouillet Dams</td>
<td>6.676 ± .101</td>
</tr>
<tr>
<td>2 Rambouillet Sires</td>
<td>8.076 ± .090</td>
</tr>
<tr>
<td>3 ( F_1 ) Ewes</td>
<td>7.441 ± .094</td>
</tr>
<tr>
<td>5 ( F_1 ) Sheep</td>
<td>8.072 ± .114</td>
</tr>
<tr>
<td>2 ( F_1 ) Rams</td>
<td>9.019 ± .113</td>
</tr>
<tr>
<td>4 Hampshire Dams</td>
<td>10.092 ± .278</td>
</tr>
</tbody>
</table>
The sex differences in the different generations are as follows: Hampshire, 0.096; Rambouillet, 1.400; and in the F₁ generation 0.948 for those with Hampshire sires and 1.578 for those with Rambouillet sires.

In the case of the crossbreds with Hampshire sire and Rambouillet dam the inheritance of fineness was definitely blended and showed no sex-linked tendency. However, in the crossbreds with a Rambouillet sire and a Hampshire dam the inheritance of fineness indicates a tendency towards sex linkage, as the crossbred ewes were even finer than their Rambouillet sires. One must consider that the crossbred ewes, although finer than their Rambouillet sires, are not nearly as fine as the Rambouillet dams, so sex-limitation of fleece fineness is a most powerful factor here and the sex-linkage is only superficial. The F₁ generation has a large sex

FIGURE 3.
F₂ (Second Crossbred Generation) Ewe No. 422.
difference in comparison with the parental breeds, and this would naturally tend to put opposite sexes closer together in wool fineness.

In order to see if density of fleece has the same reaction in inheritance as fineness of fleece the sexes of the $F_1$ generation have been separated and the data compared with the parental generations:

<table>
<thead>
<tr>
<th></th>
<th>Average Density</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Hampshire Sire</td>
<td>$2054 \pm 160$</td>
</tr>
<tr>
<td>2 $F_1$ Rams</td>
<td>$3381 \pm 191$</td>
</tr>
<tr>
<td>9 $F_1$ Sheep</td>
<td>$3978 \pm 126$</td>
</tr>
<tr>
<td>7 $F_1$ Ewes</td>
<td>$4149 \pm 153$</td>
</tr>
<tr>
<td>7 Rambouillet Dams</td>
<td>$7265 \pm 289$</td>
</tr>
</tbody>
</table>
2 Rambouillet Sires ........................................ 5522 ± 376
3 F₁ Ewes .................................................. 4278 ± 201
5 F₁ Sheep .................................................. 4049 ± 149
2 F₁ Rams .................................................. 3705 ± 203
4 Hampshire Dams ........................................ 2140 ± 164

There is no indication of sex-linked inheritance of fleece density. Inasmuch as density of fleece and fineness of fleece are closely associated, it would seem logical to assume that the sex linkage in fineness is only superficial and is due primarily to sex limitation.

Density of fleece is definitely intermediate in inheritance and shows a distinct blending.

Segregation of Body and Fleece Characters in the Crossbreds.

The F₂ individuals showed a very interesting segregation of body and wool characters which are normally associated together. Three of the F₂ ewes, Ear Tag Nos. 422, 442, and 443, are shown
in Figures 3, 4, and 5. In Ewe No. 422 the head and color markings resembled the Hampshire type; the body conformation was that of a Hampshire; but the wool, on the contrary, was similar to that of a Rambouillet. In Ewe No. 422 the Hampshire color markings were very pronounced, yet the sloping rump and fine, dense wool of the Rambouillet type were also conspicuous. Ewe No. 443 showed all of the visual characteristics of a purebred Rambouillet, but the wool measured coarser than either of the other two ewes mentioned. A compilation of the average measurements of fleece fineness and density for two fleeces for each of the ewes mentioned above gave the following figures:

<table>
<thead>
<tr>
<th></th>
<th>Mean Fineness .0001 Inch</th>
<th>Average Density</th>
</tr>
</thead>
<tbody>
<tr>
<td>$F_2$, Ewe No. 442</td>
<td>6.150</td>
<td>4144</td>
</tr>
<tr>
<td>$F_2$, Ewe No. 422</td>
<td>6.976</td>
<td>3495</td>
</tr>
<tr>
<td>$F_2$, Ewe No. 443</td>
<td>7.466</td>
<td>3522</td>
</tr>
</tbody>
</table>

The wedge-shaped appearance of the wool staples on Ewe No. 442 would indicate a fleece of great density, which was confirmed by the laboratory analysis. The other two fleeces are difficult to judge by eye, but both plainly show a fine wool character. Apparently body and fleece characters are not inherited as unit characters, for the Hampshire body and face coloring appeared with a Rambouillet fleece.

**CONCLUSIONS**

*The Inheritance of Fleece Fineness.*

The results indicate a blended inheritance in the $F_1$ generation, which is in agreement with the published results of Kronacher (1925, 1926), Terho (1923), and Pauly (1919). The maximum variation which could take place in the preparation and measurement of the samples could not affect the intermediate position of the $F_1$ generation in fineness of fleece as compared with their Hampshire and Rambouillet parentage. In the $F_2$ generation there appeared to be a distinct segregation to the Rambouillet parentage in fineness of fleece. Although the number of individuals in the
crossbred generations was rather small, still there was a remarkable uniformity of fleece fineness throughout which gives reliability to the results obtained. This type of inheritance agrees with most of the experiments with other animals and plants in that there is a blended inheritance in the $F_1$ generation and a segregation in the $F_2$ generation. It also agrees with the results obtained by range sheepmen, who find little variation in the first crossbred generation but do encounter considerable variation in the second crossbred generation, even though the sire is usually a purebred of one of the parental types instead of a crossbred, as is the procedure in genetic experiments.

**CHART No. 1.**

**THE EFFECT OF THE BREED OF THE SIRE ON THE INHERITANCE OF FLEECE FINENESS IN THE FIRST FILIAL GENERATION.**

Maximum Allowable Error is Three Times the Probable Error of Mean Fineness.

![Chart with data](chart.png)
CHART No. 2.

THE EFFECT OF THE BREED OF THE SIRE ON THE INHERITANCE OF FLEECE DENSITY IN THE FIRST FILIAL GENERATION.

Maximum Allowable Error is Three Times the Probable Error of Average Density.

Based on Samples from Seven Body Regions of Each Sheep.

Density Units—Number of fibers in thousands growing on a square skin area measuring one-half inch on a side.

When first examining the data and Chart No. 1 it would appear that those crossbreds with Rambouillet sires showed sex-linkage, but on closer analysis this seeming relationship is found to be a case of strong sex limitation. This interpretation is further strengthened by the data and Chart No. 2, which show that fleece
density is definitely intermediate and shows no tendency whatever of sex-linkage.

**The Inheritance of Fleece Density.**

The results obtained indicate a definitely blended inheritance in both of the crossbred generations. The maximum difference due to errors of sampling and determination would be around 500 fibers, which would not affect the results, as the differences between the purebred parents and the crossbred generations are much greater.

Density did not act as a sex-linked character, for all of the sheep of both sexes were definitely intermediate and the only variation was a sex-limitation between the sexes.

**The Relationship Between Body and Fleece Characters.**

Body and fleece characters are not correlated in animals of the $F_2$ generation. Visual inspection according to breed type showed Ewe No. 422 to be intermediate, Ewe No. 442 to be definitely Hampshire, and Ewe No. 443 to be definitely Rambouillet. However, fineness and density of fleece in these individuals did not support the visual inspection by breed type. Ewe No. 443 was the coarsest and sparsest in fleece and Ewe No. 442 was the finest and densest in fleece. Body and fleece characters were not associated in inheritance, for a Hampshire body appeared with a Rambouillet fleece and vice versa.

**Recapitulation.**

The chief difficulty with this experiment was the small number of sheep and the fact that no back-crosses or $F_3$ generation sheep were produced.

The crossbred generations, although small, were remarkably uniform and showed a great possibility in crossbreeding, if the two parental types are similar.

This fact is brought out by the outstanding success which practical breeders have had in fixing an intermediate type when the two parental types were similar in wool type, in contradiction to the difficulty encountered when the parental types were dissimilar.
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