ON THE GENETIC CONSTITUTION OF JERSEY CATTLE, AS INFLUENCED BY INHERITANCE AND ENVIRONMENT¹

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The high class dairy cow has taken its present form first because of its survival value in nature and second because of centuries of controlled breeding. In both instances the constitution toward which the breeding tended was approached without conscious knowledge of how inheritance was achieved. It was a case of evolution rather than exact breeding based on genetic factors and a known method of inheritance. Yet, after all, this is the way in which man and most of his economically important animals and plants evolved. It is significant to take such a population, analyze it for the mode of inheritance of the characters involved, and amount of heterozygosis which is now extant within the population, determine present distribution of this inheritance, and from this information formulate a picture of the forces which have been at work to guide the animal of today to its present form. The data of this paper and their analyses are presented as a contribution to the quantitative interpretation of this problem as far as it relates to Jersey cattle.

The Island of Jersey lies in the English Channel, but a few miles from the French mainland. There is little doubt but that the remote ancestors of the Jersey breed of cattle were identical with the common stock found on this neighboring mainland, where cattle of similar form and color can still be seen. In the 18th century the cattle of this island, not 30 miles around, were set apart from those of the rest of the world by laws prohibiting the importation of any cattle. These laws have been in force since 1763, or for about 40 generations in the life scale of cattle. The Royal Jersey Agricultural Society has systematically tried to standardize the animals by drawing up scales of points and guiding the breeding operations of the individual farmers. The Jerseys of America were imported from this island stock, most of the importations being from the latter quarter of the 19th century to the present day. The million or so progeny from these imported cattle have been kept separate from the other cattle by registration of pure breeding. They have become distributed over the whole United States.

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A population of 6000 animals scattered over 15 States will obviously vary in heredity and environment, feeding, care, et cetera. If the conformation of these animals is dependent on the variations of inheritance which have been available to such groups, then the parent and offspring and fraternal correlations will furnish a measure of the effect of inheritance. Similarly, if the variations of environment are to be factors in the determination of the size of these animals, then the uniformity of the animals within one herd, as contrasted with those in another, as determined from the proper correlations, measures this effect. But both measures have some part of the other variable within them. Parent and offspring correlations are, in the main, freed from the influences of common environmental variations since years elapse between the growth period of the parent and that of the

FIGURE 1.—Photographs of Jersey cows showing the points used in making the measurements studied herein.

offspring. This is especially true where the parents and offspring are reared in different herds. The fraternal correlations are not so one-sided a measure of the inheritance as they include also the environmental element of common rearing. The possible influence of selective breeding based on the external appearance of the animal because of its effect on the ancestral correlations enters into this comparison. These questions may be approached through the use of the excellent data on the American Jersey Cattle. (The American Jersey Cattle Club Directors, realizing that the future of any coordinated effort in dairy cattle breeding depends largely on accurate, well analyzed knowledge of all phases of the problem, have had collected the body of information herein described.)

These data include the following measurements on the bull's or cow's type: estimated weight, height at withers, heart girth, paunch girth, width at hips, body length and rump length. Figure 1 shows the relative position

of the measurements taken. About 300 bulls and 6000 cows were measured. The animals come from herds in 15 different States distributed quite generally throughout the United States. Two capable, experienced dairy cattle men took all of the measurements; one man, Mr. RANDOLPH, took all but about 800. The ages, parentages, et cetera of these animals are known through their registration in the herd books. All of the measurements utilized for this study have been age corrected so that all records are strictly comparable for this variable. The volume of material is sufficient to cover the immediate questions: (1) The relation between the sire's conformation and that of his daughters; (2) The correlation between the dam's conformation and that of her daughters; (3) The relation between the types of the full or half sisters; and (4) The assortive mating between sire and dam. (For the study of these data from the viewpoint of conformation and its relation to milk yield et cetera see the literature list (1).)

THE RELATION BETWEEN THE SIRE'S CONFORMATION AND THAT OF HIS DAUGHTERS

For this comparison, there are available 736 pairs of sires and their daughters, some of the pairs being formed by the same sire with different daughters. If the type of the sire is transmitted to the daughter it would be expected that the daughter would resemble the sire's type. By contrasting the measurement of the sire with that of his daughters, it is possible to determine the degree of relationship which exists between their types. The amount of this relationship will be due primarily to the cow's inheritance and secondarily to her environment (such as nutrition, care, et cetera) Table 1 shows the average daughter's size for given conformational measurements of the sires.

The comparison of the sire's type with that of his daughter as shown in table 1 indicated that there is a direct relation between the sire's size and his daughter's conformation. The larger the sire in any given conformational measurement, the larger his daughters tend to be. Thus, sires with a weight of 1025 pounds have daughters whose average weight is 725 pounds, and sires whose weight is 1575 pounds have daughters whose average weight is 1030 pounds. The results, however, are quite irregular, showing that the relation is not a close one. A similar relationship may be drawn for the measurements of sire and daughter in height at withers, depth at withers, heart girth, and paunch girth.

The irregular line of figure 2 represents the actual average daughter's measurements for the given sire's measurements shown in table 1. The straight line shows the general average trend of these measurements. The heavy portion of the line represents the average daughter's measurements which are based on more than 10 individuals.

TABLE 1
Relation between sires' conformations and those of their daughters.

WEIGHT*	HEIGHT AT WITHERS*		DEPTH AT WITHERS		HEART GIRTH		PAUNCH GIRTH		WIDTH AT HIPS		BODY LENGTH		RUMP LENGTH	
	DAUGHTERS' AVERAGE	SIRES'	DAUGHTERS' AVERAGE	SIRES'	DAUGHTERS' AVERAGE	SIRES'	DAUGHTERS' AVERAGE	SIRES'	DAUGHTERS' AVERAGE	SIRES'	DAUGHTERS' AVERAGE	SIRES'	DAUGHTERS' AVERAGE	SIRES'
775	870	47.5	47.0	26.5	26.5	67	70.0	77	83.0	16.5	18.5	31.0	35.7	19.5
975	685	48.5	46.7	28.5	27.3	71	67.0	79	86.6	17.5	19.2	33.0	36.3	20.5
1025	725	49.5	47.2	29.5	27.0	73	69.8	81	82.0	18.5	19.4	35.0	36.2	21.5
1075	970	50.5	47.6	30.5	27.3	75	69.5	83	85.3	19.5	19.7	37.0	—	22.5
1125	895	51.5	47.3	31.5	27.7	77	70.0	85	87.0	20.5	20.1	39.0	36.1	23.5
1175	885	52.5	48.3	32.5	27.8	79	70.5	87	85.1	21.5	19.9	41.0	37.0	24.5
1225	900	53.5	48.2	33.5	27.1	81	72.0	89	87.3	22.5	21.5	43.0	38.4	25.5
1275	910	54.5	48.1	34.5	27.6	83	71.9	91	87.2	23.5	21.5	45.0	39.2	21.8
1325	895	55.5	49.7	35.5	28.7	85	71.2	93	89.4	24.5	21.1	47.0	40.5	
1375	930	56.5	51.0	37.5	28.8	87	74.2	95	85.8					
1425	925	58.5	48.5			89	70.6	97	88.2					
1475	940							99	89.0					
1525	950							101	89.7					
1575	1030							103	91.6					
1625	970							105	87.9					
1675	1000							107	88.4					
1725	925													

* Weight in pounds, other measurements in inches

These results clearly demonstrate a relation between the size of the sire and the size of his daughter. The relation, however, is not very exact, allowing a fairly large variation in either direction. Two factors in the cow's

FIGURE 2.—Relation between sire's size and daughter's size in Jersey cattle.

development may bring about such a resemblance between the sire and his daughter: the first is the heredity for size which the sire transmits to his daughter; the second is the condition such as feeding and care which surround each, tending to make them resemble each other. In view of the fact that most sires are grown in other herds and are purchased at an age

when it would be difficult to influence their size, it seems fair to interpret these correlations as due to heredity. The correlations show that the breeder of dairy cattle may reasonably expect his choice of type in the sire to tend to produce daughters which will themselves resemble the sire's type to some degree. As the correlations are quantitatively not high, the residual or uncontrolled variation which would be expected in the type of such daughters would still be large.

If the sire's conformation for one given body measurement, say, height at withers, is compared with the body measurement of the daughter for perhaps body length, it is found that here too there is an intimate relation between the sire's size and the daughter's size. In other words, if the sire selected is of large conformation in a given body part, he tends to beget a daughter of large conformation for other given parts.

The correlation coefficients and prediction equations on which the above conclusions are based are found in table 2.

TABLE 2
Relation between the measurements of the sire and the measurements of his average daughter.

SIRE'S	DAUGHTER'S								SIRE'S AVERAGE SIZE	STANDARD DEVIATION
	WEIGHT	HEIGHT	DEPTH	HEART	PAUNCH	WIDTH	BODY	RUMP		
	AT WITHERS	AT WITHERS	AT WITHERS	GIRTH	GIRTH	AT HIPS	LENGTH	LENGTH		
Weight	.34	.33	.27	.29	.31	.34	.39	.29	1399 ± 11.4	164 ± 8.1
Height at withers	.29	.31	.33	.35	.33	.38	.30	.31	52.2 ± .14	2.0 ± .10
Depth at withers	.14	.19	.29	.28	.38	.38	.34	.32	32.0 ± .12	1.7 ± .08
Heart girth	.11	.13	.17	.30	.38	.35	.36	.33	80.4 ± .26	3.7 ± .18
Paunch girth	.08	.06	.12	.18	.31	.32	.34	.24	93.1 ± .46	6.6 ± .32
Width at hips	-.01	.07	.09	.32	.32	.65	.44	.59	21.1 ± .12	1.7 ± .08
Body length	.04	.22	.18	.28	.42	.35	.42	.33	41.3 ± .25	3.0 ± .17
Rump length	.10	.12	.08	.37	.34	.57	.43	.51	22.5 ± .10	1.4 ± .07
Daughter's size	933 ± 3.0	47.8 ± .04	27.6 ± .03	71.2 ± .09	87.5 ± .14	20.4 ± .03	37.6 ± .07	20.8 ± .03		
Standard de- viation	121 ± 2.1	1.6 ± .03	1.4 ± .02	3.5 ± .06	5.6 ± .10	1.4 ± .02	2.4 ± .05	1.2 ± .02		

Probable errors: < .06

Sires' and average daughters' conformation

Daughters' weight	= 582 + .25 sires' weight
Daughters' height at withers	= 34.9 + .25 sires' height at withers
Daughters' depth at withers	= 20.0 + .24 sires' depth at withers
Daughters' heart girth	= 48.4 + .28 sires' heart girth
Daughters' paunch girth	= 63.0 + .26 sires' paunch girth
Daughters' width at hips	= 9.1 + .54 sires' width at hips
Daughters' body length	= 23.9 + .34 sires' body length
Daughters' rump length	= 11.0 + .44 sires' rump length

The correlations on the left to right diagonal line of table 1 are for the measurements alike in sire and daughter. These correlations are in general larger than those where the measurement taken on the sire is different from the measurement taken on the daughter. Such variations result from differential development and from the action of unlike factors in inheritance which affect the body parts separately. Other analytical material is necessary to bring this point into sharp detail.

The block of nine correlations at the extreme lower-right hand corner for the interrelations of width at hips, body length and rump length are distinctly larger than those for the other measurements. This fact will be noted in all of the following tables.

The size of the correlations is also important. Considering like measurements of sire and daughter, the first five measurements have correlations which are somewhat lower than those expected on random assortment of the Mendelian factors on which size may depend. (For a more extended discussion of this question with regard to milk yield and butter fat, see papers cited in reference 2 of the Literature Cited.) The other three are large enough or in one case too large. The quantitative facts, while pointing strongly to the inheritance of these characters along customary multiple factor Mendelian lines, need further amplifications by the data which follow.

INFLUENCE OF DAM'S CONFORMATION ON THAT OF HER DAUGHTERS

The data for the relation between the type of dams and the type of their daughters are more extensive than those of the sires and their daughters, there being practically twice as many daughter and dam pairs. There are 1549 measured daughters which come from measured dams. Furthermore at least half of these daughter-dam pair measurements include different dams, whereas not more than 125 different sires were actually included in the measurements, most of the 736 measurements coming from sires which had more than one daughter. The data on the relation between the dam and daughter are therefore more reliable in this sense than those between sire and daughter. They are more obviously influenced by environment also as the dam and daughter are frequently raised in the same dairy barn. The mean types of the dams and daughters are shown in table 3.

The measurements of table 4 support the conclusion that the dam's conformation predicts the daughter's probable form. The results, however, are fairly irregular, indicating that the relation is not a close one. The data of table 3 are presented in graphical form in figure 3.

The irregular line in figure 3 shows the actual average daughter's size for a given conformation of the dam. The heavy line shows those points based on more than 10 daughters in determining the average. The straight line

TABLE 4
Relation between the conformation of the daughter and that of her dam.

DAMS' MEASUREMENTS	DAUGHTERS' MEASUREMENTS									
	WEIGHT	HEIGHT AT WITHERS	DEPTH AT WITHERS	HEART GIRTH	PAUNCH GIRTH	WIDTH AT HIPS	BODY LENGTH	RUMP LENGTH	DAMS' AVERAGE SIZE	STANDARD DEVIATION
Weight	.37	.32	.26	.26	.24	.15	.18	.20	917 ± 1.9	113 ± 1.4
Height at withers	.25	.40	.27	.25	.16	.19	.19	.25	47.6 ± .03	1.7 ± .02
Depth at withers	.21	.31	.32	.35	.27	.34	.30	.38	27.5 ± .02	1.5 ± .02
Heart girth	.18	.27	.32	.42	.34	.43	.34	.44	71.1 ± .06	3.5 ± .04
Paunch girth	.15	.23	.28	.37	.35	.36	.33	.38	87.5 ± .10	5.4 ± .06
Width at hips	.10	.21	.26	.40	.33	.59	.50	.58	20.3 ± .02	1.6 ± .02
Body length	.16	.29	.33	.36	.29	.49	.49	.46	37.1 ± .05	2.4 ± .03
Rump length	.11	.25	.31	.43	.34	.58	.49	.64	20.5 ± .02	1.4 ± .02
Daughters' average size	905 ± 2.1	47.6 ± .03	27.5 ± .02	70.7 ± .06	87.0 ± .10	20.2 ± .02	37.1 ± .05	20.5 ± .02		
Standard deviation	120 ± 1.5	1.6 ± .02	1.4 ± .02	3.7 ± .04	5.7 ± .07	1.5 ± .02	2.3 ± .03	1.3 ± .02		

Probable errors 0.02 when r less than 0.3, otherwise the probable errors are 0.01.

Daughters' weight = 540 + .398 Dams' weight
 Daughters' height at withers = 28.7 + .398 Dams' height at withers
 Daughters' depth at withers = 18.9 + .312 Dams' depth at withers
 Daughters' heart girth = 38.7 + .450 Dams' heart girth
 Daughters' paunch girth = 54.4 + .373 Dams' paunch girth
 Daughters' width at hips = 8.9 + .555 Dams' width at hips
 Daughters' body length = 19.3 + .481 Dams' body length
 Daughters' rump length = 8.0 + .612 Dams' rump length

indicates the average weighted trend of the data as determined from the proper equations indicated in table 4.

The size of the daughters of a small Jersey cow compared with the size of

FIGURE 3.—The relation between the conformation of the dam and the average conformation of her daughter.

the daughters of a large Jersey cow indicates what size may mean to the offspring when considered on the basis of the extremes of the race. If the dam is 575 pounds, the average size of the daughter is 769 pounds. If the

dam is 1225 pounds, the average size of the daughter is 1028 pounds. An increase in size of 650 pounds for the dam has resulted in an average increase in size for the daughters of 259 pounds. For height at withers dams of 41.5 inches have, on the average, daughters of 45.2 inches in size. Where the dam is 51.5 inches at the withers, the average daughter's size is 49.2 inches. It is clear that the daughters tend to approach the average although they still show the effect of the dams from which they come. An increase of 10 inches for the size of the dam at height at withers has resulted in an increase of 4 inches for the daughter. A similar condition is found for the other body measurements.

The correlation coefficients and the proper equations for relating the size of the dam to that of the daughter are given in table 4.

The data of table 4 are comparable with those of table 2 for the sire. The average correlation coefficient between the daughters and sires on like measurements is 0.39 and that for the dams and daughters is 0.45. These correlations are not significantly different although they indicate a slight influence of the more common environment of the dam and daughter. If we are to interpret these relationships as due to the inheritance of size on a multiple factor basis the numerical value is somewhat low. The interrelation of the unlike body parts shows somewhat the same tendency. The mean correlation coefficient for the sires is 0.27 and that for the dams is 0.30.

RELATION BETWEEN THE CONFORMATIONS OF FULL SISTERS

Full sisters are, from an inheritance standpoint, as closely related individuals as it is possible to have in only one generation of matings. It would be expected that full sisters would resemble each other closely if inheritance in any way played a part in determining the conformation of the animal. It would also be expected, in view of the fact that most full sisters are brought up under the same conditions, in the same barn, by the same owner, that environment too would be an important factor in bringing about a close resemblance between such relatives. The effect of environment would undoubtedly be much greater for such full sisters than for either a sire and his daughter or a dam and her daughter. The results of the comparison of full sisters are important in showing the combined influence of these two factors in molding the conformation of the animal to the desired type. The measurements on 292 full sisters, making a total of 802 pairs, have been compared for the eight items of conformation.

The results of this study show that the conformations of full sisters are more closely related in the different measurements than are either sire and daughter or dam and daughter. The correlation coefficients showing the degree of these relationships are given in table 5. The close relation which

TABLE 5
Relation between the conformation of one sister with that of her full sister.

FULL SISTER'S MEASUREMENTS	SISTER'S MEASUREMENTS	CORRELATION COEFFICIENTS	MEAN	STANDARD DEVIATION
Weight	Weight	.49	936 $\pm$ 3.3	125 $\pm$ 2.3
Height at withers	Height at withers	.43	48.0 $\pm$.05	1.66 $\pm$.03
Depth at withers	Depth at withers	.33	27.7 $\pm$.05	1.38 $\pm$.03
Heart girth	Heart girth	.40	71.6 $\pm$.10	3.57 $\pm$.07
Paunch girth	Paunch girth	.37	88.2 $\pm$.14	5.08 $\pm$.10
Width at hips	Width at hips	.65	20.5 $\pm$.04	1.44 $\pm$.03
Body length	Body length	.54	37.6 $\pm$.12	2.53 $\pm$.08
Rump length	Rump length	.64	20.7 $\pm$.04	1.29 $\pm$.02

Full sister's weight	= 475.2 + .49 sister's weight
Full sister's height at withers	= 27.5 + .43 sister's height at withers
Full sister's depth at withers	= 18.5 + .33 sister's depth at withers
Full sister's heart girth	= 43.0 + .40 sister's heart girth
Full sister's paunch girth	= 55.2 + .37 sister's paunch girth
Full sister's width at hips	= 7.1 + .65 sister's width at hips
Full sister's body length	= 17.4 + .54 sister's body length
Full sister's rump length	= 7.4 + .64 sister's rump length

exists between these full sisters may be indicated in the following way. If the full sisters of cows weighing 800 pounds are compared with the full sisters of cows weighing 900 pounds, the difference in the average weight of these full sister groups would furnish an indication of the influence of differences of 100 pounds of weight on the weight of another full sister. By such a comparison, it is found that an increase in any of the type measurements results in an increase in the type measurements of the second full sisters as follows: A cow which weighs 100 pounds more than another cow tends to have full sisters 49 pounds heavier than those of the smaller cow. Similarly, for cows differing by one inch in size, the larger cow tends to have full sisters 0.42 inches larger in height at withers, 0.34 inches in depth at withers, 0.40 inches in heart girth, 0.37 inches in paunch girth, 0.65 inches in width at hips, 0.54 inches in body length, and 0.64 inches in rump length. It will be noted that the rates of increase are essentially the same for the four measurements, height at withers, depth at withers, heart girth, and paunch girth. Those for width at hips, body length, and rump length are considerably greater. The results are throughout concordant in showing the marked influence of the cow's type on that of her full sister.

The correlation coefficients measuring the relation between full sisters, together with the equations showing the mean values for the measurements, are found in table 5. The average correlation is 0.48, a correlation which is quite similar to that expected for full sisters on random mating and complete determination by heredity. In view of the divergence of the first five correlations from the values of the last three, this relation has little meaning without the other data which are to follow.

RELATION BETWEEN THE TYPE OF ONE HALF SISTER WITH THAT OF
ANOTHER WHEN THE SIRE IS THE COMMON PARENT

Half sisters may have a common sire or a common dam. On an inheritance basis they should have approximately only half the inheritance in common which is found for full sisters.

On the other hand, half sisters have the same opportunity with full sisters to be affected by the different feeding, management and selection practices of the various farms from which they come. Most half sister groups come from the same farms rather than different farms and would therefore tend to be alike both because of their inheritance and their environment. Taking these factors into account, the degree of resemblance between full sisters on the one hand would be in its simplest form:

$$1/2 \text{ heredity}^2 + \text{environment}^2$$

while for half sisters:

$$1/4 \text{ heredity}^2 + \text{environment}^2$$

The expectation would consequently be that the half sisters would resemble each other less than full sisters in their size measurements; the differences being interpreted as the effects of the environment. If selection and care, et cetera, have no effect, then the half sisters should resemble each other only half as much as the full sisters. If environment plays an important role, the half sisters will be nearly as much alike as the full sisters. If heredity has no effect the half sisters will be as much alike as full sisters. The full sister groups and half sister groups, coming as they do from all manner of farms each of which have their chance to influence the conformation of pairs of sisters, give the environmental factors full play and push to the background the influence of heredity. Any explanation of the results must take cognizance of the influence of the two components of heredity and environment so that the facts may be truly comparable with those previously obtained in the parent and offspring groups.

If the cow's conformation be contrasted with that of her half sister, on the same basis as that used for the full sisters, it is found that for an increase of 100 pounds in weight the larger cow tends to have half sisters 38 pounds heavier than the smaller cow. An increase of one inch in any of the body measurements results in the larger cow having half sisters larger by the following amounts: height at withers 0.34 inches, depth at withers 0.28 inches, heart girth 0.37 inches, paunch girth 0.31 inches, width at hips 0.67 inches, body length 0.60 inches, and rump length 0.50 inches. It is clear that the half sisters do not resemble each other to quite the same extent as full sisters do. It is also noted that the first five measurements tend to have the same relative effect, whereas the last three tend to have a much greater effect, so far as the influence of the size of one half sister

on that of the other is concerned. Some factor, not as yet clear, tends to make the cows resemble each other more closely in width at hips, body length, and rump length than they do for the other five measurements, weight, height at withers, depth at withers, heart girth, and paunch girth.

The correlations measuring these relationships are shown in table 6.

TABLE 6

Relation between the conformation of one sister with that of her half sister on the sire's side.

HALF SISTER'S MEASUREMENTS	SISTER'S MEASUREMENTS	CORRELATION COEFFICIENTS	MEAN	STANDARD DEVIATION
Weight	Weight	.38	920 ± 1.3	116 ± .9
Height at withers	Height at withers	.34	47.7 ± .02	1.68 ± .01
Depth at withers	Depth at withers	.28	27.6 ± .02	1.45 ± .01
Heart girth	Heart girth	.37	71.4 ± .04	3.71 ± .03
Paunch girth	Paunch girth	.31	87.8 ± .06	5.48 ± .04
Width at hips	Width at hips	.67	20.6 ± .02	1.51 ± .01
Body length	Body length	.50	37.7 ± .03	2.44 ± .02
Rump length	Rump length	.60	20.9 ± .02	1.38 ± .01

Half sister's weight = 574 + .38 sister's weight
 Half sister's height at withers = 31.5 + .34 sister's height at withers
 Half sister's depth at withers = 19.8 + .28 sister's depth at withers
 Half sister's heart girth = 44.8 + .37 sister's heart girth
 Half sister's paunch girth = 60.7 + .31 sister's paunch girth
 Half sister's width at hips = 6.8 + .67 sister's width at hips
 Half sister's body length = 18.8 + .50 sister's body length
 Half sister's rump length = 8.4 + .60 sister's rump length

RELATION BETWEEN THE CONFORMATION OF ONE HALF SISTER WITH THAT OF ANOTHER WHEN THE DAM IS THE COMMON PARENT

Half sisters with a common dam have the same common inheritance as half sisters with a common sire.

If the influence of one half sister upon another be determined in the manner previously used, it is found that a cow which is 100 pounds heavier than another will tend to have half sisters 39 pounds heavier than those of the smaller cow. Similarly the cow which is larger by one inch for the other body measurements will have sisters larger by the following amounts: 0.32 for height at withers; 0.26 for depth at withers; 0.42 for heart girth; 0.38 for paunch girth; 0.55 for width at hips; 0.48 for body length; and 0.60 for rump length. These results show clearly that the size of the cow materially affects the size of her half sisters. This result is again most pronounced for width at hips, body length, and rump length, but is significant for weight, height at withers, depth at withers, paunch girth, and heart girth.

The correlation coefficients of table 7 for the interrelation of these half sisters' measurements have a mean value of 0.42. This value is identical with that of the half sisters on the sire's side and somewhat less than that for the full sisters.

TABLE 7

Relation between the conformation of one sister with that of her half sister on the dam's side.

HALF SISTER'S MEASUREMENTS	SISTER'S MEASUREMENTS	CORRELATION COEFFICIENTS	MEAN	STANDARD DEVIATION
Weight	Weight	.39	917 ± 2.7	117 ± 1.9
Height at withers	Height at withers	.32	47.7 ± .04	1.66 ± .03
Depth at withers	Depth at withers	.26	27.5 ± .03	1.44 ± .02
Hearth girth	Hearth girth	.42	71.1 ± .08	3.53 ± .06
Paunch girth	Paunch girth	.38	87.5 ± .13	5.66 ± .09
Width at hips	Width at hips	.55	20.3 ± .03	1.46 ± .02
Body length	Body length	.48	37.1 ± .06	2.33 ± .04
Rump length	Rump length	.60	20.5 ± .03	1.29 ± .02

Half sister's weight	= 557	+ .39 sister's weight
Half sister's height at withers	= 32.2	+ .32 sister's height at withers
Half sister's depth at withers	= 20.3	+ .26 sister's depth at withers
Half sister's heart girth	= 41.5	+ .42 sister's heart girth
Half sister's paunch girth	= 54.3	+ .38 sister's paunch girth
Half sister's width at hips	= 9.2	+ .55 sister's width at hips
Half sister's body length	= 19.3	+ .48 sister's body length
Half sister's rump length	= 8.2	+ .60 sister's rump length

ASSORTIVE MATING IN JERSEY CATTLE

By assortive mating is meant the tendency of breeders to mate individuals which are alike. This similarity may be taken as a whole or it may be for some given part of the body. Assortive mating is thus a distinct and fundamental function in any breeding, whether the procedure be deliberately controlled or not.

In regard to one character, milk yield, it was found that assortive mating did not occur to the extent which might be expected. This was no doubt due in large part to the fact that milk yield is a relatively obscure character requiring a large volume of records for its appreciation and control, a fact tending to reduce the number of those willing to give it sufficient attention to make for an effective assortive mating coefficient. The case for the body characteristics of the dairy cow is not of this kind. The relative size of any of the characters may be readily appreciated by simply looking at the cow. Dairy-men are continually making comparisons of this kind and naturally become expert in taking into account such things as relation of size to age, thus making the selection more effective.

Assortive mating coefficients thus have an interest to all breeders because they measure the effective selection and breeding which is taking

place within the breed for the given character. They have a further interest in that the degree to which the parents are selected for a given character markedly influences the amount of resemblance which will be found between the parents and their offspring.

If assortive mating is to be a real force in molding the characteristics of a breed it must do several things. The first and most important is that the sires to be used in the different herds must, in large part, come from superior parents. The sires selected for actual breeding must themselves be the best of the progeny of such parents. Sires of this calibre should then have the best mates which the breed affords. Some appreciation of how active is this selective breeding may be had by a comparison of the relative sizes of the sires and the cows to which they are bred. The results of this comparison for the eight body measurements of conformation are shown in the averages which follow; the sires being divided into groups, from the smallest to the largest, three groups in all and their mates' average sizes determined.

WEIGHT		HEIGHT AT WITHERS		DEPTH AT WITHERS		HEART GIRTH	
SIRE	MATE	SIRE	MATE	SIRE	MATE	SIRE	MATE
1199	880	49.9	47.4	29.7	27.3	74.3	70.0
1430	925	52.0	48.0	32.1	27.5	80.0	71.0
1570	975	54.5	47.6	34.8	27.5	84.2	72.0

PAUNCH GIRTH		WIDTH AT HIPS		BODY LENGTH		RUMP LENGTH	
SIRE	MATE	SIRE	MATE	SIRE	MATE	SIRE	MATE
84.0	85.6	19.1	19.5	37.1	36.2	21.2	19.9
92.0	88.6	20.8	20.2	41.1	36.8	22.5	20.6
99.1	88.0	23.0	22.0	43.5	38.5	24.3	21.8

It will be recalled that all measurements presented are mature form measurements. The data cited above were obtained in the following manner. There were 103 matings of sires and dams in which the sire's weight was less than 1350 pounds. These sires' weights averaged 1199 pounds. They were bred to cows whose average weight was 880 pounds. There were 167 matings in which the sire's weight ranged between 1350 and 1500 pounds with an average of 1430 pounds. They were bred to cows averaging 925 pounds. Seventy-seven matings had sires whose weights were above 1500 pounds. These sires averaged 1570 pounds in weight and were bred to cows averaging 975 pounds in weight. There is a distinct increase in the weight of the sires' mates as the weight of the sires increases. This correlation is carried through the other data particularly for the width at hips, body length and rump length. These results may be seen graphically in figure 4.

The degree of selection practiced in the Jerseys is evidently pronounced for some of the regions of the body conformation, less in others and almost non-existent in the remainder. The regions chosen for emphasis in breeding are width at the hips, body length and rump length. Less effective selection

FIGURE 4.—Relation between the size of the sire and the size of his mates for Jersey cattle.

is seen in body weight, heart girth and paunch girth. Little selection is practiced for height at withers and depth at withers. Herd owners very evidently believe that if they have cows which have wide hips, long bodies or rumps, that these cows should be bred to bulls having the same qualities,

whereas if their cows have narrow hips, short bodies or rumps, they should be bred to bulls which, relatively speaking, have equally narrow hips, short bodies and rumps. A like, though less extreme, belief also appears to exist with regard to the weight, heart girth and paunch girth. The matings with regard to the height at withers and depth at withers appear to be almost random matings, a sire high at the withers being proportionately as often bred to cows which were low at the withers, high at the withers, or medium in height.

Two factors appear to be capable of giving the degree of assortive mating observed. The first is that breeders may believe that the conformational characteristics, width at hips, rump length and body length, and, to a lesser degree, weight, paunch girth and heart girth in the order named are factors of importance in indicating production. If such a belief is sufficiently strong to cause these points to have a financial premium the desired sires and dams would be concentrated into the hands of the wealthy, the less desired stock would be in the herds of breeders with less wealth, thus giving the observed results. This situation could be accentuated by a second factor working in conjunction with it. This second factor is the tendency, perhaps stronger in the Jersey breed than in most others, of confining the breeding closely within family lines. If these family lines differ by characteristics such as width at hips, body length, et cetera, these characteristics being inherited and selected according to the particular whim of the breeders establishing the family, they would tend to make diverse lines for these characteristics. A population composed of such distinct families would give the assortive mating coefficients like those observed. In passing it is of point to suggest that it is unfortunate that the points of conformation most important to production were not emphasized in this selection: weight and heart girth.

The relative intensity of the selective or assortive breeding going on within the herds of Jerseys in this country is best appreciated by an examination of the correlation coefficients between the measurements of sires and their mates. These correlation coefficients are given in the tables which follow.

TABLE 8
Correlation coefficients between the sire's measurements and those of his mates.

CORRELATION COEFFICIENTS	
Weight	$0.26 \pm .03$
Height at Withers	$.08 \pm .04$
Depth at Withers	$.07 \pm .04$
Hearth Girth	$.18 \pm .03$
Paunch Girth	$.22 \pm .03$
Width at Hips	$.65 \pm .02$
Body Length	$.40 \pm .03$
Rump Length	$.52 \pm .03$

The first five assortive mating coefficients of table 8 correspond well with those which PEARSON (3) has calculated for stature, span and forearm length in man. The last three coefficients differ from either set in being much larger. The size of these coefficients suggests that they are in part responsible for the observed difference in the ancestral correlations of these same groups. The analysis of this point is presented in the following section.

RELATIVE INFLUENCE OF HEREDITY AND ENVIRONMENT ON CONFORMATION WITHIN THESE JERSEYS

The somatic appearance of an animal is due, first, to the genetic constitution of the fertilized egg and, second, to the environmental opportunity which is afforded the egg for development up to adult size. Assortive mating based on somatic appearance of the animal would consequently be attributed to both heredity and environment.

The definite tendency of Jersey breeders to breed within families would give the assortive mating coefficients a different emphasis. The families within the Jerseys are genetically different in origin. The average environment as represented by care, climate, feeding, et cetera, is throughout essentially the same between the different families. There are good, bad and indifferent cattlemen growing cattle in each family. The magnitude of the assortive mating coefficient when the breeding is carried on within such sub-groups is consequently dependent on their genetic background.

These two interpretations appear to be the major possibilities in analyzing the coefficients of assortive mating. There is another possibility, however; namely, that in taking the measurements the standard of measurement was different between the men making the measurements. This possibility can be eliminated since the correlations for the data of the two men derived separately lead to essentially the same numerical results. To remove any possible objection on this ground we shall consider only the data taken by one man, measuring the larger series of about 5000 animals.

As WRIGHT, FISHER and others (4, 5) have pointed out, the parent and offspring correlations are less than the full sister correlations by an amount equal to the effect of the common environment or, as FISHER (6) has shown to the influence of dominance. In our case any difference between the sire and daughter correlations and the dam and daughter correlations might be considered due to the more common environment of dam and daughter in their development. In his systems of mating, WRIGHT² has analyzed these assumptions and derived general formulae for them. His symbols are h^2 determination of size by heredity, d^2 determination of heredity by dominance deviations, e^2 determination of size by the environment com-

² The writer is indebted to Dr. WRIGHT for much in the discussion which follows.

mon to full or half sisters, m the correlation between genetic constitution of mates, and m_1 correlation between genotypes of different mates. The effects of the common environment and of dominance could theoretically be combined in all gradations. Such gradation would offer serious complication in the analysis of the problem. An estimate of the effect of common environment and dominance can be reached, however, (1) by assuming the dominance effect to be non-existent, and (2) by assuming the environmental effect to be absent and the dominance to account for the differences. By contrasting the two results it is then possible to see what effect each of the variables really has. The equations which follow on the various assumptions are listed below:

(1) Assortive mating is somatic and the genetic factors are without dominance.

$$r_{sd} = \frac{m}{h^2} \quad r_{so} = r_{do} = 1/2h^2(1 + r_{sd})$$

$$r_{oo} = 1/2h^2(1 + m) + e^2 \quad r_{oo}' = 1/4h^2(1 + 2m + m^1) + e_1^2$$

Where s = sire, d dam, o daughter, oo full sister and oo^1 half sister.

(2) Assortive mating as above, but difference between dam and daughter correlations and sire and daughter correlations assumed due to the more common environment of dam and daughter as contrasted with that of sire and daughter. The only change which this assumption makes in the above equations is

$$r_{sd} = 1/2h^2(1 + r_{sd}) \text{ as before but } r_{do} = 1/2h^2(1 + r_{sd}) + e^2$$

(3) Assortive mating as above but with genetic factors showing dominance and no effect of environment.

$$r_{sd} = \frac{m}{h^2(1 - d^2)} \quad r_{so} = r_{do} = 1/2h^2(1 - d^2)(1 + r_{sd})$$

$$r_{oo} = 1/2h^2(1 - \frac{d^2}{2})(1 + m) \quad r_{oo}' = 1/4h^2(1 - d^2)(1 + 2m + m^1)$$

(4) Assortive mating is genetic and no dominance of factors, environment as before.

$$r_{sd} = h^2m \quad r_{so} = r_{do} = 1/2h^2(1 + m)$$

$$r_{oo} = 1/2h^2(1 + m) + e_1^2 \quad r_{oo}' = 1/4h^2(1 + 2m + m^1) + e_1^2$$

The correlation coefficients which are derived from the series of measurements taken by the man measuring the largest series are shown below. These correlations will be noted to be entirely similar to those derived from the combined data of both men. There was consequently no divergence of the standard used by the two men in measuring their animals.

TABLE 9

	r_{so}	r_{do}	r_{sd}	r_{eo}	r_{so}' sire	r_{so}' dam
Weight	0.349	0.382	0.212	0.493	0.353	0.291
Height at Withers	0.267	0.336	0.013	0.383	0.306	0.223
Depth at Withers	0.359	0.312	0.108	0.304	0.283	0.219
Heart Girth	0.350	0.436	0.218	0.450	0.381	0.416
Paunch Girth	0.299	0.376	0.204	0.383	0.320	0.377
Width at Hips	0.686	0.622	0.607	0.688	0.614	0.579
Body Length	0.407	0.500	0.326	0.492	0.505	0.513
Rump Length	0.569	0.679	0.571	0.705	0.615	0.629

The solution of the various equations under the above assumptions is shown below.

The data of table 10 enable us to form some judgment regarding the influence of the various factors which affect size inheritance. The hypotheses considered are the major simple ones. Theoretically they could be combined in a variety of ways. The results from such combinations would be intermediate, however, so that conclusions arrived at on the basis of this material would be essentially correct for such intermediate hypotheses.

The data under hypotheses (1) and (2) with assortive mating somatic and no dominance of the genetic factors for size and that for (4) with assortive mating genetic and no dominance of these same factors, give the factor environment all the possible credit it can have in determining the constitution of these Jersey cattle. The data show that the environmental effects are negligible. In fact it will be noted that several of the constants take negative values. The facts in these dairy cattle consequently agree with those of PEARSON and LEE (3) on human constitution in showing but little effect on the constitution of the environmental variation which differentially played upon the individuals within the populations studied.

The hypothecating of dominance in the factors for size as seen in (3) leads to high values for the effect of heredity; three values being in fact indeterminate. The values for the correlation between the genotypes of mates are also high, four out of the eight being indeterminate. These facts seem to give suitable grounds for discarding the dominance hypothesis for the size factors in these dairy cattle.

Further information by which to differentiate between the effectiveness of the other hypotheses is furnished by the genetic correlations for the ancestral combinations as calculated from these data.

The consequences following from these three hypotheses as seen in tables 10 and 11 certainly suggest that (4), assortive mating of genetic origin and no dominance is not applicable to these Jersey cattle. The genetic correlations are throughout too high. Such correlations would require the Jerseys to be split into families which were only bred within each other and never

TABLE 10
Relative influence of heredity h^2 , environment e^2 , dominance d^2 , and the correlation of genotypes m , m^1 .

	(1)				(2)				(3)				(4)			
	h^2	e^2	m	m^1	h^2	e^2	e^1	m^1	h^2	d^2	m	m^1	h^2	e^2	m	m^1
Weight	0.60	0.15	0.13	-0.14	0.58	0.17	0.10	-0.19	1.22	0.50	0.13	0.88	0.52	0.13	0.41	0.32
Height at Withers	0.60	0.06	0.08	0.21	0.53	0.10	0.07	0.10	0.85	0.30	0.08	0.62	0.59	0.08	0.02	0.20
Depth at Withers	0.61	-0.02	0.07	0.41	0.65	-0.04	0.07	0.67	0.68	0.12	0.07	0.53	0.56	-0.03	0.19	0.18
Heart Girth	0.65	0.08	0.14	0.68	0.58	0.13	0.09	0.13	0.98	0.34	0.14	1.19	0.57	0.06	0.38	0.63
Paunch Girth	0.56	0.07	0.11	0.75	0.50	0.11	0.08	0.10	0.85	0.34	0.11	1.26	0.47	0.05	0.43	0.70
Width at Hips	0.81	0.08	0.50	0.55	0.85	0.04	-0.06	0.57	1.13	0.28	0.50	0.94	0.70	0.03	0.87	0.48
Body Length	0.68	0.07	0.22	1.10	0.61	0.12	0.09	0.20	1.11	0.30	0.22	1.53	0.58	0.04	0.56	1.12
Rump Length	0.79	0.13	0.45	0.59	0.72	0.19	0.11	0.41	1.30	0.39	0.45	1.23	0.68	0.08	0.84	0.51
Average	0.66	0.08	0.21	0.63	0.63	0.11	0.20	0.20	0.32	0.21	0.32	0.21	0.58	0.46	0.46	0.46
	$\pm .02$	$\pm .01$	$\pm .04$	$\pm .03$	$\pm .01$	$\pm .01$	$\pm .04$	$\pm .04$	$\pm .02$	$\pm .02$	$\pm .04$	$\pm .04$	$\pm .02$	$\pm .02$	$\pm .06$	$\pm .06$

outside. This type of breeding is partly true but inbreeding should be widespread if it were as active as the correlations under (4) would necessitate.

TABLE 11
Genetic correlations.

	(1)			(2)			(4)		
	r_{po}	r_{oo}	$r_{oo'}$	r_{po}	r_{oo}	$r_{oo'}$	r_{po}	r_{oo}	$r_{oo'}$
Weight	0.61	0.56	0.28	0.61	0.56	0.26	0.70	0.70	0.53
Height at Withers	0.51	0.54	0.34	0.51	0.53	0.31	0.51	0.51	0.31
Depth at Withers	0.55	0.53	0.39	0.55	0.54	0.45	0.60	0.60	0.39
Heart Girth	0.61	0.57	0.49	0.61	0.56	0.47	0.69	0.69	0.60
Paunch Girth	0.60	0.56	0.50	0.60	0.55	0.48	0.72	0.72	0.64
Width at Hips	0.80	0.75	0.64	0.80	0.76	0.65	0.93	0.93	0.80
Body Length	0.66	0.61	0.64	0.66	0.66	0.63	0.78	0.78	0.81
Rump Length	0.79	0.73	0.62	0.79	0.71	0.59	0.92	0.92	0.80

Hypotheses 1 and 2 are essentially the same in view of the lack of any environmental effect. The results are, considering their probable errors, reasonable although the variation covered is quite wide. The greatest complicating factor is the half sister correlations which are too large. The best hypothesis would seem to be that part of the assortive mating is somatic and part genetic, the factors for size being without dominance and mating taking place in such a manner as to form partially non-interbreeding families.

That variation in heredity is the main cause of the variation in the size of Jersey cattle is evident from this analysis. The close relation between the genotypes of the mates has resulted from the type of breeding. It is of interest to note how far this inbreeding and selection has been carried by the herd owners within their individual herds and how much residual variation

TABLE 12
Correlation coefficients for the relation of dam and daughter type within certain herds.

HERD NO.	WEIGHT	HEIGHT AT WITHERS	DEPTH AT WITHERS	HEART GIRTH	PAUNCH GIRTH	WIDTH AT HIPS	BODY LENGTH	RUMP LENGTH	NO. OF PAIRS
19	-0.22	-0.13	-0.04	-0.01	0.03	-0.01	0.15	0.02	27
27	-0.03	0.10	-0.32	-0.11	-0.20	0.08	0.31	0.20	25
47	0.06	-0.38	0.26	0.09	-0.31	0.08	0.17	0.10	23
52	0.45	0.34	0.27	0.43	0.28	0.32	0.16	0.39	20
58	0.53	0.49	0.65	0.32	0.49	0.34	0.18	0.60	27
69	0.30	0.26	0.18	0.17	0.35	0.51	0.35	0.16	27
77	-0.15	0.23	-0.13	-0.12	-0.02	-0.15	-0.15	0.15	50
78	0.06	0.25	0.01	-0.02	-0.02	-0.02	-0.12	0.04	63
88	0.33	0.34	0.44	0.30	0.31	0.15	0.15	0.21	27
102	0.03	0.20	0.18	0.05	-0.04	0.04	0.26	0.13	39
203	-0.02	0.39	0.20	0.12	-0.05	-0.08	0.07	0.34	31
Mean	0.12	0.19	0.15	0.11	0.07	0.11	0.13	0.20	

still exists which the individual breeder may utilize in further change of the constitution of his cows. This information may be derived from the correlations of conformations of cows within the individual herds. Because of the reduced number of animals available within individual herds only the correlations between daughter and dam, half sisters with a common sire and half sisters with a common dam have any meaning. These correlations are tabulated below for those herds which have 20 or more such pairs.

Table 12 shows that there is a fairly wide variation between the different herds in the amount of residual variation which exists within them. Some herds could change the form of their cattle by further selective breeding. The average residual heredity which remains out of the total which could have existed for the particular herd is rather small. This fact is further brought out in tables 13 and 14 for the two classes of half sisters.

TABLE 13
Correlation coefficients for the relation between the types of half sisters with a common sire.

HERD NO.	WEIGHT	HEIGHT AT WITHERS	DEPTH AT WITHERS	HEART GIRTH	PAUNCH GIRTH	WIDTH AT HIPS	BODY LENGTH	RUMP LENGTH	NO. OF PAIRS
19	0.02	0.00	-0.04	0.00	-0.03	0.02	0.01	0.09	960
27	0.13	-0.02	0.05	-0.03	-0.03	-0.07	-0.04	-0.01	418
47	0.01	-0.05	0.03	-0.06	-0.05	-0.03	-0.06	-0.04	514
52	-0.04	0.11	-0.02	-0.05	-0.05	0.01	0.07	-0.01	346
58	-0.08	-0.10	0.06	-0.03	-0.05	0.13	0.00	0.00	850
69	0.08	-0.01	-0.02	0.09	0.05	0.04	-0.04	0.09	486
77	0.00	0.18	0.02	0.01	0.06	0.10	0.14	0.01	3644
78	0.10	0.07	0.16	0.21	0.15	0.33	0.15	0.19	3610
88	-0.02	0.06	-0.06	0.00	0.03	0.11	0.24	0.03	768
102	0.09	0.06	0.12	0.11	0.03	0.09	0.08	0.29	1462
203	-0.03	-0.01	-0.01	-0.23	-0.05	0.14	-0.05	-0.03	484
Mean	0.02	0.02	0.02	0.00	0.01	0.08	0.05	0.06	

TABLE 14
Correlation coefficients for the relation between the types of half sisters with a common dam.

HERD NO.	WEIGHT	HEIGHT AT WITHERS	DEPTH AT WITHERS	HEART GIRTH	PAUNCH GIRTH	WIDTH AT HIPS	BODY LENGTH	RUMP LENGTH	NO. OF PAIRS
19	-0.23	0.13	-0.21	-0.33	-0.26	-0.42	0.05	-0.33	50
27	-0.13	0.38	0.02	0.47	-0.08	0.17	-0.42	-0.07	22
47	-0.22	-0.49	-0.07	-0.60	-0.17	-0.33	-0.20	-0.45	22
52	0.22	-0.36	-0.11	0.00	-0.35	-0.33	-0.17	-0.13	20
58	0.03	-0.25	-0.34	0.40	-0.20	0.15	-0.13	0.42	38
69	0.13	0.02	0.25	-0.06	0.23	-0.11	0.08	0.36	36
77	0.25	0.37	-0.11	0.47	0.37	0.51	0.24	0.29	44
78	0.31	0.19	0.18	0.19	0.09	0.24	0.10	0.30	116
88	0.07	-0.23	0.14	0.14	0.00	-0.09	-0.21	-0.33	34
102	-0.06	0.20	0.09	0.04	-0.01	-0.13	0.01	0.17	74
203	-0.39	-0.13	-0.57	-0.58	-0.55	-0.19	-0.03	-0.24	20
Mean	0.01	-0.02	0.06	0.01	-0.06	-0.05	-0.05	0.00	

The data of tables 12, 13 and 14 show that the Jersey herds have been differentiated into types which are quite pure in their inheritance. These types are different for different herds. The effect of the methods of breeding which have been employed have been to produce family groups which are rather homogeneous. To bring in genetic variability on which to work for further change would necessitate the interbreeding of some of these groups.

SUMMARY

This paper presents a summary of the body constitution of Jersey cattle as it is found after centuries of evolution under domestication and separation from other cattle for a period of nearly 200 years. The cattle utilized are pure-bred Jerseys owned within 15 states of the United States. Nearly 6000 relatively high-grade Jerseys form the basis for this study.

Data are presented to show the amount of residual inheritance for body constitution which remains within the breed as a whole and on the individual farms where the breeding is carried on. The parent and offspring and sibship correlations are presented. These correlations show that inheritance accounts for most of the variation in the size of these cattle, such environmental differences as do exist playing but little part in the ultimate constitution of these animals. The data show high coefficients of assortive mating. These are particularly noticeable for the hip width, body length and rump length. These coefficients are sufficiently large to indicate the separation of the Jersey cattle into non-interbreeding groups, each of these groups being characterized by a definite type. Study of the residual variation, subject to the control of the inheritance, which is left within the groups shows that it has been much reduced in the cattle of any one herd. The individual owners have consequently utilized to nearly its full measure the inheritance which was present initially within the breed. Further selection within the herds consequently must be devoted to the more refined points, or if extensive changes in type are desired resort must be had to crosses between families of the desired types.

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