INHERITANCE OF THE COMPREST TRAIT
IN HEREFORD CATTLE

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TABLE OF CONTENTS

LIST OF TABLES

INTRODUCTION

During the past 25 years an increased consumer demand for smaller cuts of beef led to the marketing of younger, lighter-weight beef cattle than those marketed at the turn of the century. The demand for high grading, light-weight cattle caused breeders to select more intensely for cattle which would fatten at an early age. The advent of the practice of retailing pre-packaged beef in self-service super markets increased the demand for these light-weight, high grading carcasses.

During the late thirties and early forties there appeared in two of the major beef breeds a very early-maturing, compact type of breeding which was thought to have much merit in meeting this changed consumer demand. Forbes (1946) made the following observations about the "comprest" Herefords: "Then, out of nowhere, came "comprest" Herefords - and they were really a sight to behold. Although of popular Hereford bloodlines, the new type differed from anything theretofore seen. Extremely low-set on ideal underpinning, with smooth, bulging quarters and deep, wide middles to match with short, thick necks and beautiful heads, the calves and yearlings were sensational." Although the term "comprest" was usually restricted to the Herefords, a similar trait in Shorthorns was referred to as "compact". Some breeders envisioned these comprest cattle as having the ability to produce a desirable finish at an early age on limited amounts of grain or on pasture alone. Show ring preference, especially in the fat steer classes, reflected the shift in consumer demand for this new type. According to Stonaker (1952) the winnings of the comprest type began in 1941 with the grand champion steer at the National Western Livestock Exposition, Denver, Colorado. Since then animals of comprest type have won many of the steer shows in this country.

The trend toward smaller, earlier-maturing cattle apparently occurred without much regard for other productive qualities of these animals. Weber (1951), in a report which summarized a study supported by the American Hereford Association to compare the grazing and feedlot performance of small-, medium-, and large-type steers, made the following statement: "Most breeders and feeders probably would agree now that a shift toward blockier, earlier-maturing cattle was necessary for economic reasons associated in part at least with consumer demand for smaller beef cuts. But ultimate objectives, with respect to size and type of breeding cattle and breeding procedures that should be followed in attaining these objectives, have been subjects of considerable discussion and controversy." In a summary of this report, Weber stated: "The results of these tests indicate that medium-size cattle tend to combine the gaining ability of large cattle and the finishing ability of small cattle without sacrifice of efficiency of gain." However, the data presented did not make the above statement too obvious.

Knox (1957) reviewed the effect of type on performance and carcass characteristics in Hereford cattle. He also reported the results of type studies at the New Mexico station. He concluded that type did not effect feed efficiency, carcass quality, or rate of maturity. However, the compact type did possess the ability to fatten at lighter weights. Data at the New Mexico station indicated that large-type cows had a higher lifetime production as measured by pounds of calf produced and a greater life expectancy than compact-type cows.

Since little or no information was available relative to the productive traits of these small, early maturing cattle, a project was initiated in the Fall of 1949 at the Oklahoma Agricultural Experiment Station to compare the breeding and feeding performance of large-type (conventional) and small-type (comprest) Hereford cattle. The purposes of the investigation presented in this paper were to study the mode of inheritance of the comprest trait within a line of Hereford cattle and to develop an objective means of classifying the animals within this line. It was also believed that the gene responsible for the recessive (snorter) type of dwarfism might be related to the factor(s) responsible for the comprest trait. Therefore, the relationships which might exist between the comprest trait and the recessive type of dwarfism were also studied.

REVIEW OF LITERATURE

The Compress Trait in Hereford Cattle

Forbes (1946) stated that the TO Ranch at Raton, New Mexico, was one of the first to start breeding "compress" Herefords. Colorado Domino 68th., a bull purchased by the TO Ranch from the Wyoming Hereford Ranch at Cheyenne, Wyoming, appeared to be the foundation for this herd of compress Herefords. Colorado Domino 68th. was sired by Colorado 21st., whose dam, Duchess Astor, also possessed this same "compress" type and therefore Forbes credits her as being the foundress of "compress" Herefords.

Safley (1949) took 20 different body measurements from a group of 39 conventional type and 18 compress type Hereford steer calves at approximately one year of age. The calves were classified as to type by judges from the Animal Husbandry staff at Colorado A&M College. The measurements showing the smallest amount of overlap and the average differences between the two types were (1) length of cannon bone, 2.7 cm.; (2) height of chest, 5.9 cm.; (3) hip height, 11.0 cm.; and (4) wither height, 9.3 cm.. The conventional type steers had the largest average for all twenty measurements. On the average the compress type steers were deeper in the chest in relation to length of cannon bone and wither height than the conventional type steers. There was no overlap between the two types for the ratios of depth of chest to length of cannon bone and weight to wither height, the conventional type steers showing the largest ratio in the latter case. Considering the four measurements given above, differentiating measurements were given for classifying twelve month-old Hereford steers. These were (1) length of cannon bone, 20.1 cm.; (2) height of chest, 48.5 cm.; (3) hip height, 107.3 cm.; and (4) wither height, 101.8 cm.. All animals having at least three body measurements less than the above were classified as comprest and all animals having at least three measurements greater were classified as conventional type.

Stonaker et al. (1952) reported a highly significant mean difference in wither height and in length of cannon bone between 63 conventional and 24 comprest Hereford steers at approximately one year of age. The conventional type were 10.1 cm. taller at the withers and 2.8 cm. longer in their cannon bone than the comprest animals. While on feed the conventional animals gained .35 pound per day more than the comprest calves. All of these differences were significant at the 1% level. There was no significant difference between digestible nutrients required per hundredweight gain when each steer was fed until he graded low choice or had developed approximately one-half inch of fat over the ribs.

Willey et al. (1951) found a significant difference in average daily feed-lot gain between a group of seven comprest and seven regular type Hereford calves. The regular type gained .19 pound more per day than the comprest animals during the 285 day feeding period. They found no significant differences in feed consumption, feed efficiency, or dressing percentage between the two types.

Stonaker (1954) reported the results of comprest X comprest and compress X normal matings in cattle of Hereford breeding. Comprest X normal matings resulted in 50 comprest and 55 normal offspring, which closely approximated a 1:1 ratio. Each of five comprest bulls that were mated to comprest cows sired at least one dwarf. The dwarfs were generally, but not always, badly crippled or "crooked-legged". Wither height measurements at birth showed a difference of 4.2 inches between the dwarf and normal calves and a difference of 2.5 inches between the comprest and normal calves from comprest X comprest matings. He hypothesized that this type of dwarfing was due to a single partially dominant gene with CC dwarf, Cc comprest, and cc normal. On this basis a chi-square test was made on the comprest X comprest and comprest X normal matings shown below:

	Progeny						
	Dwarf		Comprest		Normal		
Matings	Obs.	Exp.	Obs.	Exp.	Obs.	Exp.	Chi-Square
Comprest X Normal	0	0	50	52	55	52	.04
Comprest X Comprest	14	11	17	22	13	11	1.91

A chi-square value of .04 for comprest X normal matings and 1.91 for comprest X comprest matings did not refute this hypothesis. He concluded that the comprest type of dwarfism was suggestive of the dwarfing action found in the Dexter breed.

Chambers et al. (1954a) reported the results of three-years' study involving comprest matings. In 1951 three comprest Hereford bulls were mated to a group of comprest Hereford cows and in 1952 two of the same bulls were mated to the same group of cows. From 45 such matings 37 offspring were produced of which eleven were definitely dwarfs. Three of the dwarf calves were of the "crooked-legged" type, five of them were "straight legged", and three dwarfs were very extreme and were not further classified because they were stillborn. Four early stage abortions or resorptions were known to have occurred. In 1953 two known dwarf-carrier Hereford bulls of non-comprest breeding and one known dwarf-carrier Angus bull were bred to 24 of these comprest cows and seven of their yearling heifers. Of 27 calves dropped, six were dwarfs, but none were of the "crooked-legged" type. One resorption or abortion occurred during early pregnancy. Five of the dwarfs were Herefords and one was a cross-bred Angus X Hereford. They concluded that the genes responsible for dwarfism in comprest and conventional Hereford and Angus cattle were either allelic or that the comprest cattle in this test carried the recessive dwarf gene in a high frequency.

Chambers et al. (1954b) reported that small-type (comprest) Hereford heifers weighed 34 pounds less at weaning than large-type (conventional) Hereford heifers, although the small-type heifers were approximately nine days older than the large-type heifers. The large-type heifers gained .16 of a pound more per day during the wintering periods and outweighed the small-type by 100-150 pounds at four years of age. Photographic measurements indicated that the large-type cows were approximately two and one-half inches higher at the withers and chest floor, three inches longer of body, and about one-half inch deeper of chest than the small-type animals. The small-type were more variable in weights and body measurements than the large-type.

Similar Traits in Other Breeds of Cattle

Crew (1923) described the Dexter breed of cattle and stated that they probably originated as a result of a cross between native Irish Kerry (black) and Red Devon. He cites the Kerry and Dexter Herdbook as describing the standard of excellence for the Dexter as follows (abbreviated):

Head - short and broad with great width between the eyes; muzzle large with distended nostrils.

Body - shoulders of medium thickness; hips wide; quarters deep and thick; flat, wide loin; straight underline; legs short (especially from knee to fetlock) strong and well placed under the body, which should be as close to the ground as possible.

Color- black or red.

Weight - bulls not over 900 pounds and cows not over 800 pounds.

Two undesirable characteristics were occasionally encountered in the breed - "bad tailhead" (tail originating forward along the back and arching upwards and backwards) and a combination of bent forelegs with inwardly turned hoofs.

Since the black Dexter was very popular at that time it became desirable to produce a true-breeding line. However, when Dexter X Dexter matings were made a deformed and still-born calf was produced. These abnormal calves appeared in all herds of Dexter cattle in numbers that ranged from 5-30% of the total births. Crew described these calves as follows: "The abnormalities which these still-born calves exhibited were constant, and so characteristic that the fetus is known as a "bull-dog" calf. The cranium is bulging, the nose markedly depressed, the lower jaw protruding, the upper lip is slit, baring the teeth, while the swollen tongue, thrust far out, curls up over the nose. Owing to the disproportionate development of the buttocks, the tail seems to have its origin far up on the back; usually there is a gaping deficiency of the abdominal wall through which the intestines pass to form a large umbilical hernia. The skin hangs loosely in folds; there is abundant subcutaneous fat. The limbs are ridiculously short and the digits unusually separated."

The following figures were supplied by English Dexter breeders: Total births - 646; Normal calves - 530; "Bull-dog" calves - 116. This is approximately one abnormal calf in every 5.5 births. Crew stated that the mating of Dexter X Dexter resulted in the production of four classes of calves in such proportions as to suggest that the Dexter was a Mendelian di-hybrid in respect to color and size. In an attempt to interpret the "bull-dog" calf, Crew proposed the following mode of inheritance: The original Dexter had the genetic composition $Bb(S\ l_1\ l_2)\ (s\ l_1\ l_2)$, B being the gene for black color, S being the gene for Dexter type, and l_1 and l_2 representing two other loci on homologous chromosomes. During the formative period of the breed two independent mutations occurred, L_1 and L_2, which intensified the action of the S gene with an additive effect. These mutations seemed to be linked to the factor S. Therefore, the genetic constitution of the "bull-dog" calf would be $(S, L_1\ L_2)\ (S, L_1\ L_2)$, omitting the genes for color.

Hutt (1934) in a review of lethal traits in domestic animals, stated that approximately one-fourth of the calves born from Dexter X

Dexter matings were "bull-dog" dwarfs. However, these same matings also produced Kerry-type cattle with longer legs and narrower heads than the Dexter. The correct Dexter type was apparently due to the presence in the heterozygous state of a partially dominant gene which caused the short legs and brachycephaly (head short and broad) considered good type in that breed. Segregation of genes produced the "bull-dog" dwarf, homozygous for the character, and the Kerry-type animal which lacked the gene entirely. This was confirmed by the fact that when Dexters were crossed with the longer-legged Kerry, no "bull-dog" dwarfs were produced.

Lush (1930) reported the occurrence of hereditary shortleggedness in cattle on several Texas ranches which he termed "duck-legged". The cattle were normal in every respect except that they appeared to be four to six inches shorter of leg than normal cattle. He proposed that it was the result of a single dominant gene and might be identical to the less extreme forms of dwarfness in the Dexter-Kerry cattle of Ireland, although there were no actual numbers on which to base this hypothesis.

Johansson (1953) reported on a type of achondroplasia observed in dairy cattle in Sweden. Achondroplasia has been defined as a form of dwarfing due to a disease affecting the long bones of the limbs before birth. One normal bull of the Swedish Red and White breed was mated to unrelated cows of mixed dairy breeding and produced 28 normal and 25 malformed calves (13 males and 12 females). The latter had a moderately bulging forehead, the upper jaw and the legs below the knee and hock were reduced in length and "flexed pasterns" occurred usually on the hind feet. The malformations were more extreme in males than in females. Only one bull and four heifer calves were raised. The bull was literally a dwarf and never reached potency to copulate. The heifers were less abnormal in size, conformation and behavior but their fertility and their milk yield after calving were subnormal. A comparison of body measurements is given below:

	Achondroplasts		Normal Animals	
No. of animals	4- ♀	1- ♂	14- ♀	6- ♂
Av. age, months	43	30	42	22
Height at withers, cm.	126.5	122	130.8	132.8
Depth of body, cm.	68.3	67	72.4	72.8

It was assumed that the defective animals were heterozygous for a gene for achondroplasia and that this gene had arisen by mutation in the pregerminal tissue of the sire of the malformed calves.

Stonaker et al. (1944) reported a small, thick, shortlegged type in the Shorthorn breed which he termed "compact". This "compact" type was distinguishable at birth and was distinct throughout life. Some of the animals had a tendency to be heavy in the shoulders and a bit crooked in the legs. The Kuhrt family near Edson, Nebraska was one of the first to begin concentrating the blood of this type. A compact bull bred by the Kuhrts was used in the Crews and Crews herd at Haigler, Nebraska, and compact bulls from Crews and Crews were used in the Lindgren herd, Wray, Colorado, and in the Colorado State College herd, Ft. Collins, Colorado.

In the Fall of 1953 unselected calf crops of the Kuhrt, Crews, and Lindgren herds were classified according to type. In the Crews and Lindgren herd all calves were out of "standard" type cows; in the Kuhrt herd 27 of the cows were of compact type and 20 were of standard type. All bulls were of compact type. They were out of standard cows by compact bulls. These results are given below:

Herd	Dam's type	Calves: Actual Compact	Calves: Actual Standard	Calves: Expected Compact	Calves: Expected Standard
Crews	Standard	43	31	37	37
Lindgren	Standard	21	17	19	19
Kuhrt	27 Compact 20 Standard	24	18	27	15

Five cows classified in the Kuhrt herd did not have calves, but which five were not known, so they were included in figuring the frequency of the compact gene at .29. Stonaker suggested that this trait was due to a single dominant gene since (1) no compact calves were produced from previous standard X standard matings in these herds, (2) compact X compact matings in the Kuhrt herd yielded only compact and standard, and (3) no more extreme degree of compactness was noted from compact X compact matings than from compact X standard matings. However, ten years later Stonaker (1954) reported extreme Dexter-type dwarfs had been observed from compact X compact matings, although no data were presented to substantiate this. He concluded that this type of dwarfism was suggestive of the Dexter-type dwarfism reported by Crew.

Mead et al. (1946) observed a herd of grade (mostly Jersey) milk cows in which a dwarfism problem had appeared. A group of mature cows was divided visually into normal and mutant types. Ten were classified as normal and 13 as mutant. Body measurements were taken on the cows and the mean differences between the two types were (1) height at withers, 13.8 cm.; (2) length of leg, 10.2 cm.; (3) length of body, 15.0 cm.; (4) depth of chest, 3.9 cm.; and (5) heart girth, 9.6 cm. The normal animals had the largest values for all measurements. All mutant animals traced to the Jersey bull Alta's Oxford of Alta Cresta (366491), who was also small in type. Since mutants appeared in the first calf crop of Oxford and his parents were of normal size, they assumed that it was due to a dominant mutation. Results of mating Oxford to unrelated normal heifers were:

	Normal	Mutant	Unclassified[a]	Chi-square
Observed	22	30	8	1.23 P = .30
Expected	26	26		

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[a] The eight unclassified animals were sold before the study was initiated.

When Oxford was mated to a mutant heterozygous cow, an achondroplastic type calf was produced resembling the dominant lethal of the Dexter breed. Because of this resemblence the two types of inheritance were assumed to be identical.

Gregory (1956) discussed several different types of dwarfism. These were short-headed (snorter) dwarfs and long-headed dwarfs in the Hereford and Angus breeds and two different Shorthorn types designated III_A and III_B, the latter being characterized by a heavy body with short legs. Different crosses between these four types of dwarfs within and between the Hereford, Angus and Shorthorn breeds yielded various numbers of comprest-like progeny and dwarfs of the above types. From these results Gregory concluded that all of the dwarf phenotypes tested were a part of the same genetic complex and that modifying genes were involved which differentiated specific phenotypes.

Koger _et al_. (1955) reported on several different types of dwarfism observed in Florida. Small, compact Brahmans which were termed "midgets" were believed to be caused by a recessive or an incompletely dominant gene with variable penetrance. A "guinea" condition was also reported in crossbred and Florida native cattle which was similar in expression to "comprest" Herefords and "midget" Brahmans. He reported that the mode of inheritance was apparently due to a dominant or an incompletely dominant gene, but apparently was a different gene than "comprest" in Herefords. No data were presented to substantiate this statement.

Dollahon _et al_. (1957) at the University of Florida stated the "midget" condition in Brahmans was inherited as an incomplete dominant or a recessive trait. The offspring from two midget X midget matings were midgets. A midget Brahman X long-headed Angus mating produced a dwarf which was similar to the midget but appeared less viable. The mating of a midget Brahman and a "snorter" Hereford produced a stillborn offspring, which by anatomical classification was a snorter dwarf. He reported that the "guinea" condition in Florida crossbred and native cattle appears to have descended from the Dexter. Both guinea X guinea and snorter Hereford X guinea matings produced guinea offspring. The number of matings of this type was not presented.

Damon (1958) hypothesized that the small-type Brahman cattle were the result of simple recessive inheritance, although he had no data to demonstrate this.

Gregory (1954) reported a condition of "wry" calves which appeared rather uniformly in calves of both Hereford and Angus breeding. The animals possessed distinct dwarf features but all afflicted animals were characterized by crooked forelegs. He proposed that this "wry" condition was produced by a specific interaction of one comprest gene with two conventional dwarf genes, although no supporting data were presented.

MATERIALS AND METHODS

The experimental animals used in this study consisted of 25 small-type (comprest) Hereford females and all their classifiable offspring during the years 1952 through 1957. Measurements from 25 large-type (conventional) Hereford females were used only to establish a means of classification. Fourteen Hereford bulls and one Angus bull were used in the comprest Hereford line. These bulls were selected to represent the various genotypes under study. These included comprest bulls, non-comprest bulls carrying the recessive dwarf gene, and non-comprest bulls supposedly free of the recessive dwarf gene. All the above animals were included in Project 670 of the Oklahoma Agricultural Experiment Station entitled "Improvement of Beef Cattle by the Application of Breeding Methods".

The 25 comprest females were purchased at weaning from the Bar 13 Ranch at Sheridan, Wyoming, during the Fall of 1949. All the heifers were descendents of Colorado Domino 68th., most of them through his son, Comprest Conqueror. About half the heifers were out of small-type cows with the other half being from dams of medium size. All were sired by small-type bulls. The 25 large-type heifers were purchased at the same time from three different breeders near Hereford, Texas. They were all moved to the Ft. Reno Experiment Station during October of 1949. Both types were managed under typical range conditions and were fed limited amounts of protein supplement during the winter. The bulls were either selected from other lines at the station or purchased from various breeders in an attempt to keep inbreeding at a minimum.

The heifers in both lines were bred to calve first in the Spring of 1952 when they were three years of age. All subsequent calf crops were likewise dropped in the spring of the years included in this study. A total of 165 calves was dropped during this study. A maximum of 154 calves within the comprest line was used to test any one hypothesis.

All foundation animals and their offspring were photographed behind a grid at weaning time. The grid was constructed of metal rods which were spaced six inches apart vertically and twelve inches apart horizontally. All animals were weaned in September or October with the exception of the foundation animals whose weaning photographs were taken in December of 1949. Similar photographs were taken of the foundation animals at various intervals from weaning to maturity. A number of heifers in the comprest line were saved each year to be added to the breeding herd.

From these photographs measurements were taken of height of withers, height at floor of chest, depth of chest, and length of body from pin bones to point of shoulder. All measurements were taken directly from the photographs and were estimated to the nearest tenth of an inch. These measurements served as a basis for classifying the animals involved in the study on the theory that the comprest gene, and possibly the recessive dwarf gene, brought about a reduction in size of the animal.

Correlations between the measurements by different individuals on the foundation comprest heifers at approximately 18 months of age were estimated. The formula used for computing the correlations is given on the next page.

$$r = \frac{\Sigma x_1 x_2}{\sqrt{(\Sigma x_1^2)(\Sigma x_2^2)}}$$

x_1 = measurement by individual 1
x_2 = measurement by individual 2

Correlations between measurements on the foundation compress females at different stages of maturity were calculated using the above formula where x_1 was the measurement at one age and x_2 the measurement at a later age.

Repeatability estimates of measurements made by the same person on the foundation compress females at 18 months of age were calculated. The formula used was:

$$R = \frac{\Sigma x_1 x_2}{\Sigma x_1^2}$$

x_1 = first measurement
x_2 = second measurement

The range in the ages at the time the first photographs of the foundation heifers were taken was from 257 to 321 days for the compress line and from 228 to 266 days for the large-type line. This indicated that an age correction for the body measurements was needed. It was decided to correct to 210 days of age since this would be approximately the average age at which the progeny from these lines would be photographed. The correction was made by simple regression of the measurement being corrected for on age. The regression formula was:

$$b = \frac{\Sigma xy}{\Sigma x^2}$$

x = age
y = measurement

Differences between regression coefficients for each measure between the two lines were tested by analysis of covariance techniques as described by Snedecor (1956).

Correlations between 210 day corrected measurements and actual mature measurements on the foundation compress females were calculated to determine how well the earlier measurements describe the mature animal. The same correlation formula given earlier was used to estimate this relationship. In these correlations x_1 was the age corrected measurement and x_2 was the actual mature measurement.

Wither height, height at floor of chest, and length of body were found to be different between the two lines. Depth of body was essentially the same for both lines. Therefore, the three measurements showing mean differences were used to develop a method of classification. It was decided that the most efficient method of classification would be to use these three measurements in the development of a discriminant function. The procedures developed by Fisher (1950) were used in this study and are described in Appendix A. In general, the discriminant function maximizes the ratio of the difference between the specific line means to the standard deviation within lines. One foundation female in each line was omitted in developing this function because they were not typical of the two lines to which they were assigned. This left 24 heifers in each line from which to compute the discriminant function.

After the discriminant function was developed, coefficients of variation ($s/\bar{x}$) were calculated for each corrected measurement within each line (wither height, chest height, and length of body), for the sums of the corrected measurements for each animal within each line, and for the discriminant function values derived for each animal within each line.

Component analyses for the same variables mentioned above were computed to determine the relative importance of the sources of variation (between lines and within lines) and to indicate the relative efficiency of the discriminant function for classification as compared to single measurements or the sums of the three measurements for individual animals.

The weanling measurements of all progeny within the comprest line were corrected to 210 days of age by the regression techniques developed for the foundation lines. The corrected measurements for each animal were used in computing a discriminant function value.

The age corrected mean values for each measurement within each foundation line were applied to the discriminant function, resulting in a mean discriminant function value for each line. The mean ($\bar{y}$) of the comprest line and the standard deviation (S.D.) computed from the pooled variance served as the basis for objective classifications, since the work reported in this paper was entirely within the comprest line. A certain range of these parameters was designated to each genotype of the three modes of inheritance considered in this study.

Due to the fact that the dwarf calves were easily identifiable at birth and seldom lived to weaning age, all dwarfs were classified by visual appraisal. The bulls involved in this study were also visually classified. All visual classifications were made by the project leader of this experiment. All foundation females and their offspring were classified by their discriminant function values. These data were analyzed by a chi-square "goodness of fit" test.

The foundation heifers and their progeny had also been classified visually by the project leader. A chi-square test was made on the results obtained by using these classifications.

A gene frequency analysis was made on the basis of the visual classifications described above. The zygotic ratios computed from the gene frequencies served as a basis for comparison to the observed ratios, making a chi-square test applicable.

A correlation between visual classifications and discriminant function classifications was estimated.

The mean body measurements for comprest and non-comprest animals classified by visual means and by the discriminant function were calculated.

Three hypotheses on the mode of inheritance of the comprest trait were tested based on classifications made with the discriminant function. The first hypothesis was that the comprest trait was due to a single pair of autosomal genes with partial dominance. The genotypes, phenotypes, and basis for classification are summarized below:

Genotype	Phenotype	Basis for Classification[a]
CC	dwarf	visual
Cc	comprest	$\bar{y} \pm 2$ S.D.
cc	normal	$> \bar{y} \pm 2$ S.D.

The second hypothesis was that three allelic genes (C, c^d, c) were responsible for the variations in body size and proportions. Both C and c^d would affect body size, but C would have the more drastic effect. The classification of the various genotypes is shown below:

Genotype	Phenotype	Basis for Classification[a]
CC	dwarf	visual
Cc^d	dwarf	visual
c^dc^d	dwarf	visual
Cc	comprest	$< \bar{y} \pm 1$ S.D.
cc^d	non-comprest (carrier)	$\bar{y} \pm 1$ S.D. to $\bar{y} \pm 2$ S.D.
cc	non-comprest (clean)	$> \bar{y} \pm 2$ S.D.

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[a] $\bar{y}$ is the mean discriminant function value for the comprest line;
S.D. is the standard deviation within lines;
$>$ is a symbol which signifies greater than;
$<$ is a symbol which signifies less than;
$\pm$ is a symbol which signifies plus and minus.

The third hypothesis tested was that the variation in body size and shape was due to two independent pairs of genes, designated *Cc* and *Dd*. Both *C* and *d* would reduce body size, but *C* would have the more marked effect. Either *CC* or *dd* or both in the homozygous state would result in a dwarf. This theory is summarized below:

Genotype	Phenotype	Basis for Classification[a]
CCDD	dwarf	visual
CCDd	dwarf	visual
CCdd	dwarf	visual
Ccdd	dwarf	visual
ccdd	dwarf	visual
CcDd	extreme compress	$< \bar{y} - 1$ S.D.
CcDD	compress	$\bar{y} \pm 1$ S.D.
ccDd	non-compress (carrier)	$\bar{y} \pm 1$ S.D. to $\bar{y} \pm 2$ S.D.
ccDD	non-compress (clean)	$> \bar{y} \pm 2$ S.D.

Under these various hypotheses, the bulls involved in this test were classified as listed on the following page.

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[a] $\bar{y}$ is the mean discriminant function value for the compress line;
S.D. is the standard deviation within lines;
$>$ is a symbol which signifies greater than;
$<$ is a symbol which signifies less than;
$\pm$ is a symbol which signifies plus and minus.

Year	Bull	Classification First theory	 Second theory	 Third theory
1952	S-17	Cc	Cc	CcDd
	S-22	Cc	Cc	CcDd
	S-33	Cc	Cc	CcDd
	182	cc	cc	ccDD
1953	S-17	Cc	Cc	CcDd
	S-33	Cc	Cc	CcDd
1954	DU-1	cc	cc^d	ccDd
	HC-2	cc	cc^d	ccDd
	48	cc	cc^d	ccDd
1955	D-95	cc	cc	ccDD
	BRL	cc	cc	ccDD
1956	4-24	Cc	cc^d	ccDd
	4-30	Cc	Cc	CcDd
	4-34	cc	cc	ccDD
1957	420	Cc	cc^d	ccDd
	450	cc	cc	ccDD
	469	cc	cc	ccDD

Four bulls (S-17, S-22, S-33, and 4-30) were of compress type from compress breeding. Two bulls (420 and 4-24) were of compress type but not of compress breeding. The three bulls used in 1954 (DU-1, HC-2, and 48) were of medium type and were known to carry the recessive (snorter) dwarf gene. Five bulls (182, D-95, BRL, 450, and 469) were of medium or large type and were supposedly free of the recessive dwarf gene.

Bull 4-34 was a non-compress segregate from compress breeding and was predicted to be free of the recessive dwarf gene based upon X-ray classification.

The first hypothesis (one pair of genes) was also tested on the basis of visual classifications of all progeny. Visual classifications on the theories of a multiple allelic series and two pairs of genes were available for the first three calf crops (1952 through 1954) and served as the basis for a chi-square test. For testing the theory of three allelic genes, the $\underline{cc^d}$ genotype was assigned to those animals in the compress line which bordered between compress and non-compress in type. In assigning genotypes for the theory of two independent pairs of genes, approximately half of the foundation compress females were assumed to carry the recessive dwarf gene. Therefore, only the smallest half of the compress females were assigned the genotype CcDd.

A gene frequency analysis was made on the last two hypotheses mentioned above, i.e. - three allelic genes and two pairs of independent genes. In analyzing the results it was assumed that only dwarf, compress, and non-compress animals were distinguishable. Therefore, the expected zygotic classes were divided only into these three types for comparison with the observed types.

The proposed genotypes for all bulls remained the same when testing hypotheses on the nature of inheritance of variations in type of animals classified by both visual means and the discriminant function.

RESULTS AND DISCUSSION

Methods of Classification

Correlations between photographic measurements taken by different individuals on 24 foundation comprest females at approximately 18 months of age were calculated. Correlations found were .97 for height at withers, .96 for height at floor of chest, .88 for depth of body, and .95 for length of body. All correlations were significant at the 1% level. These correlations indicate that the variations in photographic measurements taken by different people are relatively unimportant.

The repeatability of photographic measurements by the same person was estimated on the same group of animals indicated above. The estimates of repeatability were .98, .87, 1.00 and 1.00 for height at withers, height at floor of chest, depth of body and length of body, respectively. The repeatability for height of chest was the lowest of the four measurements taken. This might have been due to the fact that unconscious corrections were made for the position in which the animal was standing the second time the measurements were taken. In general, all of the repeatabilities were high enough that single measurements would be relatively accurate as compared to averages of two or more measurements.

Correlations between weanling measurements and measurements taken at different stages of maturity were estimated on the same group of females. These are presented in Table I. The weanling measurements were all

TABLE I CORRELATIONS BETWEEN WEANLING MEASUREMENTS AND MEASUREMENTS AT DIFFERENT STAGES OF MATURITY ON 24 COMPREST FEMALES

	12-1-49 (weaning)			
	Ht. at withers	Ht. at chest	Depth of body	Length of body
9-14-50 (18 mos. old)				
Height at withers	.87**			
Height at chest		.69**		
Depth of body			.57**	
Length of body				.58**
9-14-51 (30 mos. old)				
Height at withers	.64**			
Height at chest		.49*		
Depth of body			.37	
Length of body				.48*
9-4-53 (maturity)				
Height at withers	.59**			
Height at chest		.54**		
Depth of body			.08	
Length of body				.16

* Significant at 5% level of probability.
** Significant at 1% level of probability.

significantly correlated with the same measurements at 18 months of age. The correlation between depth of body at weaning and at 30 months of age was not significant. All other correlations were significant, but they were not as large as those obtained between the two earlier photographs. Only height at withers and height at chest floor at weaning were significantly correlated with the same measurements at maturity ($P < .01$). Height at weaning was more closely associated with mature height than were depth and length of body at weaning and at maturity.

The unadjusted mean differences observed between the comprest and and non-comprest foundation heifers at the time of the first photographs were 2.7 inches for wither height, 2.3 inches for chest height, and 2.9 inches for length of body. The two groups did not differ in depth of body. The non-comprest line had the largest mean values for those measurements which were different. Since no mean difference was found between the lines in respect to depth of body, this measurement was omitted from further study.

The age correction for body measurements at weaning was accomplished by simple regression techniques. The regressions were computed on the 24 foundation females within each line (comprest and conventional). The regression coefficients for wither height on age were .017164 for the comprest line and .017938 for the conventional line. The regression coefficients for height at chest floor on age were .001965 for the comprest line and .000501 for the conventional line. Regression of .036358 and .023387 were observed for comprest and conventional animals, respectively, for length of body on age. Since neither of the regression coefficients for any of the measurements were significantly different between lines (Appendix B), an average of the two regressions for each measurement was used as the basis for correction factors. It was felt that this average regression would allow more accurate classifications to be made since both comprest and non-comprest animals were segregating in the comprest line. The average regressions were .017551 for wither height on age, .001233 for chest height on age, and .029872 for length of body on age. The formula used for correcting measurements to 210 days of age was:

$$\text{C.M.} = X - (\text{Age} - 210)\ \bar{b}$$

Where: C.M. = corrected measurement

X = actual measurement

Age = actual age in days at time of photograph

$\bar{b}$ = average regression coefficient for measurement being considered

All measurements (wither height, chest height, and length of body) from both lines of foundation females and for all progeny from the comprest line were corrected to 210 days of age by the above method. Regression coefficients based on the body measurements from all progeny in both lines might have been a more accurate basis for age correction factors due to the larger numbers involved.

The age corrected mean differences between the two foundation lines at the time of the first photograph were 3.1 inches for wither height, 2.5 inches for chest height, and 3.6 inches for length of body. The large-type line had the largest average values for all three measurements. It was felt that these differences could serve as a basis for developing an objective classification system for separating comprest and non-comprest segregates.

The correlations between the 210 day corrected measurements and mature measurements on the foundation compress females were .71 ($P < .01$) for wither height, .49 ($P < .05$) for height at chest, and .29 (non-significant) for length of body. This indicates that the age correction had the greatest effect on wither height and length of body. Chest height was not appreciably affected by the correction.

The ranges of corrected measurements in the compress foundation line were 32.2 to 37.1 inches for height at withers, 14.0 to 17.9 inches for height of chest, and 31.9 to 40.0 inches for length of body. In the conventional foundation line ranges of 35.3 to 41.6 inches for wither height, 17.2 to 21.0 inches for chest height, and 36.5 to 44.1 inches for length of body were observed. The least amount of overlap between the two lines was in the measurement for height at chest floor. This might indicate that length of leg is the most important difference between compress and non-compress animals.

As was indicated in the previous section, the 210 day corrected body measurements on the 24 females in each line were used to develop a discriminant function. The procedures used are shown in Appendix A. The following equation was obtained which could be used to derive a numerical value (Y) for each animal by substituting the age adjusted measurements for X_1, X_2, and X_3:

$$Y = X_1 + 6.862489\,X_2 + 1.083064\,X_3$$

Where:

$Y =$ discriminant function value

$X_1 =$ corrected measurement for wither height

$X_2 =$ corrected measurement for chest height

$X_3 =$ corrected measurement for length of body

The discriminant function placed nearly seven times as much emphasis on chest height as on either wither height or length of body. This was due to the fact that the two lines differed most consistently in height of chest. Approximately equal emphasis was given to wither height and length of body by the function.

All 210 day corrected measurements were applied to the formula and Y values were obtained for each animal. The corrected means for each foundation line were applied to the formula to derive the mean Y value for each line. The mean for the comprest line was 183.537105 and for the conventional line it was 207.692358, with a mean difference between the two lines of 24.155253. The standard deviation for the Y values was 8.975586. Therefore, a certain amount of overlap between the two lines for respective Y values was observed. Eleven of the 48 foundation animals were in this overlap range. Since there are undoubtedly many factors which affect variations in body size other than the ones considered in this study, the overlap was not surprising.

The coefficients of variation (C.V.) for Y values were 3.68% for the conventional line and 5.33% for the comprest line. Therefore, the comprest line was more variable in body measurements than the conventional line. This may have been due to an inability to select perfectly for the comprest trait in establishing the foundation line.

Coefficients of variation for each corrected measurement within the foundation lines were obtained. In the comprest line the coefficients of variation were 3.69% for height at withers, 6.86% for height at floor of chest, and 4.67% for length of body. The coefficients of variation for the conventional line were 3.70% for wither height, 4.29% for chest height, and 5.72% for length of body. For wither height there was little or no difference in the relative amount of variation between the lines. However, height of chest was over 50% more variable in the compress line than in the conventional line. The conventional line was somewhat more variable in length of body than was the comprest line.

For the sums of the corrected measurements for each animal, the comprest line had a C.V. of 4.16% and the conventional line had a C.V. of 3.90%. This is in general agreement with the above results, indicating that the comprest line varied more in body measurements than the conventional line.

The component analyses for each corrected measurement, for the sums of corrected measurements for each animal, and for the discriminant function values are presented in Table II. As compared to the sums of measurements, the discriminant function increased the variance between lines by only 4.1%. This was probably due to an inability to select perfectly for each type in establishing the foundation lines, thereby increasing the amount of overlap for body measurements between the two lines. The fact that the discriminant function placed more emphasis on height at chest floor is understandable, since this measurement had the greatest variance between lines for any single measurement. The function placed somewhat more emphasis on length of body than on height at withers, although the variance between lines was greater for the latter. The only evident explanation for this is that the mean difference between lines for length of body was greater than for height at withers.

Visual classifications were also made on the foundation animals and their offspring. This method of classification depends on the ability of the individual or individuals making the classifications. There is the

TABLE II COMPONENT ANALYSES FOR DISCRIMINANT FUNCTION VALUES, SUMS OF CORRECTED MEASUREMENTS, AND INDIVIDUAL CORRECTED MEASUREMENTS

	Source	d.f.	M.S.	E.M.S.	Percent of total var.
[a]	Total	47			
	Between lines	1	7,048.68	$\sigma^2+24\sigma_L^2$	79.0%
	Within lines	46	77.06	σ^2	21.0%
[b]	Total	47			
	Between lines	1	991.90	$\sigma^2+24\sigma_L^2$	74.9%
	Within lines	46	13.67	σ^2	25.1%
[c]	Total	47			
	Between lines	1	110.42	$\sigma^2+24\sigma_L^2$	71.1%
	Within lines	46	1.84	σ^2	28.9%
[d]	Total	47			
	Between lines	1	77.01	$\sigma^2+24\sigma_L^2$	77.7%
	Within lines	46	.91	σ^2	22.3%
[e]	Total	47			
	Between lines	1	149.11	$\sigma^2+24\sigma_L^2$	59.6%
	Within lines	46	4.10	σ^2	40.4%

[a] Component analysis for discriminant function values.

[b] Component analysis for sums of corrected measurements.

[c] Component analysis for height at withers.

[d] Component analysis for height at chest floor.

[e] Component analysis for length of body.

possibility of bias entering into the classifications. Knowledge of pedigree or of previous treatment could affect visual classifications. Visual appraisal has the advantage that more factors can be appraised during classification than by the system developed above.

Hypotheses Tested

Three different hypotheses on the mode of inheritance of the comprest trait were tested using discriminant function values as the basis for classification. The hypotheses were (1) one pair of genes, (2) three allelic genes, and (3) two pairs of independent genes. The same hypotheses were also tested on the basis of visual classifications. A gene frequency analysis was computed for the second and third hypotheses listed above based on visual classifications.

The first hypothesis tested using discriminant function values as the means of classification was that the inheritance of the comprest trait was by a single pair of genes (C and c) exhibiting partial dominance. The results of this analysis are presented in Table III. Three different types of matings resulted in a total of 136 classified progeny during the period from 1952 through 1957. A chi-square of 1.53 was observed for 53 comprest X comprest matings. This value was not large enough to signify rejection. In the second type of mating (comprest X non-comprest), five dwarfs were observed when none were expected. Under most circumstances this would be a basis for rejecting the hypothesis. However, it was known that the recessive dwarf gene was also present in some of the bulls, thereby confusing the observed results. If these five dwarfs were assumed to be of the recessive type and were eliminated from the analysis, a chi-

TABLE III OBSERVED AND EXPECTED TYPES OF OFFSPRING BASED ON THE HYPOTHESIS OF ONE PAIR OF GENES[a]: CLASSIFICATION BY DISCRIMINANT FUNCTION

			Progeny						
			Observed			Expected			
	Type of mating	No. of matings	Dwarf	Cc	cc	Dwarf	Cc	cc	Chi-square
b	Cc X Cc	53	17	25	11	13.25	26.50	13.25	1.53 .50>P>.25
	Cc X cc	69	5	36	28	0	34.50	34.50	
	cc X cc	14	1	3	10	0	0	14	
c	Cc X cc	48	0	29	19	0	24	24	2.08 .25>P>.10
	cc X cc	11	0	2	9	0	0	11	
d	Cc X Cc	53	17	25	11	13.25	26.50	13.25	1.53 .50>P>.25
	Cc X cc	21	5	7	9	0	10.50	10.50	
	cc X cc	3	1	1	1	0	0	3	

---

[a] CC - dwarf; Cc - comprest; cc - non-comprest.

[b] Results of all matings; 1952-1957 calf crops, inclusive.

[c] Results of matings eliminating bulls known or suspected to be carrying recessive dwarf gene: 1952-1957 calf crops, inclusive.

[d] Results of matings including only bulls known or suspected to be carrying recessive dwarf gene: 1952-1957 calf crops, inclusive.

square of 1.00 (non-significant) results. In the third type of mating (non-comprest X non-comprest), one dwarf and three comprest animals were observed but none were expected. If we assume that the dwarf was of the recessive (snorter) type, then the comprest animals could possibly be due to errors in classification or to some expression of this gene in heterozygotes.

The second part of Table III includes only those matings involving bulls that were believed to be free of the recessive dwarf gene. Out of 48 comprest X non-comprest matings no dwarf calves were produced, with a non-significant chi-square of 2.08. This tends to substantiate the earlier belief that the recessive type of dwarfism was confusing the results. Out of 11 non-comprest X non-comprest matings, two unexpected comprest animals were observed. As mentioned above, these animals could be the result of errors in classification or of the heterozygous expression of the recessive dwarf gene.

The third part of this table included only matings to bulls which were known or suspected to be carrying the recessive dwarf gene. Here again dwarf animals occurred when not expected under the hypothesis assumed, which adds evidence to the theory that the recessive dwarf gene was confusing the results.

The second hypothesis was that this trait was due to three allelic genes (C, c^d, c). This hypothesis was based on the theory that $\underline{c}^d$ gene might account for the unexpected dwarfs that appeared. There were six different types of matings for a total of 136 offspring. The results of these matings are presented in Table IV. Five of these mating types resulted in unexpected offspring. This hypothesis was able to account

TABLE IV OBSERVED AND EXPECTED TYPES OF OFFSPRING BASED ON THE HYPOTHESIS OF THREE ALLELIC GENES[a]: CLASSIFICATION BY DISCRIMINANT FUNCTION

		Progeny								
		Observed				Expected				
Type of mating	No. of matings	Dwarf	Cc	cc	cc^d	Dwarf	Cc	cc	cc^d	Chi-square
Cc X Cc	30	14	5	5	6	7.50	15.00	7.50	0	
Cc X cc	30	0	12	11	7	0	15	15	0	
cc X cc	11	0	0	9	2	0	0	11	0	
Cc X cc^d	29	6	9	11	3	7.25	7.25	7.25	7.25	5.07 $.25 > P > .10$
cc X cc^d	24	1	6	10	7	0	0	12	12	
cc^d X cc^d	12	2	3	3	4	3	0	3	6	

[a] CC, Cc^d, c^dc^d - dwarf; Cc - comprest; cc^d - non-comprest (carrier); cc - non-comprest (clean).

for most of the dwarfs, since only one occurred that wasn't expected. However, 15 of $\underline{cc}^d$ type and nine of $\underline{Cc}$ type were observed when not expected. This would indicate that either the system of classification was in error or that the hypothesis was invalid.

Table V gives the results obtained under the third hypothesis; i.e. - the comprest trait is due to two independent pairs of genes (Cc and Dd). Under this theory either $\underline{CC}$ or $\underline{dd}$ would result in a dwarf. Out of nine classes of matings, five resulted in unexpected types of progeny. Three of the remaining four classes yielded chi-square values that were in the region of rejection. Either the hypothesis or the method of classification should be questioned.

There are several factors which might have caused the method of classification to be in error, most of them being associated with the method by which the measurements were secured. The weanling photographs of the foundation heifers which served as the basis for developing the discriminant function used in this study were the first attempt at this station to secure measurements by this method. Certain mistakes were made in technique which limited its accuracy. The position of the animal in relation to the grid and the camera is one of the primary sources of error in photographic measurements. The camera used to take these photographs was mounted on a tripod and focused on the center of the grid. Therefore, the animal should be standing as near to the grid as possible and in the center of the chute to prevent distortions. Also, weanling calves are more nervous and do not stand in position as well as older cattle. Therefore, calves were not always "set up" properly to yield accurate photographic measurements.

TABLE V OBSERVED AND EXPECTED TYPES OF OFFSPRING BASED ON THE HYPOTHESIS OF TWO INDEPENDENT PAIRS OF GENES[a]: CLASSIFICATION BY DISCRIMINANT FUNCTION

Type of mating	No. of matings	Progeny										Chi-square
		Observed					Expected					
		Dwarf	CcDd	CcDD	ccDd	ccDD	Dwarf	CcDd	CcDD	ccDd	ccDD	
CcDd X CcDd	6	2	0	0	3	1	2.62	1.50	.75	.75	.38	10.19 $.05 > P > .025$
CcDd X CcDD	24	12	1	4	3	4	6	6	6	3	3	11.17 $P \cong .025$
CcDd X ccDd	13	2	0	3	1	7	3.25	3.25	1.62	3.25	1.62	24.23 $P < .005$
CcDd X ccDD	6	0	0	2	2	2	0	1.50	1.50	1.50	1.50	2.00 $.75 > P > .50$
CcDD X ccDd	16	4	2	4	2	4	0	4	4	4	4	
CcDD X ccDD	24	0	2	8	5	9	0	0	12	0	12	
ccDd X ccDd	12	2	1	2	4	3	3	0	0	6	3	
ccDd X ccDD	24	1	1	5	7	10	0	0	0	12	12	
ccDD X ccDD	11	0	0	0	2	9	0	0	0	0	11	

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[a] CCDD, CCDd, CCdd, Ccdd, ccdd - dwarf; CcDd - extreme compress; CcDD - compress; ccDd - non-compress (carrier) ; ccDD - non-compress (clean).

Some of the mistakes mentioned above had been recognized and corrected at the time the 18 month photographs were taken. To indicate the relative inaccuracy of the weanling photographs to predict mature size, correlations between 18 month photographic measurements and subsequent measurements on the foundation animals were calculated. These correlations are presented in Table VI. All correlations were highly significant ($P < .01$) except the one for depth of body between the 18 month measurements and mature measurements. Whether a cow has calved or not will greatly influence her depth of body measurement and probably accounted for the size of the observed correlation for this measurement. If these correlations were compared to those in Table I, it will be seen that the 18 month photograph was a better indication of mature size than the weanling photograph. This was due in part to the fact that certain photographic errors had been corrected. Some of the maternal influences had also been reduced at 18 months of age. Also, these later correlations would naturally be higher since age differences between measurements had been reduced.

Although the weanling photographs and subsequent measurements of the foundation females were subject to several sources of error, it was necessary to use them in developing the objective method of classification. This was essential because the animals to which the discriminant function was to be applied must be comparable to those used in developing the function. Since most of the offspring were photographed only at weaning, it was necessary to develop the discriminant function on the weanling photographs of their dams.

Although the accuracy of this particular discriminant function may be questionable when derived from such data as these, its potential should

TABLE VI CORRELATIONS BETWEEN 18 MONTH MEASUREMENTS AND SUBSEQUENT MEASUREMENTS ON 24 COMPREST FEMALES

	9-14-50 (18 mo. old)			
	Ht. at withers	Ht. at chest	Depth of body	Length of body
9-14-51 (30 mo. old)				
Height at withers	.88**			
Height at chest		.77**		
Depth of body			.90**	
Length of body				.77**
9-4-53 (maturity)				
Height at withers	.76**			
Height at chest		.80**		
Depth of body			.45*	
Length of body				.57**

* Significant at 5% level of probability.
** Significant at 1% level of probability.

not be overlooked. If a discriminant function is based on accurate data, it will probably be the best objective means available for classifying units into two or more groups. Therefore, more use could be made of discriminant functions in biological research to eliminate the bias inherent in human judgement.

Since the accuracy of classification of the individual animals in this particular case was doubtful, it was decided to test the three theories on the basis of visual classifications.

The first hypothesis tested was that the comprest trait was due to a single pair of partially dominant genes. These results are presented in Table VII. The first part of this table presents the results of all matings, resulting in 154 classifiable offspring. A chi-square of 3.33 (non-significant) resulted from 49 comprest X comprest matings. The chief discrepancies were that too many dwarfs and too few non-comprest animals were observed. In the other mating groups unexpected progeny were observed and therefore eliminated a chi-square test.

The second part of the table includes only those matings in which the bulls were believed to be free of the recessive dwarf gene. The comprest X non-comprest matings resulted in a chi-square of .51, which was non-significant. This substantiated the earlier belief that the recessive dwarf gene was confusing the results. As under the discriminant function classifications for the one pair of genes theory, non-comprest X non-comprest matings resulted in two comprest animals which were not expected, supposedly due to errors in classification.

When matings with bulls known or suspected to be carrying the recessive dwarf gene were analyzed, a larger number of dwarfs were observed

TABLE VII OBSERVED AND EXPECTED TYPES OF OFFSPRING BASED ON THE HYPOTHESIS OF ONE PAIR OF GENES[a]: VISUAL CLASSIFICATIONS

			Progeny						
			Observed			Expected			
	Type of mating	No. of matings	Dwarf	Cc	cc	Dwarf	Cc	cc	Chi-square
b	Cc X Cc	49	17	24	8	12.25	24.50	12.25	3.33 .25>P>.10
	Cc X cc	77	5	37	35	0	38.50	38.50	
	cc X cc	28	1	4	23	0	0	28	
c	Cc X cc	49	0	22	27	0	24.50	24.50	.51 .50>P>.25
	cc X cc	22	0	2	20	0	0	22	
d	Cc X Cc	49	17	24	8	12.25	24.50	12.25	3.33 .25>P>.10
	Cc X cc	28	5	15	8	0	14	14	
	cc X cc	6	1	2	3	0	0	6	

[a] CC - dwarf; Cc - comprest; cc - non-comprest.

[b] Results of all matings: 1952-1957 calf crops, inclusive.

[c] Results of matings eliminating bulls known or suspected to be carrying recessive dwarf gene: 1952-1957 calf crops, inclusive.

[d] Results of matings including only bulls known or suspected to be carrying recessive dwarf gene: 1952-1957 calf crops, inclusive.

than were expected. The appearance of unexpected dwarfs in the two types of matings where none were expected strongly indicates the presence of the recessive dwarf gene.

In general, the results obtained on the basis of visual classifications and on discriminant function classifications for this hypothesis were essentially the same. The chief distinction was that more animals were visually classified as non-comprest than by the discriminant function.

A correlation of .54 ($P < .01$) was calculated between visual classifications and discriminant function classifications under the one pair of genes theory. This correlation was based on all foundation animals and their classifiable offspring. As previously mentioned the main discrepancy was due to the fact that more animals were visually classified as non-comprest than by the discriminant function.

The corrected mean measurements for comprest and non-comprest animals and the respective differences between the two types for these measurements on the basis of visual and discriminant function classifications are summarized in Table VIII.

TABLE VIII CORRECTED MEAN MEASUREMENTS OF COMPREST AND NON-COMPREST ANIMALS FOR THE TWO SYSTEMS OF CLASSIFICATION

	Discriminant function class.			Visual class.		
	Non-comprest	Comprest	Diff.	Non-comprest	Comprest	Diff.
Wither height (inches)	37.6	34.9	2.7	36.8	35.2	1.6
Chest height (inches)	18.2	16.2	2.0	17.8	16.3	1.5
Length of body (inches)	41.7	38.3	3.4	40.9	38.5	2.4

The discriminant function required comprest animals to have smaller measurements and non-comprest animals to have larger measurements than did the visual classifications. This resulted in greater mean differences between the two types under the objective classification system than under visual classifications. If the true differences between the two types were not this great, then the discriminant function would classify some animals as comprest which were really non-comprest in type. The differences between the two types under visual classifications are relatively small. It is questionable that differences of this magnitude could serve as an accurate basis for visual classifications in the absence of other criteria.

The second hypothesis tested was that the comprest trait was due to three allelic genes (C, c^d, c). Classifications were available on the foundation animals and their progeny from 1952 through 1954. Five different types or classes of matings resulted in a total of 61 offspring. These results are presented in Table IX. Two of the classes yielded unexpected genotypes and one resulted in a highly significant chi-square value when tested. There were too few animals in the other classes for any conclusions. Most of the observed discrepancies were in the Cc and $\underline{cc^d}$ classes. If these two genotypes had a similar effect on body size, it would have been difficult to distinguish between them. Therefore, part of the observed inconsistencies might have been due to an inability to separate these two genotypes because they had a similar phenotypic expression.

Table X presents the results of 60 matings based on the hypothesis that the trait under study is due to two pairs of independent genes (Cc and Dd). From eight different classes of matings only two resulted in unexpected types of offspring. All other classes yielded non-signif-

TABLE IX OBSERVED AND EXPECTED TYPES OF OFFSPRING BASED ON THE HYPOTHESIS OF THREE ALLELIC GENES[a]: VISUAL CLASSIFICATIONS

		Progeny								
		Observed				Expected				
Type of mating	No. of matings	Dwarf	Cc	cc	cc^d	Dwarf	Cc	cc	cc^d	Chi-square
Cc X Cc	29	11	13	2	3	7.25	14.50	7.25	0	
Cc X cc	4	0	1	3	0	0	2	2	0	1.00 $.50 > P > .25$
Cc X cc^d	23	5	12	6	0	5.75	5.75	5.75	5.75	12.65 $P \cong .005$
cc X cc^d	2	0	0	2	0	0	0	1	1	2.00 $.25 > P > .10$
cc^d X cc^d	3	1	2	0	0	.75	0	.75	1.50	

[a] CC, Cc^d, c^dc^d - dwarf; Cc - comprest; cc^d - non-comprest(carrier); cc - non-comprest(clean).

TABLE X OBSERVED AND EXPECTED TYPES OF OFFSPRING BASED ON THE HYPOTHESIS OF TWO INDEPENDENT PAIRS OF GENES[a]: VISUAL CLASSIFICATIONS

Type of mating	No. of matings	Progeny										Chi-square
		Observed					Expected					
		Dwarf	CcDd	CcDD	ccDd	ccDD	Dwarf	CcDd	CcDD	ccDd	ccDD	
CcDd X CcDd	11	5	3	3	0	0	4.81	2.75	1.38	1.38	.69	4.01 .50>P>.25
CcDd X CcDD	18	6	5	2	3	2	4.50	4.50	4.50	2.25	2.25	2.22 .75>P>.50
CcDd X ccDD	3	0	0	1	0	2	0	.75	.75	.75	.75	3.67 .50>P>.25
CcDd X ccDd	13	2	4	4	0	3	3.25	3.25	1.62	3.25	1.62	8.54 .10>P>.05
CcDD X ccDD	1	0	0	0	0	1	0	0	.50	0	.50	1.00 .50>P>.25
CcDD X ccDd	9	3	2	1	0	3	0	2.25	2.25	2.25	2.25	
ccDd X ccDd	3	1	0	2	0	0	.75	0	0	1.50	.75	
ccDD X ccDd	2	0	0	0	0	2	0	0	0	1	1	2.00 .25>P>.10

---

[a] CCDD, CCDd, CCdd, Ccdd, ccdd - dwarf; CcDd - extreme compress; CcDD - compress; ccDd - non-compress (carrier); ccDD - non-compress (clean).

icant chi-square values, although one value approached significance. This was probably the best "fit" obtained, although the deviations observed were great enough to prevent any conclusions from being made.

The methods of classification used restricted matings to a certain type; i.e. - comprest X comprest, comprest X non-comprest, etc. Unexpected progeny could be attributed to errors in classification of either sire, dam, or offspring. Misclassification of sire and/or dam would result in the most serious mistakes due to the fact that it would affect more animals than the misclassification of a single calf. Therefore, it was decided to test two hypotheses by a gene frequency analysis on the basis of visual classifications. The advantage of this type of analysis is that it does not restrict the types of individual matings but depends on the gene "pool" available in predicting expected results. This reduces the effect of errors of classification of individuals. Although this does not permit a very critical test of any one theory, it could indicate which theory has the greater probability. Under both hypotheses the gene frequencies for both the sires and the dams were calculated and expected zygotic ratios computed from these frequencies. Random mating was assumed in calculating the zygotic frequencies. These zygotic ratios were then subdivided into dwarf, comprest, and non-comprest types on the basis that these types could be visually detected in the offspring. The expected numbers were then tested against the observed numbers by a chi-square test.

The first hypothesis tested on the basis of visual classifications was that variations in type were due to three allelic genes (C, c^d, and c). Table XI presents the results of this test. Only one year's results (1954) of the six years studied deviated enough from expected values to yield a

TABLE XI OBSERVED AND EXPECTED TYPES OF OFFSPRING BASED ON THE HYPOTHESIS OF THREE ALLELIC GENES[a]: CLASSIFICATION BY VISUAL METHODS

	Gene Frequency[b]			Offspring			
Year	Gene	Dams	Sires	Type	Expected	Observed	Chi-square
1952	C	.43	.43	Dwarf	2.97	6	4.50
	c^d	.03	.00	Cc	7.16	4	.25> P > .10
	c	.54	.57	cc	4.87	5	
1953	C	.43	.50	Dwarf	5.04	5	.30
	c^d	.05	.00	Cc	9.98	11	.90>P>.75
	c	.52	.50	cc	5.98	5	
1954	C	.40	.00	Dwarf	5.75	6	17.59
	c^d	.06	.50	Cc	5.00	13	P<.005
	c	.54	.50	cc	14.25	6	
1955	C	.39	.00	Dwarf	0	0	.03
	c^d	.05	.00	Cc	10.53	11	.90>P>.75
	c	.56	1.00	cc	16.47	16	
1956	C	.39	.09	Dwarf	3.60	6	1.95
	c^d	.06	.16	Cc	10.94	11	.50>P>.25
	c	.55	.75	cc	17.46	15	
1957	C	.35	.00	Dwarf	1.25	0	4.40
	c^d	.07	.11	Cc	8.41	13	.25>P>.10
	c	.58	.89	cc	17.34	14	
Total	C	.39	.14	Dwarf	18.52	23	6.06
	c^d	.06	.14	Cc	52.60	63	.05>P>.025
	c	.55	.72	cc	75.88	61	

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[a] CC, Cc^d, c^dc^d - dwarf; Cc - comprest; cc^d - non-comprest (carrier); cc - non-comprest (clean).

[b] Gene frequencies weighted for differences in number of progeny per parent; random mating assumed in calculating zygotic ratios.

significant chi-square. Too many compres t animals and too few non-compres t animals were observed to approximate the expected values for these classes. However, this was the general trend and these deviations were great enough in the analysis for all years to result in a significant chi-square of 6.06 ($P < .05$). This might indicate that this particular theory is unfounded if the system of classification is accurate.

The theory that two independent pairs of genes were responsible for variations in type was also tested. These results are presented in Table XII. The 1954 data yielded a significant chi-square value, but this was the only year in which the deviations were great enough to signify rejection. As in the above hypothesis, too many compres t and too few non-compres t animals were usually observed. If the recessive dwarf gene also caused a reduction in body size, animals carrying this gene might have been classified as one of the compres t types. This could account for the excess of compres t animals and lack of non-compres t animals which were observed. However, these deviations were not consistent enough to result in a significant chi-square for all years studied. It appears that the hypothesis of two independent pairs of genes has the greater probability of being the true mode of inheritance, as compared to the theory of three allelic genes. Due to the lack of sensitivity of this test, however, no conclusive statements can be made.

Table XIII presents the actual results by years and by sires for visual classifications on the basis of a single pair of genes. This is presented to enable the reader to better understand the nature and results of the problems involved in this study.

TABLE XII OBSERVED AND EXPECTED TYPES OF OFFSPRING BASED ON THE HYPOTHESIS OF TWO INDEPENDENT PAIR OF GENES[a]: CLASSIFICATION BY VISUAL METHODS

	Gene Frequency[b]			Offspring			
Year	Gene	Dams	Sires	Type	Expected	Observed	Chi-square
1952	C	.43	.43	Dwarf	3.82	6	2.41
	c	.57	.57	Cc	6.72	4	.50>P>.25
	D	.80	.57	cc	4.46	5	
	d	.20	.43				
1953	C	.43	.50	Dwarf	6.25	5	.55
	c	.57	.50	Cc	9.40	11	.90>P>.75
	D	.79	.50	cc	5.36	5	
	d	.21	.50				
1954	C	.40	.00	Dwarf	3.24	6	7.42
	c	.60	1.00	Cc	8.28	12	.01>P>.025
	D	.73	.50	cc	12.48	6	
	d	.27	.50				
1955	C	.39	.00	Dwarf	0	0	.03
	c	.61	1.00	Cc	10.53	11	.90>P>.75
	D	.74	1.00	cc	16.47	16	
	d	.26	.00				
1956	C	.39	.09	Dwarf	3.21	6	2.69
	c	.61	.91	Cc	12.20	11	.50>P>.25
	D	.73	.75	cc	16.59	15	
	d	.27	.25				
1957	C	.35	.00	Dwarf	.77	0	2.90
	c	.65	1.00	Cc	9.18	13	.25>P>.10
	D	.74	.89	cc	17.05	14	
	d	.26	.11				
TOTAL	C	.39	.14	Dwarf	17.24	23	3.88
	c	.61	.86	Cc	57.20	62	.25>P>.10
	D	.75	.73	cc	71.55	61	
	d	.25	.27				

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[a] CCDD, CCDd, CCdd, Ccdd, ccdd - dwarf; CcDd - extreme compress; CcDD - compress; ccDd - non-compress (carrier); ccDD - non-compress (clean).

[b] Gene frequencies weighted for differences in number of progeny per parent; random mating assumed in calculating zygotic ratios.

TABLE XIII RESULTS OF MATINGS WITHIN A COMPREST LINE BASED ON THE HYPOTHESIS OF ONE PAIR OF GENES[a]: VISUAL CLASSIFICATIONS

Year	Sire	Type of sire	Type of dam	Progeny Dwarf	Progeny Comprest	Progeny Non-comprest
1952	182	cc	Cc	0	0	2
	S-17	Cc	Cc	1	2	0
	S-22	Cc	Cc	2	1	0
	S-33	Cc	cc	0	0	2
			Cc	3	1	1
1953	S-17	Cc	cc	0	2	1
			Cc	1	5	2
	S-33	Cc	Cc	4	4	2
1954	48	cc	Cc	1	5	2
	DU-1	cc	cc	1	2	1
			Cc	4	3	2
	HC-2	cc	cc	0	0	2
			Cc	0	3	0
1955	D-95	cc	Cc	0	0	1
	BRL	cc	cc	0	0	6
			Cc	0	11	9
1956	4-24	Cc	cc	0	1	1
			Cc	2	4	2
	4-30	Cc	Cc	4	2	0
	4-34	cc	cc	0	0	5
			Cc	0	4	7
1957	420	Cc	cc	0	1	0
			Cc	0	5	1
	450	cc	cc	0	1	8
			Cc	0	3	3
	469	cc	cc	0	1	1
			Cc	0	4	5

[a] CC - dwarf; Cc - comprest; cc - non-comprest.

SUMMARY

The purposes of this investigation were to study the mode of inheritance of the compress trait in a line of Hereford cattle and to develop an objective means of classifying the animals in this line. Relationships which might exist between the comprest trait and the recessive (snorter) dwarf gene were also studied.

The experimental animals consisted of 25 comprest Hereford females and all of their classifiable offspring during the period from 1952 through 1957. Fourteen Hereford bulls and one Angus bull, representing the various genotypes under study, were used in the comprest line. All of these animals were handled under typical range conditions at the Ft. Reno Experiment Station, El Reno, Oklahoma.

All foundation females and the progeny from the comprest line were photographed behind a grid at weaning time. Measurements of height of withers, height at floor of chest, depth of body and length of body were taken from these photographs. Depth of body was found to be essentially the same for comprest and non-comprest cattle and was eliminated from further study. The other measurements for all foundation females and their offspring were standardized to 210 days of age by regression techniques. The corrected measurements for comprest and non-comprest foundation heifers were used to develop a discriminant function. This served as the basis for objective classifications of the progeny of comprest parents on

the theory that the comprest trait reduced body size.

The foundation comprest females were more variable in body measurements than the foundation non-comprest females. The least amount of overlap between the two foundation types was in the measurement for height at floor of chest.

Although the use of the discriminant function resulted in a greater variance between lines than any single measurement or the sums of measurements for each animal, it was only slightly more effective in this respect than the measurement for height at chest floor.

Visual classifications were also available for all animals involved in this study.

Three hypotheses on the mode of inheritance of the comprest trait were tested by a chi-square "goodness of fit" test using both means of classification (discriminant function and visual). The hypotheses were (1) one pair of genes exhibiting partial dominance, (2) three allelic genes, and (3) two pairs of independent genes. A maximum of 154 calves within the comprest line was used to test any one hypothesis.

All hypotheses tested on the basis of discriminant function classifications resulted in the appearance of unexpected types of progeny. However, it was known that the photographic measurements of the animals at weaning which were used to develop the basis for classification were not very precise. Therefore, errors in classification could be responsible for the occurrence of unexpected types of progeny. In order to compare the two methods of classification, the same hypotheses were tested on the same group of animals classified by visual means. Unexpected types of offspring were observed for each theory tested, although the discrepancies generally were not as great as those observed for discriminant function classifications. The theory of two independent pairs of genes fitted the data more nearly than the other theories considered.

Gene frequency analyses were computed on the basis of visual classifications for the theories of three allelic genes and two pairs of independent genes. It was felt that this type of analysis would allow for some of the errors in classification. A significant chi-square of 6.06 ($P < .05$) was observed for the hypothesis of three allelic genes for a total of 147 matings. However, the analysis based on two independent pairs of genes resulted in a non-significant chi-square of 3.88 for 146 matings.

From these results it appears that the hypothesis of two independent pairs of genes being responsible for the variations in type is the more probable one of the theories tested. The recessive (snorter) dwarf gene may also reduce body size, but perhaps not to the extent of the comprest gene. Therefore, an animal may be classified as comprest if it carries either the comprest gene or the recessive dwarf gene. No definite conclusions can be made about the inheritance of the comprest trait due to the inaccuracies involved in the classifications used in this study.

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APPENDIX

APPENDIX A

DEVELOPMENT OF THE DISCRIMINANT FUNCTION

The discriminant function used in this study was developed according to the procedures described by Fisher (1950). The purpose of the discriminant function was to maximize the ratio of the differences between the specific means to the standard deviation within lines.

The 210 day corrected measurements used to develop the function were height at withers (X_1), height at floor of chest (X_2), and length of body (X_3) on 24 foundation females in each line (comprest and conventional). The procedures used are described below.

(1) The corrected mean values for each measurement in each line and the mean differences between lines were computed:

	Conventional	Comprest	Difference
X_1	38.1	35.0	3.1
X_2	18.4	15.9	2.5
X_3	40.0	36.4	3.6

(2) The corrected sum of squares and cross-products for measurements within each line were calculated and the respective values were added:

	Conventional	Comprest	Sum
X_1	46.10	38.72	84.82
X_2	14.39	27.44	41.83
X_3	121.38	67.04	188.42
X_1X_2	17.34	23.95	41.29
X_1X_3	44.95	35.13	80.08
X_2X_3	9.48	26.09	35.57

(3) These sums were used to construct the matrix indicated below:

$$\begin{array}{cccc} & X_1 & X_2 & X_3 \\ X_1 & 84.82 & 41.29 & 80.08 \\ X_2 & 41.29 & 41.83 & 35.57 \\ X_3 & 80.08 & 35.57 & 188.42 \end{array}$$

(4) The matrix was inverted by the abbreviated Doolittle procedure as described by Anderson <u>et</u> <u>al</u>. (1952), resulting in the inverse matrix below:

$$\begin{array}{cccc} & X_1 & X_2 & X_3 \\ X_1 & .031972 & -.023830 & -.009090 \\ X_2 & -.023830 & .046239 & .001399 \\ X_3 & -.009090 & .001399 & .008906 \end{array}$$

(5) Each row of the inverse matrix was multiplied by the observed mean differences between lines, resulting in coefficients (C) for a linear equation:

$$C_1 = 3.1(.031972) \neq 2.5(-.023830) \neq 3.6(-.009090) = \underline{.006814}$$

$$C_2 = 3.1(-.023830) \neq 2.5(.046239) \neq 3.6(.001399) = \underline{.046761}$$

$$C_3 = 3.1(-.009090) \neq 2.5(.001399) \neq 3.6(.008906) = \underline{.007380}$$

(6) C_1 was converted to unity by multiplying all C values by 146.756677. These values were the coefficients for the fitted equation or function being solved for:

$$Y = C_1X_1 \neq C_2X_2 \neq C_3X_3$$

$$= X_1 \neq 6.862489\ X_2 \neq 1.083064\ X_3$$

The corrected body measurements for each animal were then applied to the above equation and the resulting Y values served as the basis for classification.

APPENDIX B

Part I. Analysis of covariance for regressions of wither height on age.

Source[a]	d.f.	Ex^2	Exy	Ey^2	d.f.	Ed^2	M.S.
Cc	23	35,114.62	602.59	49.77	22	39.43	
cc	23	28,575.33	512.57	54.50	22	45.31	
Pooled					44	84.74	1.93
Reg. Coeff.					1	0	0
Common	46	63,689.95	1,115.26	104.27	45	84.74	

$H_o : B_1 = B_2$ $F = \frac{0}{1.93} = 0$ Non-significant d.f. = 1,44

Part II. Analysis of covariance for regressions of chest height on age.

Source[a]	d.f.	Ex^2	Exy	Ey^2	d.f.	Ed^2	M.S.
Cc	23	35,114.62	69.00	27.49	22	27.35	
cc	23	28,575.33	14.33	14.12	22	14.11	
Pooled					44	41.46	.94
Reg. Coeff.					1	.04	.04
Common	46	63,689.95	83.33	41.61	45	41.50	

$H_o : B_1 = B_2$ $F = \frac{.04}{.94} = .04$ Non-significant d.f. = 1,44

Part III. Analysis of covariance for regressions of length of body on age.

Source[a]	d.f.	Ex^2	Exy	Ey^2	d.f.	Ed^2	M.S.
Cc	23	35,114.62	1,276.70	112.21	22	65.79	
cc	23	28,575.33	668.30	139.45	22	123.82	
Pooled					44	189.61	4.31
Reg. Coeff.					1	2.65	2.65
Common	46	63,689.95	1,945.00	251.66	45	192.26	

$H_o : B_1 = B_2$ $F = \frac{2.65}{4.31} = .61$ Non-significant d.f. = 1,44

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[a] Cc - foundation comprest line; cc - foundation non-comprest line.

VITA

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