A GENETIC HISTORY OF MODERN YORKSHIRE SWINE IN CANADA
II. IMPORTANT ANCESTORS AND LENGTH OF GENERATION

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Introduction

Heredity is a universal fact and familiar to everyone, although man is often not fully conscious of its significance. It is well known that members of the same family exhibit many of the same characteristics. As a simple illustration of heredity, the offspring of a corn plant will develop into corn plants; and, an offspring of a Shorthorn cow bred by a Shorthorn bull will develop into a Shorthorn animal. Moreover any particular kind or strain of corn or cattle produces individuals of that strain. This phenomenon of inheritance is evident in man as well as in the lower forms of life. This resemblance among individuals related through descent is called heredity.

From earliest times men have shown interest in heredity. They recognized the facts that "like begets like", and that one of the most remarkable features of the process of reproductive activity is that new individuals tend to resemble their ancestors fairly closely. They realized to a less extent that offspring differ in some characteristics among themselves and from their parents, or that there is a regular pattern of variation. It is very likely that the ancient idea of purebreeding as applied to man stemmed from this first knowledge of the facts of inheritance. This idea together with the interest in human ancestry became manifest in those peoples who developed pronounced caste systems in society. Striving for purity of inheritance was most strikingly evident in Royal families. Man, in early times, began to apply this knowledge of the facts of inheritance, more or less unconsciously perhaps, in improving his beasts of burden by choosing these individuals best suited to his requirements.

The early husbandmen bred their animals without any detailed knowledge of the reproductive processes, or the principles of animal breeding. However, development and improvement of the various breeds of livestock was achieved to a considerable extent before the real science of genetics was established.

Development of distinct breeds of livestock began in England about the latter part of the eighteenth century. Breeders, inspired by Robert Bakewell who had made an outstanding contribution to breeding methods, and who had many followers, began developing groups of animals closely related to each other and similar in type. Most of the modern breeds developed in Britain came from these groups. The remarkable results achieved by these early breeders were to a large extent subsequent to the practice of isolating the descendants of particular animals whose exceptional qualities the breeder wished to perpetuate. Breeders were reluctant to make outcrosses when their own stock seemed superior to that of their neighbors. Mating largely within their own herds, and making few, if any, outcrosses inevitably resulted in a certain amount of inbreeding which proved to be an effective means of fixing the type. However, inbreeding was not the only tool employed in the development of a particular breed, selection was also practiced by the breeders in so far as it was within their power to decide which animals were to have many offspring.

The coefficients of correlation developed by Wright (1922) have made it possible to analyse in terms of inbreeding and relationship the breeding programs employed by the early breeders. Inbreeding is usually considered as the mating of animals more closely related to each other than the average within the population concerned. Relationship between two individuals is "simply the probability that, because they are related by descent, they will be alike in more of their genes than unrelated members of the same population."

Genetic studies of the different breeds of livestock indicate the amount of inbreeding practiced as well as the success of the breeding plans in concentrating or disseminating the genes of outstanding individuals. Analyses have been made of several breeds of cattle, two breeds of sheep, a number of breeds of horses, and a few breeds of swine. The Yorkshire, being the most important breed of swine in

Canada, and whose genetic structure heretofore has not been analysed, was chosen for a similar study.

Review of the Literature.

Methods of Analysis

As a natural consequence of his interest in heredity, man began to put emphasis on ancestry in human pedigrees. Even today it is not uncommon to hear someone stressing with pride the importance of a certain ancestor in his lineage. Man has long realised that the hope of his posterity was latent in his genealogy. Until comparatively recent years he had no scientific methods at his disposal by which he could analyze pedigrees and measure the actual relationship between an ancestor and its offspring. In the late nineties, Francis Galton, who was the first to apply methods of statistical analysis to the phenomenon of variation and heredity, devised a means of measuring the degree of relationship between parent and offspring; moreover, he endeavoured to determine the particular contribution which was made to an individual by each of its ancestors.

In livestock breeding the modern manner of using pedigrees was inaugurated in rural England during the latter part of the eighteenth century. Robert Bakewell initiated a constructive breeding program that was imitated by many of his followers. Without the aid of analytical methods to indicate the contribution of an ancestor back in the pedigree, he was successful in establishing scientifically sound systems of breeding. He began his constructive work about the year 1760, making use, even at this early date, of all the tools (inbreeding, outcrossing, and selection) which livestock breeders are trying to put into general use today. Bakewell bred the old Longhorn cattle, Leicester sheep, and Shire horses, and his best proven sires, some of which featured in his sire-letting practice, no doubt assumed an influential role in the improvement of British livestock.

With the increase in the number of purebred animals, as well as in the number of breeders, it became difficult for the individual breeder to remember all the foundation animals far back in the pedigrees. Consequently herd books were established not only for recording of pedigrees and to protect the purity of existing strains, but also to provide the knowledge required by the breeder when buying new breeding stock. George Coates published the first Shorthorn Herd Book in 1822. The early history of other profitable breeds of livestock, generally speaking, follows a somewhat similar pattern of development.

After the rediscovery of the Mendelian principles of heredity great strides were made in the comparatively new field of genetics. At the start of this century scientists and breeders alike began to show interest in the genetic status of the existing breeds of livestock. They wished to determine by means of pedigree study just how much inbreeding had been practiced in certain breeds of livestock and how far breeders had maintained the resemblance of the breed to prominent individuals by concentrating the blood of these influential ancestors. As a result various formulae have been brought forward in an effort to measure the intensity of inbreeding, and the degree of relationship between individuals produced by the different systems of mating.

Pearl (1917) proposed a measure of inbreeding and relationship based on a "ratio between the number of different ancestors an animal actually had and the number it would have had if there had been no inbreeding". According to Pearl the degree of relationship is, in general, proportional to the number of different ancestors which two individuals have in common out of the total number possible. His coefficients of relationship are calculated in two slightly different ways according to whether they are being evaluated in connection with inbreeding coefficients or whether they are being calculated independently. Furthermore, the coefficient of relationship is computed for each ancestral generation. Except for their historical interest, Pearl's coefficients are practically obsolete; in any case, when different systems of mating are taken account they give inconsistent results.

Wright (1922, 1923) devised coefficients of inbreeding and relationship on the basis of Mendelian inheritance. The general formula for inbreeding is

$$Fx = \sum \left[\left(\tfrac{1}{2}\right)^{n + n' + 1} (1 + Fa) \right] ,$$

where Fx is the coefficient for the individual and Fa for the common ancestor of his sire and dam, while n and n' are the number of generations between the sire and the common ancestor, and the dam and the common ancestor respectively. The coefficient "measures accurately the percentage departure from the number of homozygous factors in the random-bred stock toward complete homozygosis." In his earlier paper Wright (1922) states that it measures the correlation between uniting gametes.

Wright's formula for the coefficient of relationship is

$$Rxy = \frac{\sum \left[\left(\tfrac{1}{2}\right)^{n + n'} (1 + Fa) \right]}{\sqrt{(1 + Fx)\ (1 + Fy)}} .$$

In this formula a represents a common ancestor; x and y the two individuals whose relationship we wish to measure; n and n' the number of generations the individuals x and y respectively are removed from the common ancestor; and Fa, Fx and Fy the coefficients of inbreeding of a, x and y respectively. The coefficient of relationship is "the percentage of genes which are probably identical in the two related individuals because of their relationship by descent". Wright states that it measures the correlation between the genetic constitutions of the two individuals concerned.

The measurements of inbreeding and relationship are interdependent. An individual's inbreeding depends upon the relationship between its sire and dam. The equations connecting the two coefficients where S represents the sire, and D the dam, and X the offspring, are:

$$Fx = \frac{Rsd}{2} \times \sqrt{(1 + Fs)(1 + Fd)}\ , \text{ and } Rsd = \frac{2Fx}{\sqrt{(1 + Fs)(1 + Fd)}}\ .$$

Wright and McPhee (1925) have developed an approximate method by which much of the detail of the long method involving writing out complete pedigrees may be avoided. This method "rests on the tabulation of random samples of the pedigrees of the sire and dam." The need to count the number of generations to the closest common ancestor is eliminated; it is only necessary to note that there is a tie in the random lines back of the sire and dam. The coefficient of inbreeding becomes either 50 per cent or 0 according to whether a tie does or does not occur. Wright and McPhee have found that the shortened method is nearly as accurate as the more detailed method when determining coefficient of inbreeding for a large group, but for the individual such determination means practically nothing. The coefficient of relationship is also calculated readily by the approximate method.

Breed Analyses

Wright's coefficients have been used by several investigators in their genetic analysis of the pure breeds of livestock. A study of these Mendelian analyses clearly indicates that in at least some of the modern breeds important ancestors have noticeably influenced the characteristics of their respective breeds.

Wright (1923) was the first to initiate a method of breed analysis on the basis of the values of his Mendelian coefficients. He made a genetic study of the Duchess Family of Shorthorns as bred by Thomas Bates. Starting with Colling's stock, which was already 40 per cent inbred, Bates maintained a high relationship to Colling's bull, Favourite. Wright states that presumably there was a closer relationship of the Duchess herd to Favourite, even forty years after his death, than between an ordinary parent and offspring. It is exceptionally interesting to note too, that the relationship between Duchess cows and the bulls with which they were mated was kept at the constant point of 60 per cent. Furthermore, Bates was able to keep the percentage of inbreeding from exceeding the 49 per cent mark by constantly introducing a "dash of fresh blood". He used sires, whether bred by another breeder or himself, which had an average inbreeding of about 40 per cent. Bates was able to mold a type of Shorthorn possessing a considerable percentage of the characteristics represented by Charles Colling's bull, Favourite.

McPhee and Wright (1925) presented a rather complete genetic study of the Shorthorn breed; they found numerical measures of the genetic situation in the breed throughout its history. They chose as a base that period in the Shorthorn history just prior to the date on which Favourite was calved. The latter is considered to be one of the prominent ancestors of the breed. They found that the relationship of the whole breed to Favourite, calved in 1793, rose from 0 per cent in 1790 to 44 per cent in 1825. The comparable figure for 1920 was 55 per cent. This high relationship figure for 1920 is significant because it means that the Shorthorn breed then resembled Fvourite more than the average resemblance between sire and son among the foundation stock of Favourite's time. McPhee and Wright assumed that by 1920 such uniform diffusion of Favourite's blood had taken place that no further change was possible. Favourite may also be said to have sired the entire breed.

During what may be referred to as the second period in the development of the Shorthorns, when Amos Cruikshank began developing the Scotch type, another sire assumed great importance, namely, Champion of England. He was dropped in 1850. McPhee and Wright found that he had an inbreeding coefficient of 18.4 per cent which was nearly similar to that of the entire breed at that time (18.0). Their study further revealed that his relationship to the breed at the time of his birth was about 26 per cent, but in the years following it gradually increased by 20 per cent, so that in 1920 his relationship to the breed was 46 per cent. His relationship to Favourite was about 49 per cent, as compared with the 50 per cent for the breed average. The authors of this study considered the fact in the latter statement important because it showed "that no amount of concentrating of the blood of Champion of England could change to any appreciable extent the breed relationship to Favourite". Champion of England, an outstanding individual product of Amos Cruikshank's breeding, has been the most important sire since Favourite in affecting the character of the breed.

As part of their genetic analysis McPhee and Wright made a comparison of Champion of England's relationship to the breed with his average relationship to 20 leading Shorthorn prize-winning sires at the International Livestock Exposition in 1918-22. His relationship to the prize-winning sires was 47 per cent, which exceeds by about 1 per cent his relationship to the breed. Furthermore, they found about 21 per cent of Champion of England's blood in these animals. This figure compares favourably with Makin's calculations of 22.5 per cent. Complete pedigrees were used in Malin's analysis of the prize-winners. The authors concluded that there was no significant difference between the amount of Champion of England's blood carried by the prize-winners and the average for the breed as a whole. Finally, they state that Champion of England's blood has become so thoroughly diffused throughout the breed that no further concentration was possible.

Using Wright's formula to calculate the inbreeding coefficient for the Shorthorn breed, McPhee and Wright report a rise from 0 per cent in 1790 to 17 per cent inbreeding in 1810. By 1825 the inbreeding had risen to 20 per cent, but from that time on the inbreeding coefficient had changed slightly, being 26 per cent in 1920. This means that in 1920 the breed was 20 per cent more homozygous than the original stock. In addition, the authors found that the breed in 1920 was a fairly homogeneous unit because the inter se relationship, that is, the relation between any two random animals, was about 40 per cent.

McPhee and Wright (1926) presented a study of the British Dairy Shorthorns. Their investigation involved the selection of two groups: one a random sample of 100 cows, and the s econd, a sample of 100 high producing cows. They found that the relationship to Favourite shown by the latter group was 55.7 ± 2.4, and that shown by the former group was 56.61 2.3 per cent. The average relationship to Favourite shown by the 200 cows was 56.1 ± 1.6 per cent. The difference between this figure and 55.2 ± 2.3 per cent for the breed in 1920 was only 0.9 ± 2.8 per cent, a figure which the authors considered as insignificant.

The average coefficient of relationship between the 200 cows and Champion of England was found to be 42.1 ± 2.7 per cent. The difference between this figure and 45.5 ±

2.3 per cent for the Shorthorn breed in 1920 amounted to 3.4 ± 2.3 per cent. The large probable error fairly well nullifies any significance that may be attached to this difference. Furthermore, the authors found that, in tracing back random lines of ancestry of a Dairy Shorthorn cow, about the same proportion traced to Champion of England as in the case of a Shorthorn cow selected at random without regard to milk production.

The average coefficient of inbreeding for the 200 cows was found to be 27.5 ± 1.4 per cent while that for the 1920 Shorthorns was 26.1 ± 2.0 per cent. The difference of 1.5 ± 2.4 per cent between the inbreeding of the Dairy Shorthorns and the average inbreeding of the entire British Shorthorn breed was not considered significant. With respect to inter se relationship the authors found that "the average relationship of the milking Shorthorn cows to each other, or even to random animals of the whole Shorthorn breed, did not differ significantly from the average relationship between random Shorthorns."

Brockelbank and Winters (1931) made a study of the methods of breeding the best Shorthorns in the United States. They found that inbreeding had not been a factor in the production of show winning Shorthorns during the period 1924-1928. In the broad sense of the term, selection based on individuality, on ancestry, on progeny, or on the combinations of these in different degrees, was believed to be mainly responsible for the production of show winners. According to their study the small amount of inbreeding for the Present Day Show Winners demonstrated the fact that outcrossing too, had been practiced by the breeders. The authors concluded that "show winners tend to produce show winners, and that breeders had been making assortative matings." Finally, their study indicated that the percentage of inbreeding for the breed as a whole increased gradually.

Lush, Holbert, and Willham (1936) outlined the genetic history of the Holstein-Freisian breed of cattle in the United States, covering the period from 1880 to 1931. Their genetic study indicated that the cow De Kol 2d, had exerted more influence on the breed than any other individual. Her relationship to the breed in 1931 was 8 per cent, which practically makes her a "great grandmother of the breed." Lush et al state that she has probably furnished about one-tenth of the genes of the breed at the time this study was made. Another noteworthy fact gleaned from this study is that nearly all of De Kol 2d's relationship is direct because her sire was not found in any line except through her, and her dam was found in only eight collateral lines of descent. Eleven other prominent individuals, which had the highest relationship to the breed, were her two sons sired by her grandsons, five other sons or grandsons, and four other descendants of hers less related to her than grandsons. The only other animal of note, and unrelated to De Kol 2nd, was Netherland Prince. Though his relationship to the breed in 1931 was only 5.3 per cent, he featured as the most influential animal in the samples of 1889 and 1899.

A study of the group of high producers and prominent show animals indicated that these animals did not differ much from the breed average in their inbreeding or in their relationship to the remote ancestors.

The average length of generation in the Holstein-Freisian cattle was found to be about four and one half years. The coefficient of inbreeding for the breed was 4.0 per cent in 1931; the loss of heterozygosis was about four-tenths of one per cent per generation. The average inter se relationship had risen to 3.4 per cent in 1931, and since the actual inbreeding exceeded the expected Lush et al concluded that there may have been a mild tendency to form family lines.

Stonaker's (1943) studies of the inbreeding structure of the Aberdeen Angus breed of cattle in the United States revealed that Black Prince of Tillyfour (77) had the highest average relationship to the breed in 1939 (24.1%). He might also be considered as a grandsire to the breed. Other important ancestors include Hanton (80) with a relationship to the breed of 21.3 per cent; Rob Roy MacGregor (106), 14.9; Grey Breasted Jock (113), 15.5; Earl Marshall (1831) (80), 14.0; and Blackcap Revolution (287269), 12.0 per cent.

Furthermore, Stonaker's study has revealed that about two-thirds of Earl Marshall's relationship to the breed was direct because of his many sons and daughters, while the other third could be attributed to collateral relationship from his sibs, cousins, etc. No other important ancestor surpassed Earl Marshall in his direct relationship to the breed. This study reveals clearly that an individual may have little direct relationship to the breed but yet have high total relationship largely because of the cumulative importance of his sire's and/or dam's offspring. This situation is found in the case of Blackcap Revolution, a son of Earl Marshall. His direct relationship through his own sons and daughters constituted only 43 per cent of the total, while the remainder resulted from collateral relationship.

We learn from this study, too, that not only certain important ancestors, but groups of individuals such as a herd, vary in their influence upon a breed. Stonaker found that five herds provided about 65 per cent of the genes in the Angus breed. Of these, the most important group was the herd of Hugh Watson.

Next to the Shorthorns, the Aberdeen Angus breed of cattle is probably more highly inbred than any other breed so far studied. Stonaker found that the average inbreeding percentages of the samples of this breed in the United States in 1900, 1910, 1920, 1930, and 1939 were 8.9, 12.7, 10.8, 14.2, and 11.3 respectively. The inter se relationships in each of the five samples were 9.4, 16.3, 12.2, 6.1, and 13.3 per cent.

The average interval between generations was found to be 5.4 years.

A complete genetic history of another beef breed, the Hereford cattle in the United States, has been made by Willham (1937). He discovered that Beau Brummel, calved in 1890 and a grandson of Anxiety 4th, had the highest relationship to the breed of any of the animals in this analysis. In 1930 he was related to the breed by 24.6 per cent which is nearly equivalent to the relationship between an offspring and its grandsire. In other words, Beau Brummel then was practically a grandsire to the whole breed.

Another prominent individual was Don Carlos (33734). He was calved in 1886 and used all his life in the Gudgell and Simpson herd. As the most important son of Anxiety 4th, he held a relationship of 22.6 per cent to the breed in 1920. The fact that he was used extensively to concentrate the blood of Anxiety 4th, and that he had seven full brothers and sisters used frequently in the breed, contributed to his high relationship. Don Carlos was the sire of Beau Brummel.

Anxiety 4th, a bull imported by Gudgell and Simpson in 1881, was related to the breed by 18.5 per cent in 1930. In addition to these three bulls, there were several other animals including Lamplighter (51834), a three-quarter brother of Beau Brummel, and a few cows including Dowager 6th and Belle which had a fairly high relationship to the breed. However, it is interesting to note that nearly all of the animals which had distinctly high relationships to the Hereford breed were either ancestors, descendants or mates of Anxiety 4th.

The average interval between generations was found to be 5.4 years, a figure which is similar to that found by Stonaker for the Aberdeen Angus breed. This genetic analysis indicated that the generation interval had tended to lengthen during the years prior to 1930. The probable reason for this fact, as suggested by Willham, is that the breed perhaps was approaching an equilibrium in numbers. Such a condition, he concluded, would tend to make the average age of the animals higher than it would be if the population were still increasing rapidly in numbers. Another factor,which may have been responsible for part of this lengthening, was a tendency among the cattle breeders of the period to keep those animals originally bred by Gudgell and Simpson to the extreme end of their periods of fecundity.

Willham found an inbreeding coefficient of 8 per cent for the Hereford cattle in 1930. This amount of inbreeding represents an increase in homozygosisty of .68 per cent per generations during the period from 1860 to 1930. The inter se relationship increased gradually from 1860 to 1930 when it reached a point of about 17 per cent.

A genetic study using Wright's method was also made of the Brown Swiss breed of cattle in the United States by Yoder and Lush (1937). Their results indicated that no one animal dominated the whole Brown Swiss breed in the United States. Two bulls, William Tell in 1909 and College Boy in 1929, possessed the highest relationship to the breed, 9.2 and 9.1 per cent respectively. In this breed it appears that the cows had almost the same chance as the sires of spreading their genes to the whole breed. The highest relationship for cows was 8.6 per cent for Josie in 1909, and 7.4 per cent for Bertha M in 1929. However, the highest relationships were exhibited in the Show groups where the sires were related to the whole groups by 14.9 per cent, and the cows had values as high as 13.5 per cent and 9.5 per cent. The authors stated that sires used extensively in the show herd have a considerable chance of appearing frequently in the pedigree of a sample of Show winners.

The average interval from birth of parent to birth of offspring is 5.4 years. In 1929 the Brown Swiss breed was found to be 3.8 per cent inbred. This amount of inbreeding means that there was a loss of about one half of one per cent per generation of the existing heretogygosis. Also in the last sample the inter se relationship was found to be 4.3 per cent. Because there was a small but significant excess of actual inbreeding over the expected, the authors concluded that there may have been some tendency toward family formation.

Using the short method evolved by Wright and McPhee (1925) for examining the pedigrees of the breed population,

A. B. Fowler (1933) made a genetic study of the Ayrshire breed of cattle. However, for the purpose of obtaining full information on the systems of mating used in producing the high milk producers, as well as the average milk producers, Fowler employed the "long method" of analysis as evolved by Wright (1922). In his genetic study Fowler found that three sires from the Drumjoan herd made the most remarkable contribution to the breed as a whole because they accounted for 25 per cent of the inbreeding. Burnhouses (8) was the first bull to have an effective influence on the breed; he was found to be responsible for 18.07 per cent of the total inbreeding coefficient for the breed. His grandson, White Prince (63), assumed an important role, also, mainly because through him certain breeders endeavoured to breed for the type of animal as was represented by Burnhouses. Another interesting point about White Prince is that he is supposed to be responsible for much of the white color in the breed. The most famous sire seemed to be Hover-a-Blink (892) as 30.12 per cent of the total inbreeding coefficient is traceable to him or his descendants.

The genetic study also demonstrated the effective influence of the Drumjoan stockon the "high milk" producers of the breed. The noted herd was dispersed from Drumjoan in 1892, but even as late as 1928 the sires of this herd were responsible for the highest coefficient of inbreeding. The analysis of the "milk recorded" group revealed the widespread influence of the bull Hover-a-Blink. Of the total coefficient of inbreeding the Drumjoan herd was responsible for 18.36 per cent. Fowler states that the results clearly show the profound influence which one herd, and indeed one sire, may exert on the genetic construction of a recently established breed.

The coefficient of inbreeding for the whole breed, as calculated by Wright's short method, increased steadily from basic zero in 1877 to a mean value of 5.3 per cent in 1927.

Steele (1944) applied Wright's method to the genetic analysis of three breeds of light horses in the United States, the Thoroughbreds, Standardbreds, and the American Saddle Horses. His study showed that out of ten ancestors which occurred most commonly in modern Thoroughbred pedigrees only three made a notable contribution to the breed during its formative years. These three foundation ancestors, Eclipse, Herod, and Matchem, founded famous groups into one of which modern Thoroughbreds may be classed on the basis of the male line of descent.. Steele found that these three stallions, Eclipse, Herod, and Matchem contributed about the following proportions of genes to the modern American Thoroughbred: 11 or 12 per cent, 17 or 18 per cent, 5 or 6 per cent respectively.

Another interesting aspect of this study by Steele was his comparisons of the relationship to important ancestors between the extreme performance groups, the "stake winners" and the "poors" (those which failed to win races). He found that the differences were minor, and probably had no statistical significance.

With respect to the more recent ancestors in the Thoroughbreds Steele found that the most prolific sires of stake winners greatly surpassed the "poors" in the production of stake winners. In fact, the former group produced relatively more than 3 times as many stake winners as the "poors" did. The performance of the most prolific grandsires tells a slightly different story; this group produced relatively only about one and a half times as many stake winners as did the "poors". Steele concluded that the above results showed not only how quickly the influence of an ancestor decreases with receding generations, but also how quickly differences disappear with regard to ancestry of superior and poor performing individuals.

So far as is indicated by Steele's study, apparently no one particular individual had a dominant influence on the Standard or on the American Saddle Horse. However, it is known that three stallions, Messenger (1780-1808), Diomid (1777-1808), and Bell Founder (1815-1843) were particularly famous in the development of the Standardbred. Denmark, a Thoroughbred stallion foaled in 1830, has been regarded as the foundation ancestor of the American Saddle Horse. Steele's genetic analysis of this breed has indicated that out of 19 most frequently occurring ancestors, only one, namely, Rex Alexander, had a direct relationship to the breed as high as 10 per cent in all the samples studied.

The interval in years between the birth of the parent and the birth of the offspring exceeded 11 years in the Saddle Horse and 12 years in the Thoroughbred and Standardbred. Steele states that such a long interval constitutes a real limitation in carrying out selective breeding during the normal life span of any man.

Steele found that the three breeds, Thoroughbreds, Standardbreds, and the American Saddle Horse were inbred 8.3 per cent, 4.0 per cent, and 3.2 per cent respectively. The Thoroughbreds and the Standardbreds lost .6 per cent per generation of their original heterozygosity, but the American Saddle Horse lost 1.1 per cent. On the basis of the decrease in heterozygosity per generation, it appears that the Saddle Horse was slightly more inbred than the other two breeds. The Thoroughbreds had an inter se relationship of about 16.3 per cent for the stake winners, and 14.1 for the "poors"; whereas, the Standardbred and the American Saddle Horse had an average relationship between random animals of 8.2 per cent and 6.0 per cent respectively. According to Steele, homogeneity appeared to be increasing more rapidly in the American Saddle Horse than in the other breeds.

In his genetic analysis of the American Quarter Horse, J. Lane Fletcher (1945) applied Wright's method as did Steele in his study of the Thoroughbred, Standardbred, and the

American Saddle Horses. As was the observed case in the preceding studies, certain animals have assumed particular importance in the ancestry of the Quarter Horse. Fletcher found that only six sires were of very great importance, and only four of these appeared in the pedigree samples with about the same frequency. The four outstanding sires were Peter McCue, Hickory Bill, Traveller and Little Joe. Peter McCue was the sire of Hickory Bill, and Traveller was the sire of Little Joe. According to this study Peter McCue has been the most important sire in the breeding of the Quarter Horse. First, he has the greatest number of appearances in the pedigrees; secondly, he far exceeds his own sons in number of appearances. His relationship to the "Before 1930" sample was 6.35 per cent, while to the 1940-41 sample it was 5.68 per cent. This apparent variation of relationship to the samples was less for Peter McCue than for the other important sires. The average relationship of Hickory Bill and of Little Joe to the three samples was 3.77 per cent and 3.74 per cent respectively.

Furthermore, Fletcher's study brought out the interesting fact that only three of the frequently occurring sires in other samples were prominent in the King Ranch sample. It appears that Hickory Bill, followed by his son Old Sorrel, had the most dominant influence in King Ranch breeding. Thus the frequent appearance of Peter McCue in the King Ranch sample is incidental to linebreeding to his son and grandson. The King Ranch Horses showed a direct relationship of 6.69 per cent to Peter McCue, and 40.29 per cent to his grandson, Old Sorrel.

Fletcher's study had also demonstrated the fact that more than 50 per cent of the animals traced to at least one Thoroughbred ancestor, thus indicating that another breed has had a considerable influence upon the evolution of the Quarter Horse. Thoroughbred ancestors were present within the first four generations in the pedigrees of 97.4 per cent of King Ranch Horses. This situation indicates that King Ranch had made considerably greater use of the Thoroughbred in its breeding program than has been true with most Quarter Horse breeders.

The interval in years between generations was found to be 8.99 years, which is somewhat shorter than that found by Steele for the Thoroughbred, Standardbred, and the American Saddle Horse. The shorter generation interval in the Quarter Horse may be due to the fact that outstanding sires have not played so important a part in the breed, or perpaps the stallions were not kept in service over extremely long periods. Fletcher's analysis of the representative samples accepted for registration showed the coefficient of inbreeding to be about 1.7 per cent. The inter se relationship was found to decrease progressively from 2.46 per cent in the "Before 1930" sample to .98 per cent in the recent 1940-41 sample.Fletcher pointed out that the coefficient for inter se relationship was too small to account for the inbreeding; therefore, this trend in relationship and inbreeding probably indicated some separation into family lines.

Rhoad and Kleberg (1946) made a genetic analysis of one of the most outstanding families of the modern Quarter Horse in its formative stage. They found that King Ranch breeders, in their development of this prominent line, perpetuated Old Sorrel's exceptional qualities by consistently linebreeding to him. Four outstanding sires, all descendants of Old Sorrel, played a dominant role in this linebreeding program.

Wimpy, a double grandson of Old Sorrel and 12.5 per cent inbred to him, was generally mated to Old Sorrel's daughters who were related to Wimpy by 25 per cent. An increase of genes from Old Sorrel from 39.7 to 44.9 per cent resulted in the increase in Quarter Horse breeding among Wimpy's get. Peppy, who was 6.25 per cent inbred to Old Sorrel, was mated to daughters or double granddaughters of Old Sorrel; thus, the percentage of Old Sorrel's genes in their offspring was higher than in Peppy. The third stallion, Macanudo, A son of Old Sorrel, was mated for the most part to nieces by half-brothers and out of Quarter Horse outcross mares . This stallion more than doubled the percentage of genes from Old Sorrel in his foals. Babe Grande, son of Old Sorrel and Hickory Bill's daughter, was the fourth sire used in this experiment. About a third (36 per cent) of the genes of Babe Grande's colts derived from Old Sorrel, while the average of the dams to which he was mated was only 22.5 per cent.

This study has demonstrated that by intensive inbreeding it is possible to retain a high degree of relationship to a noteworthy foundation sire for many generations as was also demonstrated in the Duchess strain of Shorthorns by Wright(1925).

J. Lane Fletcher's second study (1946) of a light Horse breed was his analysis of the first fifty years of Tennessee Walking Horse breeding. This horse breed was not a product of planned breeding; it had been in the process of development for at least a century. However, for the purpose of this study, Fletcher considered the breed to have originated about the year 1886. He takes this year as the turning point in the breed history because Allan F-1, often considered as the progenitor of the breed, was foaled in this year. Allan F-1 was himself Standardbred, and his pedigree reveals that he had collateral relatives which became influential individuals in the history of other breeds such as the American Trotter, the American Saddle Horse, and the Morgan Horse breed. The heterogeneous origin of the Walking Horse is clearly indicated by his pedigree.

Fletcher selected five animals for his study on the basis of their assumed prominence as foundation animals, and the frequency with which they occurred in the pedigrees. He found that the two most important ancestors were Allan F-1 and Roan Allen F-38. The relationship of Allan F-1 to the 1940 group was 16.48 per cent, which means that he was more closely related to the sample as a whole than would have been the case had he been great grandsire to each animal in the sample. With his relationship of 19.44 per cent Roan Allen F-38, a son of Allan F-1, nearly approached the position of grandsire to the 1940 sample. Hunters Allen F-10 and Wilson Allen, son and grandson of Allan F-1 respectively, had a high relationship to the sample studied. It is probable that Allan's F-1 influence in the breed will be maintained at a high level through his outstanding sons and grandsons.

Fletchdr's study of the direct relationship of the five samples of the Walking Horse to the American Saddle Horse and Standardbred, has revealed that about one-fourth of the breeding had come from these two breeds. Furthermore, it is interesting to note that the 1940 sample had increased in relationship to the Standardbred but declined in relationship to the Saddle Horse.

The average interval between generations was found to be 10.02 years. The average inbreeding for the samples ranged from 1.24 per cent for the foundation animals to 3.62 per cent for these born in 1940. The average inter se relationship ranged from 2.96 per cent for the foundation sample to 6.45 per cent for those born in 1935. The 1940 group was interrelated by 5.8 per cent, which indicates that the Walking

Horse breed is a somewhat more closely knit unit than are the other breeds of Light Horses already studied.

Calder (1927) conducted similar studies of the Clydesdale in Scotland. He found that there was little inbreeding during the formative years of the breed; however, its inbreeding had risen to 6.5 per cent over a period of 60 years. The loss in heterozygosity per generation was practically on the same level as that found in the Light Horses.

Dickinson and Lush (1933), in their genetic history of the Rambouillet sheep in America, found that no one animal had a dominant influence on the breed. One animal, a von Homeyer ram, reached a relationship of 14.4 per cent to the 1896 sample. Perhaps F. M. Moore 26, deserves special mention because he had the highest coefficient of relationship to the breed in 1926. Another animal, Monarch, rose to rapid prominence within nine years after his birth. His direct relationship to the breed in 1926 was 3.7 per cent but his total relationship was 7.0 per cent. This would indicate that he, his sons and grandsons were used very extensively to make such a marked influence on so large a breed. The relationship of no animal to the breed exceeded 8.7 per cent and only few have exceeded 6.0 per cent.

The authors of this study found that the average individual animal in the breed in 1926 was about 5.5 per cent less heterozygous than the foundation animals were. The coefficient of relationship between random animals born in 1926 was 2.6 per cent, about four times as much as would have been expected if all the inbreeding had been the result of the inter se relationship within the breed. Such a condition indicates a distinct tendency of the breed to separate into families.

The average interval between the birth of the parent and the birth of the offspring was found to be 4.2 years.

Carter (1940), in his genetic history of the Hampshire sheep in the United States, found that only two animals were related to the whole breed as much as two per cent. Bentworth Herriod, who was imported from England and used extensively by the Mount Haggin Land and Livestock Co. at Anaconda, Montana, had a relationship of 2.4 per cent to the breed in 1935. His son, Heather, had a relationship of 3.0 per cent in 1935. Carter concluded that no one animal or family has ever dominated the Hampshire breed of sheep in the United States. He gives two possible reasons that may account for this lack of prominent individuals. The first reason is the relatively recent introduction of the breed to the United States as well as the large numbers in those importations. The second reason is the practice of flock registration, giving the individuals numbers rather than names, which tends to emphasize the flock rather than the individual animal.

A generation interval of 3.5 years was found in the

1925 sample and 3.8 years in the 1935 sample. A shorter generation interval is to be expected in a breed which is rapidly expanding in numbers as compared to a breed relatively stable in numbers. On this basis it is possible to explain the longer interval in 1935 when an equilibrium in numbers had been approached.

With regard to inbreeding, Carter found that about 1.4 per cent of the heterozygosis which was present in the breed in 1911 had been lost by 1925, while those born in 1935 had lost about 2.9 per cent of the heterozygosis that was present in 1914. About 0.7 to 0.9 per cent of the existing heterozygosis was lost per generation during the period studied. As for the homogeneity of the breed, he found an inter se relationship of zero in 1925, and 0.5 per cent in 1935, which was too little to explain the inbreeding. Carter concluded that some separation into family lines was apparent The natural consequence of geographic discontinuity rather than a deliberate attempt by breeders to keep families from interbreeding with each other, was perhaps the more likely reason for this separation into families.

The literature reviewed has indicated that only two breeds of swine have been studied using methods developed by Wright. Lush and Anderson (1939) made a genetic analysis of the Poland-China breed of swine in the United States. Their findings from this analysis has shown that several prominent individuals had an outstanding place in the development of the breed. Three different ancestors were at one time or another the source of more than one-eighth of the genes of the breed; these might be called great grandsires of the breed. The first was Chief Tecumseh 2d whose prominence was almost equally distributed between the two types, the "hot bloods" and the "Big Types". He was found to have contributed 13 to 15 per cent of the genes in each of the three latest samples, 1910, 1920, and 1929. Furthermore he had contributed more than ten per cent of the genes in the 1900 sample, taken just ten years after his birth. Chief Tecumseh 2d was the ancestor of the other two prominent individuals, Chief Perfection 2d, and Chief Price. Chief Perfection 2d contributed nearly 17 per cent of the genes in the breed of 1910 when the "hot bloods" were at the height of their popularity; however, with the decline in popularity of this ideal type, he assumed only a minor position. Chief Price achieved prominence when the second ideal, the "big type", came into high demand; he contributed around 12 to 13 per cent of the genes of the breed in both the 1920 and 1929 samples. Such high relationship figures are rather significant in a population as large as an entire breed.

This genetic study has also revealed that the ten foundation animals found most frequently in the pedigrees contributed 45 per cent of the genes to the breed in the 1929 sample, 46 per cent in 1930, and 30 per cent in 1910. Three animals, Jumbo 3rd, King Tecumseh, and the sow Gilmore Slick were responsible for more than half of this pool of genes. Together they contributed 25 per cent of the genes of the 1929 sample, 26 per cent of the 1929 sample, and 15 per cent of the 1910 sample.

The average interval from one generation to the next was found to be about two and one half years. The coefficient of inbreeding for the breed as a whole was 9.8 per cent in 1929. Covering the period studied, 1886 to 1929, the rate of inbreeding in the Poland China swine was sufficient to account for a loss of about .6 per cent per generation of the existing heterozygosis. Because of the fact that the actual inbreeding was higher than that expected from the inter se relationship, Lush and Anderson concluded that there had been a little formation of family lines.

The only other analysis of a breed of swine along similar lines is Rottensten's genetic study of the Landrace in Denmark (1937). On the basis of one sample Rottensten found the highest relationship of any one animal to the whole breed was 12 per cent. The average interval between generations was 2.2 years. In the period from 1897 to 1930 the inbreeding coefficient rose to 6.9 ± .7 per cent. This is equivalent to about one half of one per cent loss per generation of the existing heterozygosity. The most interesting fact here, which is somewhat contrary to the findings in other breeds, is that the actual increase in inbreeding is less than was expected from the average inter se relationship coefficient (16 ± 1.7%). It would appear then that the

Danish breeders refrained from even mild inbreeding practices.

The evolution of most of our domesticated animals is not completely known. An exception is the horse whose stages of development have been worked out rather fully by students in natural history. According to Mathew (1926), a study of the fossil remains has indicated that the history of the horse dates back some fifty million years. The evolution of the hog is not known to the same extent, but there is zoological evidence showing that the first differentiation of swine-like animals took place in the late Eocene or early Oligocene times. These swine-like ungulates, unlike the animals of the primitive ruminant group, were characterized by their simple digestive tract. The evolutionary tree (Fig. 1) shows that three distinct families, the Suidae or Pigs, the Hippopotamidae or Hippopotami, and Dicotylidae or Peccaries, have evolved from the Pig group. There are three generic types of swine of which only one, Sus, is concerned primarily in the development of the modern hog. Two species, Sus scrofa, typical representative of which is the European wild boar, and Sus vittatus (sometimes called Sus indicus), or the Asiatic wild boar, figure mainly in the origin of the domestic pig. In modern times there has been a great deal of intercrossing between various European and Asiatic strains; consequently, the ancestry of most present day breeds can be traced to both species. However, the European wild boar is most predominantly represented in the modern breeds of swine,

Fig. 1.
Evolution of the Modern Yorkshire Hog.

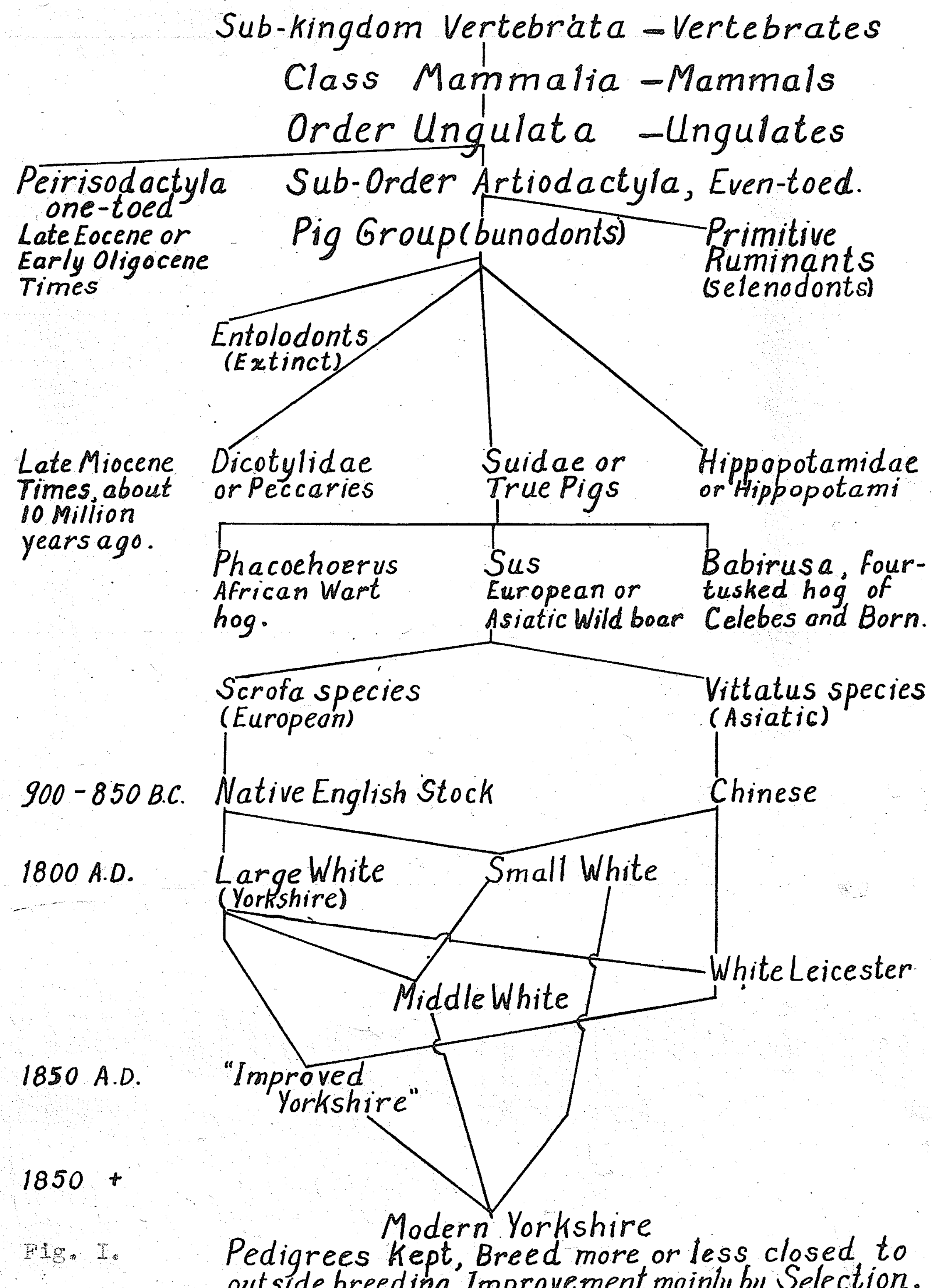


Fig. I.

particularly in the bacon breeds, while the Asiatic influence is generally recognized to figure more strongly in the pork or lard type of hog.

There is no definite evidence supporting the earliest domestication of swine, although it is believed that all farm animals were tamed to some degree long before historic times. Lydekker (1912) says that the earliest evidence of domesticated swine in Europe is perhaps afforded by remains found on the sites of the prehistoric lake-dwellings in Switzerland. However, earliest domestication probably occurred first in China about 3000 B.C. Domestication of pigs in Western Europe, and especially in the British Isles, most likely occurred a few centuries or more later. It is known that the European wild boar once inhabited the forests of Britain in great numbers, and is probably the chief strain from which the British breeds developed. Development of the present-day breeds, and the inauguration of breeding methods did not begin until the middle of the nineteenth century when man embarked on revolutionary improvements, both in industry and agriculture.

The Yorkshire or Large White, evolved in the northern counties of England,but its origin is more closely linked with the county from which it gets its American name. The ancestors of the Yorkshires were labge, coarse, leggy and narrow-backed native hogs known to have inhabited northern England for more than a century; therefore it is very likely that the European wild boar, Sus scrofa, is predominantly represented in this breed. The earliest improvement was achieved when the Large Yorkshires were crossed with the white Leicester pigs developed by Robert Bakewell. The Leicester strain, possessing smaller heads and more refinement, is believed to have originated from a cross between White Chinese and Yorkshire-bred pigs. Plumb (1920) states that the Yorkshire-Leicester cross was improved by breeding the largest and best young sows to Small Yorkshire boars. Possibly too, another Yorkshire breed, the Middle White, was used in the crosses to bring about general improvement in quality and probably to meet the demand for more refined heads. The most marked improvement of the Yorkshire began after the middle of the nineteenth century when pedigree breeding, established by Robert Bakewell, came into extensive use by many English breeders. Careful breeding and selection has resulted in further improvement of the Yorkshire.

The national Pig Breeders' Association was organized in 1884; it was incorporated in 1886 for the purpose of conducting a herd book, as well as promotion of the Yorkshire and also the Middle White, Small White, Berkshire and Tamworth breeds of swine in Great Britain.

The first importations of Yorkshires to Canada prior to 1850 were few, and the majority of these were yet unimproved. The "improved type" did not make its appearance in Canada until about 1886 and in the early herd books was known as the "Improved Yorkshire". The introduction of the

Large White to the United States occurred prior to 1840, but the improved type was not imported until 1893. In the United States where the American breeds have had a strong foothold for years the Yorkshire is not especially popular, but in Canada it has made great progress. The Yorkshire is almost synonymous with bacon production in Canada, and Canada's export bacon trade has largely depended upon the use of the breed. In 1949 there were 17093 Yorkshire pedigrees recorded in the Canadian National Records for Swine, or about 88 per cent of all the swine registered.

The Object of This Study.

In this genetic analysis of the Yorkshire breed of swine in Canada the object has been twofold:

(1) To find what influence important ancestors have exerted on the breed as a whole,

(2) To find the average length of generation.

Methods of Analyses.

The methods of investigation used in this study were developed by Wright (1922), and first applied by Wright (1923) in his Mendelian analysis of the Duchess Shorthorns as bred by Thomas Bates. Willham (1937), and Carter (1940) reviewed the published studies made using the technique developed by Wright and McPhee (1925). In addition to these, recent studies based on Wright's methods have been made of the Tennessee Walking Horse in the United States (Fletcher, 1946), the American Quarter Horse (Fletcher, 1945), and the Thoroughbred, Standardbred, and American Saddle Horses in the United States (Steele, 1944).

1. Important Ancestors.

For the present study a representative sample of 171 pedigrees was taken from among animals registered in Volume 60 of the Canadian National Records for Swine. This sample constituted one per cent of the total Yorkshire registrations in the volume; it consisted of 114 females and 57 males. The proportion of male to female registrations was determined by recording the number of male and female appearances in samples of twenty pages chosen at random from the herdbook. The "boar-sow" ratio was found to be approximately 1:2. The first step in taking the random sample of pedigrees was to ascertain the number of pages embracing all the Yorkshire registrations in Volume 60; the second step was to divide this number into regular intervals so as to yield the required number of pedigrees. Then, the animals were chosen by taking the first pedigree of the required sex--every third selection a male--on regularly spaced pages in the herdbook.

The average birth date of the animals in the sample was 1948; whereas, the base date, or the average birth date of the foundation animals was 1936. In this study of the Yorkshire breed of swine complete five-generation pedigrees have been used.

Ten ancestors, all of which appeared more than 80 times in the sample of pedigrees, were selected for consideration in this study. It is likely, no doubt, that some animals with larger collateral relationship than some of those shown in Table II may have been overlooked by the method of selecting them primarily on the size of their direct relationship.

The direct relationship of an ancestor to the breed was found by dividing the number of lines in which the particular ancestor was found by the total number of lines of descent in which it might possibly have been found. For example, if an ancestor appeared in 50 lines out of a possible 1000 lines of descent, it would have a direct relationship to the breed of 5 per cent. This relationship figure actually indicates the fraction of the genes in the breed at the date sampled which probably came from that particular ancestor.

2. Length of Generation

In determining the average length of generation the data used were the birth dates of the sample animals and of the foundation animals in the fifth generation where the ancestral lines terminated. To obtain the average length of generation the total number of years intervening between ancestors and descendants were divided by the total number of generations.

ANALYSES

1. Important Ancestors in the Yorkshire Breed of Swine in Canada.

When two individuals have one or more common ancestors a certain degree of relationship exists between them. Measuring this relationship is simply evaluating the probability that the two related individuals will have duplicate genes because of common ancestry. Because of Mendelian segregation, half of the genes of each offspring are identical with half of the genes of its parent. The rest of the genes are no more and no less apt to be alike than if the two individuals were chosen at random from a base population. However, where inbreeding has occurred these other genes will have a greater than average probability of being alike.

Animals may be related directly or collaterally, but it is also possible for two animals to be related both directly and collaterally. Direct relationship exists when one animal is the ancestor of the other, as in the case of parent and offspring, or grandson and grandsire. Animal breeders usually measure direct relationship by what they call "Percentage of blood". Figure 2. shows the "percentages of blood arranged in the form of a pedigree. The fractions résult from the halving nature of Mendelian segregation. Collateral relationship occurs if the two animals concerned are descended in part from some of the same ancestors, as in the case of half and full brothers, uncle and niece, cousins, etc.

Three of the animals listed in Table II. are fairly closely related, and thus they have accumulated considerable amounts of collateral relationship. They have a common ancestor in Ranche Sardis 9 who is the sire of both Ranche Empress 170 R and Ranche Duke 13 T, and the maternal grandsire of Woodstock Duke 9 T. Ranche Empress 170 R has a direct relationship to the breed of only 2.23 per cent, but her total relationship is 4.12 per cent, a figure which is nearly double her direct influence to the breed. This sow accumulated such a high collateral relationship because her sire, Ranche Sardis 9, appeared frequently in pedigrees where she did not appear. Similarly, Ranche Duke 13 T and Woodstock Duke 9 T have accumulated higher collateral relationships because their ancestor, Ranche Sardis 9, appeared in many other lines of descent. These two boars have the next highest total relationship to the breed of 3.63 per cent and 3.47 per cent respectively. The case of Ranche Sardis 9 is particularly interesting because his relationship to the breed is almost entirely direct; his collateral relationship to the breed is only .0045 per cent. This fact means that his parents or grandparents appeared in almost no other lines except through him.

As far as direct individual influence on the breed

				6 1/4	3 1/8
			12½		3 1/8
				6 1/4	3 1/8
		Paternal Grandsire 25%			3 1/8
				6 1/4	3 1/8
			12½		3 1/8
				6 1/4	3 1/8
					3 1/8
	Sire 50%				
			12½		
		Paternal Grandam 25%	12½		
X 100%					
			12½		
		Maternal Grandsire 25%	12½		
	Dam 50%				
			12½		
		Maternal Grandam 25%	12½		
Gen:	1.	2.	3.	4.	5.
Fractions of genes most likely to come from each ancestor	$(\frac{1}{2})$	$(\frac{1}{2})^2$	$(\frac{1}{2})^3$	$(\frac{1}{2})^4$	$(\frac{1}{2})^5$

Fig 2. Percentage of Blood arranged in the form of a Pedigree. (After Lush. 1949. Animal Breeding Plans, pp. 249)

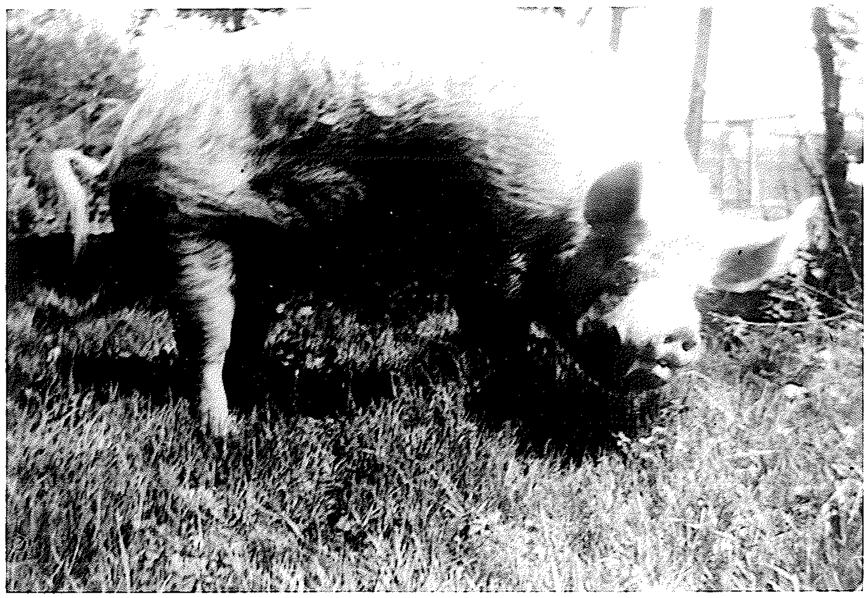


Plate I. Ranche Duke 13T, -202150-, sired by Ranche Sardis 9, is almost a great great great grandsire to the breed. His total relationship to the breed is 3.01 per cent. Ranche Sardis 9 was senior and grandchampion at the Royal Winter Fair (Toronto) in 1937. (Courtesy of Hooker Bros., Ormstown, Que.)

is concerned, Ranche Empress 170 R is surpassed in this regard only by one animal, namely, Elmira Wonder 32 R, who has a direct relationship to the breed of 2.67 per cent. It is probable that Elmira Wonder's 32 R descendants have been used a little more extensively in the breed; however, he assumes a position of slightly lesser importance than the sow mentioned above for his total relationship to the breed is only 3.01 per cent. Another animal, the only other sow listed among the ten ancestors, which perhaps deserves a mention, is Pine Grove Evergreen 28 T. She has a direct relationship to the breed of 2.1 per cent which makes her one of the four animals out of ten that have as high a direct relationship to the breed as 2 per cent, although her total relationship is only 2.6 per cent.

The ten animals listed in Table II. appeared at the ends of 26.72 per cent of the ancestral lines; in other words, they contributed directly 26.72 per cent of the genes present in the breed. Furthermore, a close study of the data in Table II. shows that there is really very little significant variation in the relationship of these ancestors to the breed as a whole.

The most remarkable fact which emerges from this study of relationships is that the Yorkshire breed of swine in Canada has not been dominated by any one prominent animal. This situation is exceptionally striking when compared with the Shorthorn breed of cattle in Britain which was 55 per cent

TABLE I

Important Ancestor which appeared more than 50 times in the sample.

Name of Ancestor	Reg. Number	Birth Date	Number of Occurrences	Percentage of Blood
Ranche Sardis 9	167046	1933	121	2.21
Ranche Duke 13 T	202150	1939	106	1.94
Aberdeen 7 T	200977	1939	100	1.83
Pine Grove Evergreen 28 T	208468	1939	115	2.10
Managra 86 S	196537	1938	60	1.10
Dungannon Sligo Hall 122P	194441	1936	56	1.02
Montville 9 U	218948	1940	84	1.54
Lacombe Prince 178 W	247383	1942	92	1.68
Elmira Wonder 32 R	190793	1937	146	2.67
Ottawa Wonder 81	160947	1933	92	1.68
Ranche Empress 170 R	189893	1937	122	2.23
Woodstock Duke 9 T	201790	1939	103	1.88
Orchard Valley Sardis 41 R	190017	1937	69	1.26
Cedar Brook Sardis 51N	179898	1935	71	1.30
Falconwood Duke 4U	220118	1940	63	1.15
Maple Lodge Valley 22N	182689	1935	62	1.13

This table gives an idea of the influence the particular animal has had on the breed through its own descendants.

TABLE II.

Ten Important Ancestors and their total, direct and collateral relationships.

Name of Ancestor	Reg. Number	Total Relationship	Percentage of Blood	Collateral Relationship
Montville 9U	218948	1.96	1.54	.42
Ranche Duke 13T	202150	3.01	1.94	1.09
Woodstock Duke 9T	201790	3.47	1.88	1.59
Pine Grove Evergreen 28T	208468	2.61	2.10	.51
Aberdeen 7T	200977	1.86	1.83	.03
Ottawa Wonder 81	160947	1.71	1.68	.03
Lacombe Prince 178W	247383	2.52	1.68	.84
Elmira Wonder 32R	190793	3.01	2.67	.35
Ranche Empress 170R	198893	4.125	2.23	1.895
Ranche Sardis 9	167046	2.2158	2.2113	.0045

Sows and boars which appeared 80 times in the samples are listed. Perhaps, some animals with larger collateral relationships than some of those shown may have been overlooked by this method of selecting them primarily on the size of their direct relationship.

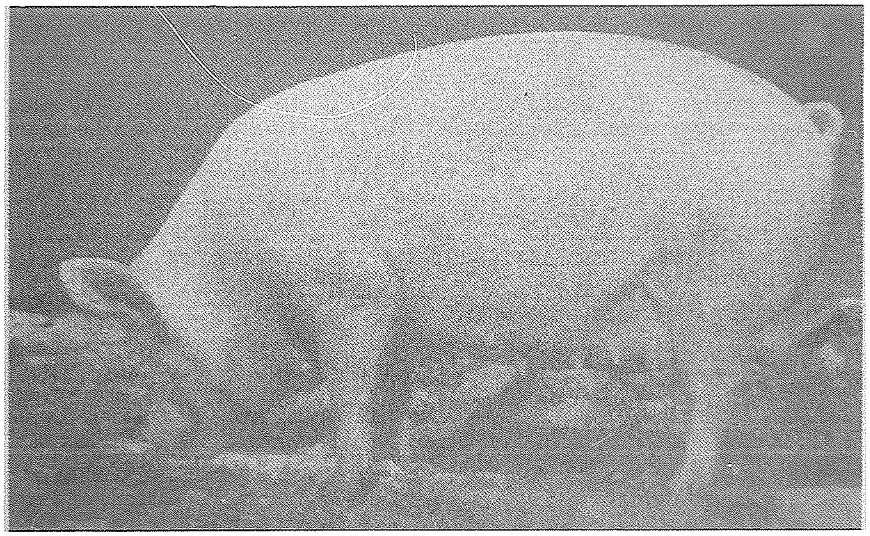


Plate II. Ranche Queen 131W, -275204-. She is a daughter of Ranche Duke 13T, and was grand-champion at the Ormstown Show. (Courtesy of Hooker Bros., Ormstown, Que.)

relatêd to Favourite and 45 per cent related to Champion of England in 1920, or when compared with the Polan China swine in the United States which was dominated by three prominent ancestors who at one time or another were great grandsires of the breed.

2. The Average Length of Generation.

For the Yorkshire breed of swine in Canada, the average length of generation was found to be 2.4 years. This figure is based upon 26,600 generations totalling 63,822 years in 5320 ancestral lines. This figure is practically the same as that found by Lush and Anderson (1939) for the Poland-China breed of swine in the United States.

DISCUSSION

1. Important Ancestors.

Individual animals do not have equal opportunity to contribute to future inheritance of the breed. Certain individuals, because of their inherent merit and partly because of such other factors as potent advertising by breeders, etc., are used in prominent herds. Males in such herds have many sons and grandsons which go to head other registered herds; therefore, they have a greater than average opportunity to contribute to the inheritance of future generations. Less popular sires have no sons which see service in purebred herds and perhaps few daughters and grandsons; consequently, the chance that the genes carried by them might be spread to the breed is decreased correspondingly. Moreover, a fair proportion of sires are put to use in grade herds where their inheritance is diffused into the population of grade animals which produce the market stock. Therefore, only a small number of sires have the opportunity to contribute to the future inheritance of the breed.

This means that the frequency of certain genes possessed by this smaller group will be increased in the breed at the expense of the deletion of genes possessed by the sires used less frequently. This effect on the gene frequency also applies to females but, because of their fewer offspring, to a less extent. Lush and Anderson (1939) summarize it by stating that the effective number of breeding animals concerned with the alteration of gene frequency is far smaller than the number of those which reach breeding age. Braun (1950) found that the effective number for the Yorkshire swine in Canada was about 96 (this is less than one per cent of the census number for the breed) calculated on the basis of random mating within a population closed to outside blood. It is very likely that in this effective group some individuals contributed a greater share of the genes to the breed than others. It is in fact borne out in this study. Three animals, Ranche Empress 170R, Ranche Sardis 9, and Elmira Wonder 32R, which appeared most often in the sample, together contributed 7.11 per cent of the genes to the breed. Some ten ancestors were found at the ends of 26.72 per cent of the ancestral lines in the sample. This figure, perhaps, is not as striking as that found for the Poland-China swine in the United States, where ten ancestors were found at the ends of 46 per cent of the ancestral lines in 1930. It indicates that the frequency of the genes of these animals has been increased in the breed to a greater extent than it would have been had random mating prevailed.

Certain factors may account for the extreme contrast between the census number and the effective number in the population of farm animals. It may be that economic conditions, potency of advertising, prominence given to show ring awards, government policies such as advanced registry, etc., give opportunity for only one or a few animals to be important at a certain time. Possibly the desire of breeders to have sons or grandsons, or other close relatives of the currently famous animals at the heads of their herds is an important factor. This practice would have the tendency to effect a rapid diffusion of the genes of those few through the breed and a corresponding decrease of the chances that any genes carried by the less popular animals would continue to exist in that breed.

The population of the Yorkshire breed of swine in Canada had increased steadily, and in recent years quite rapidly, until in 1949 the total registrations numbered 17093. This is a fairly large population, and it would seem to be almost improbable for one animal to affect the whole breed even as much as was done by those animals shown in Table II. unless breeders effect a change in the prevailing systems of breeding. Even if a boar was kept in service for an unusually long time, and his sons and grandsons were used widely to head other purebred herds their offspring would be only grandsons and great grandsons of the original animal. Moreover, if they are mated to unrelated animals the offspring will get only one-fourth and one-eighth, respectively, of their inheritance from the outstanding ancestor. If the offspring in turn are mated to unrelated individuals the influence of the important ancestor is again halved or "diluted". In general, if the descendants are continually mated to unrelated animals, then, by the fifth or sixth generation the diluting effect of this outcrossing will have reduced the ancestor's contribution to its descendants to an insignificant level.

A study of the "percentage of blood" in the pedigree, Fig. 2, clearly indicates the diluting effect of continuous outcrossing. It should be remembered that because of the part played by chance in the sampling process of inheritance, the percentages indicated in the Fig 2, are not necessarily exact for an ancestor farther back than a parent. As one goes further back in the pedigree there are more and more opportunities for chances to have altered the percentage of blood. The figure for the percentage of blood is actually the coefficient of relationship of ancestor to descendant provided, however, that both ancestor and descendant are inbred to the same extent, or not at all, and that they are not related in any other way than as ancestor and descendant.

Direct relationship, or "Percentage of blood", alone is not the sole indicator of the probable extent to which the genes of the breed as a whole are similar to those carried by an ancestor. Two animals may be found 90 times in a sample, but the first one might have no sisters or brothers, and probably none of his grandparents or great grandparents were found in the sample except in lines coming through him. The other animal with the same number of appearances might have had several sisters or brothers, uncles and cousins which were found in other lines and which had an important influence on the breed. Therefore, in such a sit-

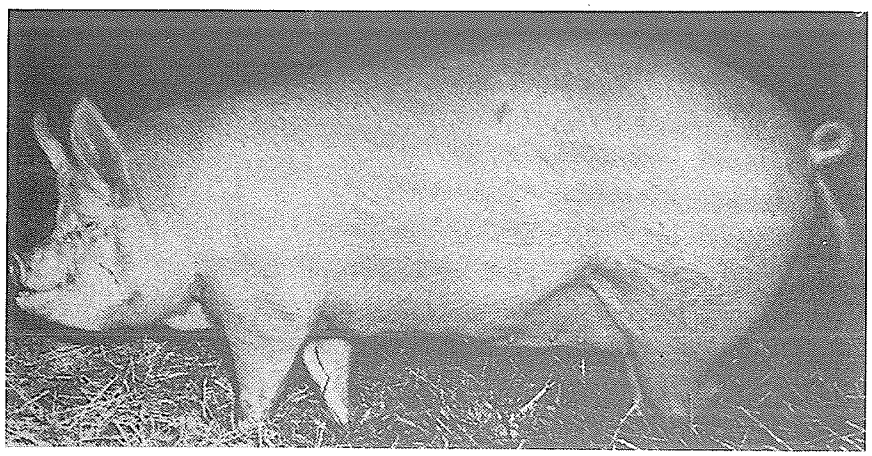


Plate III. Ranche Queen 51A, -316476-. Her sire and dam, Ranche Duke 33Y, -290149-, and Ranche Queen, -275204-, are a son and daughter of Ranche Duke 13T. She was a Reserve Senior Champion Yorkshire sow, R.W.F., 1947.
(Courtesy of Hooker Bros., Ormstown, Que.)

uation, it is evident that the second animal would be more like the breed in the genes it possessed than the first one. This fact is fairly well demonstrated in Table II. where two ancestors, Lacombe Prince 178 W amd Ottawa Wonder 81, are shown to have an equal influence individually on the breed with a direct relationship to the breed of 1.68 per cent each, but the former has a greater total relationship to the breed because of a higher collateral relationship. The total relationship of each animal to the whole breed includes both its own influence as an ancestor of the breed and its collateral relationship to the breed.

The only system of mating that could counteract the continuous diluting effect of outcrossing is one involving the mating of descendants among themselves so that relationship is concentrated towards some animal or animals regarded as unusually desirable. This is essentially the principle of the system commonly called "linebreeding". It is usually a less intense form of inbreeding,and it leads to an increase in the frequency of the genes of an important animal among his descendants, and to a corresponding decrease in the frequency of the genes of the less favoured individuals.

Fig. 3. shows a comparison between the milder form of regular inbreeding systems which might be used more readily in breeding farm animals, and the most intense systems theoretically possible. Fig. 4 shows what happens to the relationship between full brothers under the various regular

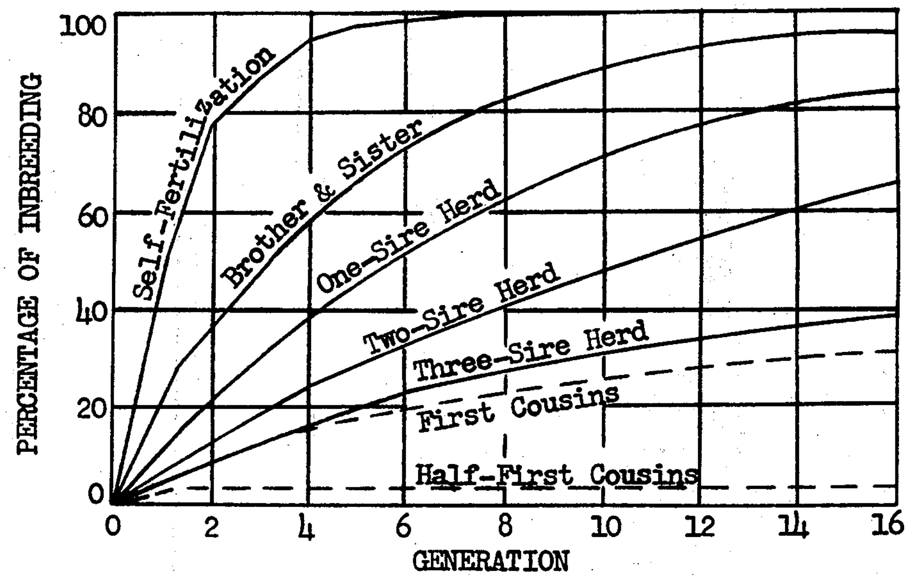


Fig. 3. The percentage of inbreeding under various systems of mating. (After Wright in Genetics, 6:172, and Lush in Animal Breeding Plans, p. 276.)

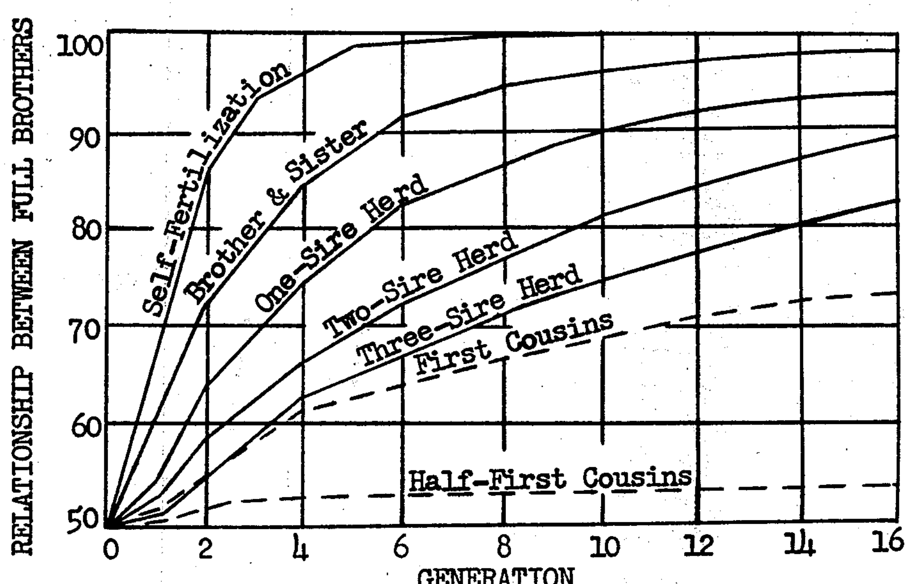
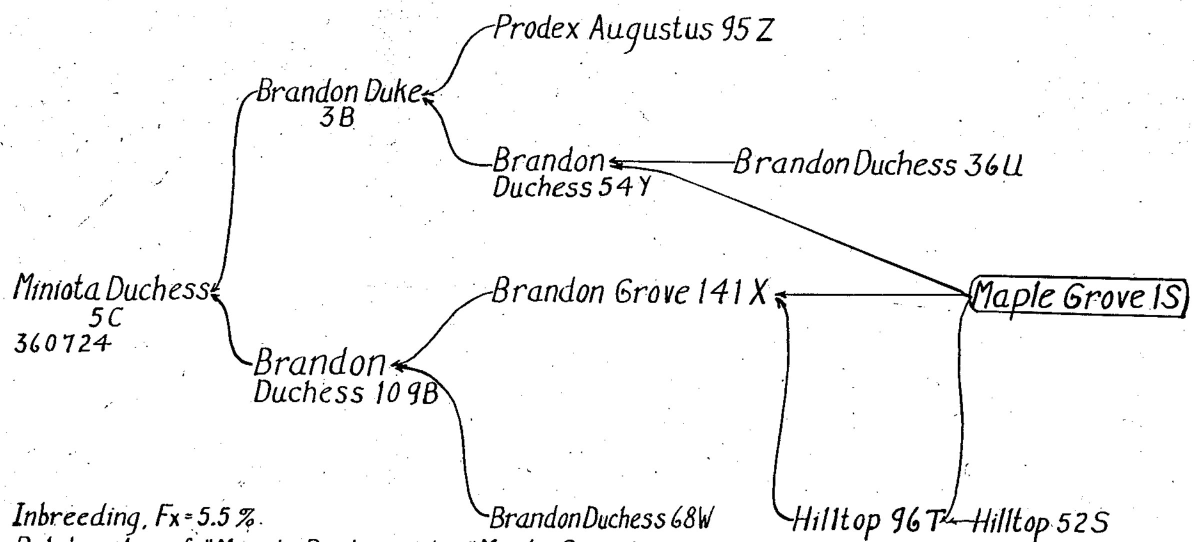
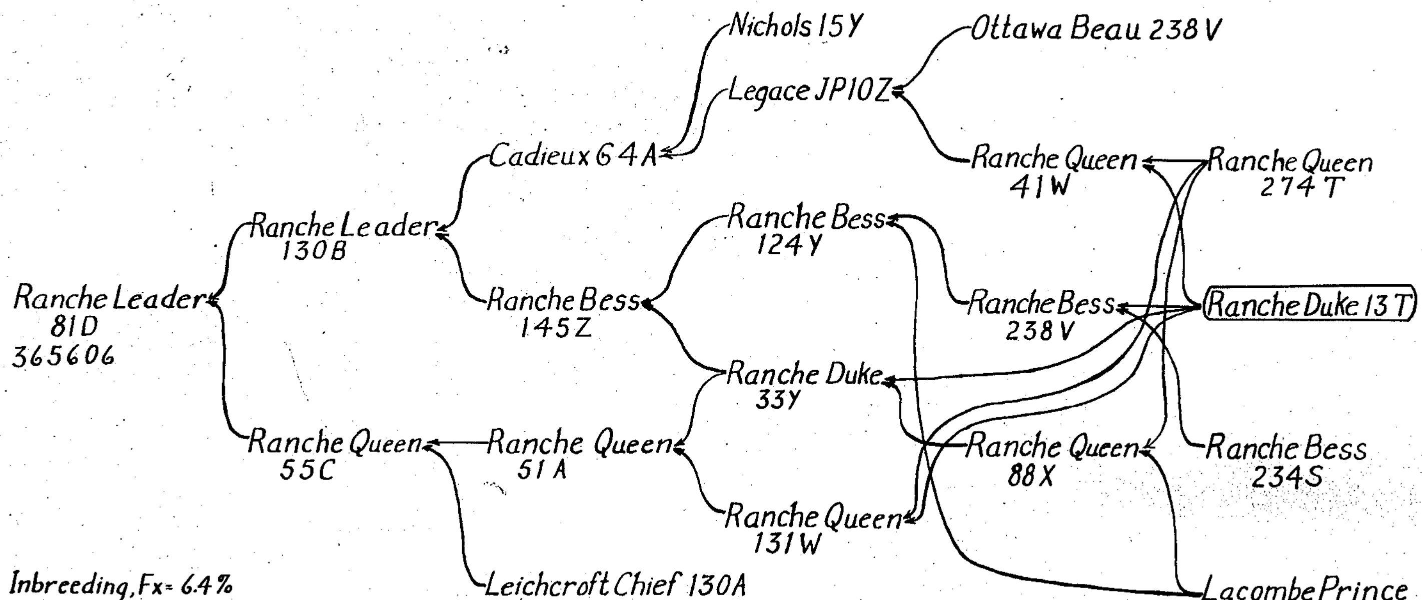


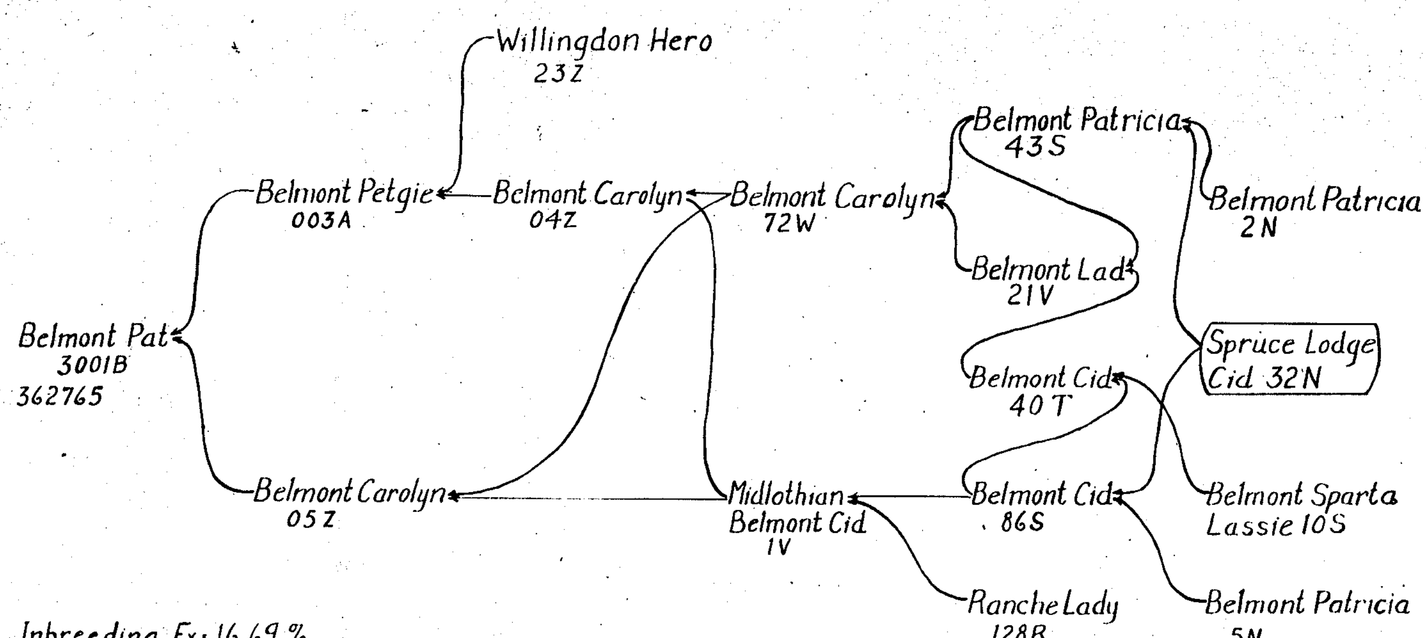
Fig. 4. The relationship between full brothers under various systems of mating. (After Wright in Genetics, 6:170, and Lush in Animal Breeding Plans, p. 277.)



Inbreeding, Fx = 5.5 %.
Relationship of "Miniota Duchess" to "Maple Grove" = 31.25 per cent.



Inbreeding, Fx = 6.4 %
Relationship of "Ranche Leader 81D" to "Ranche Duke 13 T" = 25 per cent.



Inbreeding, Fx = 16.69 %
Relationship of "Belmont Pat" to "Spruce Lodge Cid" = 21.875 per cent.

Fig. 5. Network Pedigrees of Yorshire animals showing linebreeding.

inbreeding systems.

Figure 5 shows actual samples of linebreeding practised by some breeders of the Yorkshire breed of swine in Canada. The relationship between Miniota Duchess and her ancestor, Maple Grove IS is greater than that between an ordinary grandparent and its offspring because 31.25 per cent of the genes of Miniota Duchess came from Maple Grove IS. Ranche Duke 13 T may be considered to be a grandparent of Ranche Leader 81 D, because he contributed 25 per cent of the genes present in his descendant. The network pedigree of Ranche Leader 81D also shows that there is secondary linebreeding to Ranche Duke 33Y. Belmont Pat 3001B is more highly inbred (16.69%) than the two animals already discussed. His relationship of 21.875 per cent to Spruce Lodge Cid 32N approaches nearly the relationship of an individual to its grandparent.

If most breeders of purebreds used linebreeding as the chief system of breeding, and made outcrosses only now and then to correct defects, a great number of unrelated line-bred families might be built up within the breed. It must be understood that such a system would be successful only if the fountain stock from which these families or strains were developed was average or above average merit of the breed. This formation of families within the breed would set the stage for a general improvement of the breed on a family basis, family versus family. Families which establish the reputation of being the best in the breed undoubtedly would have the greatest influence on the breed. There would be a period of grading the whole breed up towards these popular families. Inbreeding would then be used to fix the characteristics and improve the characteristics of the breed. Furthermore, these inbred families would make the breed more valuable for commercial livestock production through the use of hybridization.

It appears that most of the improvement in the Yorkshire is accomplished by mass selection, which is definitely limited in effecting rapid improvement, for Braun (1950) in his study on inbreeding and inter-relationship found that little line breeding and family formation is actually going on in the Yorkshire breed today. Family formation would of necessity focus on some important founder or founders of the family. Whether Ranche Duke 13T and Woodstock Duke 9T, or some other animal is to become as prominent an ancestor in the breed as Anxiety 4th became in the Herefords or Favourite and Champion of England in the Shorthorns in Britain depends not only on their inherent merit but also on whether a strain closely related to them is preserved. Relationship of an ancestor to his descendants will be reduced by half each succeeding generation unless breeding plans include line breeding to him.

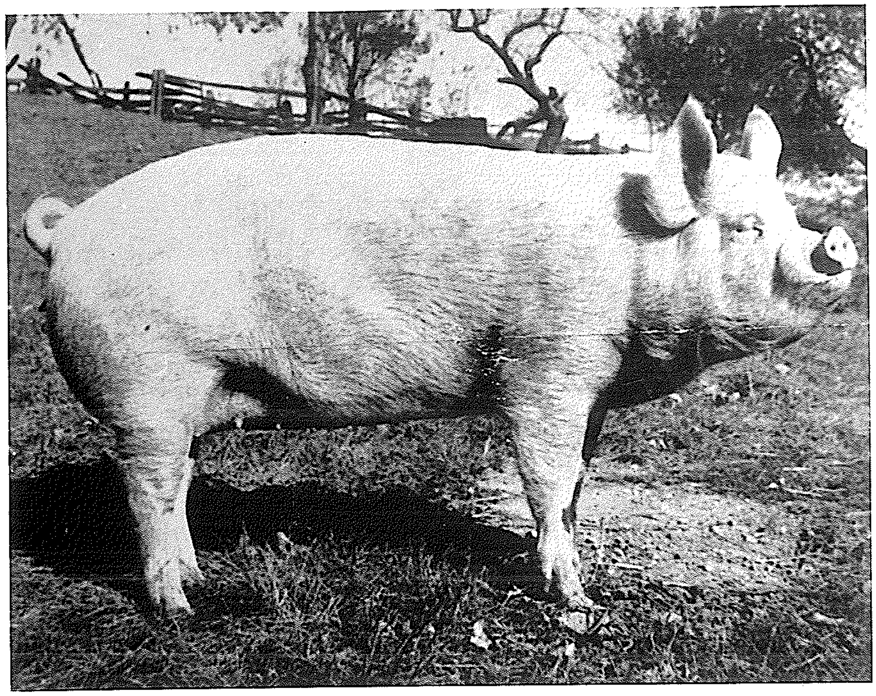


Plate IV. Ranche Bess 21Y, -283146-. She is a daughter of Ranche Bess 238V, -240665-, and a grand-daughter of Ranche Duke 13T. Her sire is Lacombe Prince 178W, -247383-. She was Junior Champion, Erin, 1944.
(Courtesy of Hooker Bros., Ormstown, Que.)

2. Length of Generation.

The average interval from the birth of the parent to the birth of the offspring represents the average age of the parent when the offspring is born. In their genetic history of the Poland-China swine in the United States, Lush and Anderson (1939) have stated that most sows and boars have their first litters born when they are about one year old, but enough sows and boars are kept in use until they are three or four years old so that the average age of the parent when the pigs are born is raised from the physiological minimum of about one year to the two and a half years actually found for that breed. In most livestock breeding, generally speaking, the breeder's policy of keeping outstanding sires or dams in service over extremely long periods of time usually results in a longer generation interval for the breed. For example, Fletcher (1945) found a generation interval of 8.99 years for the American Quarter Horse, while Steele (1944) found a longer interval (12 years) for the Thoroughbred and Standardbred breed of horses. The shorter interval in the Quarter Horse is probably due to the fact that outstanding stallions were not kept in service for long periods of time.

The status of the breed population affects the length of generation (Carter, 1940). The generation interval has a tendency to be short when the breed is rapidly expanding in numbers, and tends to be somewhat longer when the population number approaches an equilibrium.

The average interval between one generation and the next is a matter of practical importance in the breeding of any livestock. Several reasons account for this significance of the generation interval. In the first place, it will aid the breeder to calculate the time required to attain a certain goal in his breeding plans. If he wishes to fix the characteristics of some worthy individual by some system of linebreeding, the generation interval will enter into his plans of what he can accomplish within a certain time. Secondly, the generation interval is useful in estimating what has been achieved in a certain length of time in the past by the breeding systems employed. Another reason is that, from the economic point of view, the breeder can make use of this information in making rough estimates of the replacement rate for the breeding stock, and the average number of offspring he can reasonably expect from animals retained for breeding purposes.

Register Number 202150

Breed Yorkshire

- **SIRE** Ranche Sardis 9, No. 167046, Bred by
  - Oak Lodge Sardis 147, No. 145926, Bred by
    - Rosedale Masterpiece 2, No. 126392
      - Oak Lodge Masterpiece 110, 92249
        - Oak Lodge Sardis 63 79922
        - Amulree Lucy 13 81541
      - Orchard Valley Lady, 105516
        - Pine Grove Rosedale 8 84119
        - Alliston Helen 96548
    - Oak Lodge Sunbeam 690, No. 135102
      - Oak Lodge Vim 310, 107622
        - Oak Lodge Prior 100 92259
        - Oak Lodge Violet279 94010
      - Oak Lodge Sunbeam 679, 113883
        - Oak Lodge Famous283 70517
        - Oak Lodge Sunbeam 162 71121
  - Ranche Queen, No. 137945, Bred by
    - Sherwood Duke 3, No. 102067
      - MacDonald Morvin Duke 22, 80506
        - Morvin Duke 3 68733
        - College Queenie 25 53115
      - Keppoch Lassie, 85131
        - Superior 6 65978
        - Ravenwood Girl 3 72207
    - Ranche Frances 2, No. 131735
      - Sylvestre A6, 117383
        - Simon 2 101499
        - Sophia 94391
      - Ranche Frances, 125981
        - Ranche Colonel 101480
        - Oak Lodge Queen Bess 163 102956
- **DAM** Ranche Queen 214R, No. 193508, Bred by
  - Glenafton Empress 42P, No. 184116, Bred by
    - O.A.C. Conqueror 315, No. 167820
      - O.A.C. Conqueror 132, 146199
        - Wilt Dale Excelsior113080
        - O.A.C. 4314 134255
      - O.A.C. 4318, 134257
        - Pine Grove Glory 119293
        - O.A.C. 3462 101594
    - Stevenson Empress CB 24-58, No. 167453
      - Ottawa Wonder 81, 160947
        - Frederiction Duke 11 146579
        - Ottawa Maple Leaf 57 156570
      - Stevenson Empress CB 12-12, 161212
        - Orchard Valley Emperor 14 132364
        - Stevenson Princess 4 139682
  - Ranche Queen 25N, No. 178571, Bred by
    - Springbrook Pat, No. 155368
      - Dixon Dan, 137776
        - Spruce Orchard Pat 3 123047
        - Greenwood Queen 14 123198
      - Hillcrest Princess11, 140543
        - Springbrook Monarch102022
        - Boswall 10 107021
    - Ranche Queen 23, No. 167603
      - Oak Lodge Sardis 147, 145926
        - Rosedale Masterpiece 2 126392
        - Oak Lodge Sunbeam 690 135102
      - Ranche Princess, 157276
        - Spruce Orchard Pat 3 123047
        - Ranche Queen 137945

Fig. 6.

SUMMARY

Using complete five generation pedigrees a genetic analysis of the Yorkshire breed of swine in Canada has been made to determine the important ancestors and the length of generation. A representative sample of 171 pedigrees including 114 females and 57 males was chosen as at random as possible from among Yorkshire registration in Volume 60 of the Canadian National Records for Swine. From this study the following conclusions were made:

1. No one animal has dominated the Yorkshire breed of swine in Canada between 1936 and 1948. The relationship to the breed of the ten most important ancestors did not vary greatly, although three animals exceeded slightly 3 per cent and one 4 per cent. The relationship to the breed of the remaining six ancestors averaged about 2 per cent. These ten ancestors together appeared at the ends of 26.72 per cent of the ancestral lines in the sample, or they may be said to have contributed about 26.72 per cent of the genes present in the breed.

2. The length of generation was found to be 2.4 years. This figure compares favourably with the interval of 2.5 years found between generations for the Poland-China breed of swine in the United States.

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