producing homozygosity and prepotency or genuine "fixity" of type. It produces uniformity within the various inbred lines but marked differences between lines. Thus, it leads to the apparent paradox of a very non-uniform breed composed of very uniform lines or families. Because of its family-forming power, inbreeding can make selection much more effective, especially in cases where there is much epistasis. Inbreeding which is directed toward keeping relationship to some admired ancestor high (i.e., linebreeding) is a combination of selection and inbreeding particularly useful for perpetuating favorable epistatic effects of certain gene combinations.

Outbreeding promotes individual merit by tending to conceal recessive genes. It remedies damage done by inbreeding and is useful for introducing desirable genes into a population which lacks them. Because it destroys family distinctness, covers recessives and scatters favorable epistatic combinations, outbreeding hinders progress in breed improvement except in those cases where a little outcrossing is necessary to introduce desired genes into a family which lacks them. Outbreeding is primarily a method for the producer of market animals.

The breeding of outwardly similar individuals together has practically no effect upon homozygosis or prepotency but does increase immediately the average resemblance between parent and offspring. That happens merely because the parents are chosen for their resemblance to each other and each offspring has a chance to inherit from both parents genes which will make it seem like them both. Mating like to like increases the proportion of extreme individuals and decreases the proportion of intermediates, thereby making the population more variable provided no accompanying selection is practiced. The effects of mating like to like are limited by the correlation between genotype and phenotype and cannot be extreme unless that correlation is high. Hence, in practice, assortive mating based on somatic resemblance and unaccompanied by selection does little but increase the variability of the population. Mating unlikes together to correct defects, where both are too extreme but in opposite directions, makes the population more uniform and keeps it nearer to an intermediate type. The mating of somatic unlikes has little effect on homozygosis. It is a very useful breeding system wherever the goal is an intermediate, particularly in a species where fertility is moderate and some of the extreme individuals must be used for parents.

PLANS FOR INDIVIDUAL BREEDERS

For All Kinds of Breeders:

1. Decide what kind or type of animal and what level of production

would be ideal for the breeder's own individual circumstances and local conditions.

2. Find what living animals most nearly have the genes needed to produce that ideal animal.
   a. By judging and testing each animal.
   b. By paying some attention to the merit of recent ancestors and close collateral relatives.
   c. By studying the progeny of each animal.
3. Obtain, as far as can be done at reasonable prices, those animals which come nearest to having the ideal genes and let each have offspring in numbers proportional to the closeness with which its heredity approaches the ideal.

FOR BREEDERS OF PUREBREDS:

4. Keep the future herd closely related to the best animals of the present and of the recent past, letting the relationship to poor or ordinary animals be diluted by the natural halving effect of the processes of inheritance.
5. Outcross only when it is necessary to prevent some serious defect from being fixed on the whole flock or herd. The higher the average individual merit of the herd and the farther the breeder has gone in his line-breeding program, the milder and more tentative such outcrosses should be.

FOR BREEDERS OF MARKET ANIMALS:

4. Outbreed so far as that can be done without using animals of distinctly poorer heredity than would be available if related individuals were mated together. By using sires which are closely bred but unrelated to the females on which they are to be used, the maximum of heterosis and individual merit can be kept without losing as much in uniformity as if the sires were not closely bred themselves.

The first step in any animal breeding program is to decide what is ideal. Until a breeder knows what kind of animal he wants, he is stopped in his tracks and can neither select the best nor discard the worst. Somewhat indefinite words, such as best, worst, poorer, better, more productive, meritorious, etc., have intentionally been used in this book instead of more precise words in discussing selection and kindred problems because the purpose was to discuss ways of attaining the goals the breeder wants and not to enter into the subject of what ideal for each kind of animal would be most profitable. Each breeder needs to consider his own physical and biological resources, his own markets and his own personal inclinations to decide what characteristics his ideal

animals should possess. Naturally a beginning breeder would defer somewhat to the opinions of those who have had more experience under somewhat similar conditions, but his own conditions may be different from those of the men from whom he is receiving advice. It seems likely that the matter of local adaptability will receive more attention in the future than it has in the past. Probably there will always be at least enough interchange of breeding stock to keep that from being overdone. The ideal must often be a compromise between satisfying the market and satisfying one's own local conditions most completely. Conceivably the butcher's interest in high dressing percentage and high quality of meat, if carried too far, might result in animals with vital organs too small for them to be as healthy and thrifty as the farmer wishes, while the animals which would suit the farmer best because they were healthiest, most robust, largest, and quickest growing might be too big, bony, and coarse to suit the butcher. The commercial ideal is largely dependent upon economic conditions which can change much more rapidly than the breed average can be changed. Because of this it is natural not to follow a current economic change as far as would be wise if one could be certain that the change would be permanent. Sometimes the farmer's ideal and the breeder's ideal are not quite identical. That may have a rational basis wherever the commercial ideal is an intermediate, but most of the females in the farmer herds are far to one side of that ideal. For example, in the 1930's the Danes were striving to lengthen their hogs to meet better the demands of their British market. Since most sows were too short, the breeder ideal was for even longer hogs than the bacon factories wanted. They hoped that extremely long boars would produce from the farmers' sows pigs about right in length. The breeder ideal may, however, differ only in stressing some details of breed type or in following some current fashion which has gone farther than economic conditions justify. A word of caution should be added about paying too much attention to what is said to be the customer's demand. It is difficult to be sure just what the customers do want, and many a man has gone to considerable trouble to satisfy the supposed demands of his customers only to find that an insignificant portion of them really wanted these peculiar characteristics enough to pay extra money for them.

That the ideal degree of development of a characteristic may be quite different in animals intended for different purposes is illustrated by the following quotation from a most interesting book[1] concerning the breeding of German Shepherd dogs for various kinds of service:

[1] Humphrey, Elliott, and Warner, Lucien. 1934. *Working dogs.* Baltimore: The Johns Hopkins Press. 253 pp.

"There are several characteristics which do not bear the same relationship to all forms of service. A trait may be essential to the excellent performance of certain work but nonessential or even detrimental to the proper execution of other services. The reader will find it convenient to refer to the accompanying chart:

Form of Service	Olfactory Acuity	Nose Obedience	Aggressiveness	Distrust
Police (frontier, penitentiary, etc.)	+	+	++	−
Trailing	++	++	+	−
Liason	+	+	−	+
Blind guiding	−	++	+	−
Sanitary (Red Cross)	+	0	0	−
Herding	+	+	+	0
Companion	0	0	+	−

In this chart, ++ indicates that the trait is essential in its highest developed form; +, that it is desirable to at least a limited degree; −, that the presence of the trait is detrimental to good work; and 0, that its presence or absence is unimportant."

The second step in the breeder's plans—finding which animals most nearly have the genes he wants—has been discussed in detail in chapters 12 to 19. It is useless to institute an elaborate search for perfect animals, because in few if any cases have such animals yet been born. The breeder will always be under the necessity of compromising, getting animals which are above average as a whole but which are below average in some respects, taking care that at no time do all of his breeding animals have the same defect. Only in rare cases will the breeder know the Mendelian formula for more than a few genes in his animals. He will never see genes but can judge whether or not they are present only by the effects they produce, either in this animal itself or in some of its close relatives. In point of time, pedigree selections come first; but in most populations they are less dependable than selections based on the individual's own characteristics or on the characteristics of its progeny. Individual selection of the parents keeps the animals which would have had the worst pedigrees from being born. If individual selection has been extreme among the parents, there is only a little room left for pedigree selections among the progeny, especially among the female progeny. Individual selections are usually more accurate than selections on pedigree or selections on progeny except in the case of characteristics which can be expressed only in the other sex, but if the worst individuals have been discarded without being tried as breeding animals, the progeny test when it first becomes available brings fresh evidence from an entirely new direction and for the moment offers more possibilities for further progress than can be had by paying attention to the remaining differences between pedigrees and individualities of those which have already survived the earlier cullings on those two bases. Inbreeding seems to deserve more use than it has yet received as a means

of finding which animals have the best genes. Not only does it uncover recessives more surely than any other method, but it also increases the relationship between the inbred animal and its parents and other relatives so that the animal's pedigree and the merits of the family to which it belongs become more dependable as indicators of its own genes than can be the case with animals which are not inbred. Considerable inbreeding is necessary if family selection is to be very effective. A breeder can sometimes get help in finding which of his young males have the best genes by leasing for progeny-testing in other herds those which have such good pedigrees and such good individuality that he might wish to use them himself if their progeny prove them good. There may be more of these than he can progeny-test himself, and leasing them will give him a larger number from which to choose in bringing back the ones which would improve his own herd the most. The costs of such a plan would come from some increase in the possibility of disease transmission and the possibility that the lease price might be less than could be had for these animals by outright sale. Perhaps the possibilities for business disagreements are numerous enough to be important. Leasing young sires for progeny-testing is not a new idea. Bakewell was famous for his annual ram-lettings. The plan seems to deserve wider use than it has generally received.

The third step in the practical breeder's plan is to get the animals which have the most nearly ideal heredity, so far as he can afford to buy them, and to let them reproduce at rates in proportion to how nearly ideal their heredity is. There will be some things about each animal which are not ideal, but in breeding for its good qualities one must breed for these undesired ones also. The gene is the unit of inheritance, but the animal is the smallest unit which can be chosen or rejected for breeding purposes. To breed exclusively from one or two of the best animals available would tend to fix their qualities, both good and bad, on the herd. In fact, that is the essence of what happens under extreme inbreeding. Moreover, the breeder will make at least a few mistakes in estimating which animals have the very best inheritance. Hence, in a practical program the breeder will hesitate to use too extensively even a very good sire. With as many as four or five sires in use at all times and no one of them used far more extensively than the others, the danger of fixing traits on the whole herd against selection is small. Perhaps it may be ignored for many animal generations. Where no inbreeding is practiced, this danger practically disappears because the next sire, being unrelated, will rarely have many of the same undesired genes as his predecessor.

The breeder is far from having full power to decide how many offspring each of his animals shall have. Some of the animals will die or

become sterile or will be prevented in other ways from leaving as many offspring as the breeder wants. Females from which he wants a herd sire may persist in producing only daughters for several years. Consequently, some animals from which he really did not want so many offspring must leave more to make up for the offspring he does not get from the animals he prefers.

The fourth step in the plan for the breeder of purebreds is to stay with the best individuals, once he has found them. This is the essential object of linebreeding. It utilizes the laws of Mendelian inheritance to hold at a nearly constant level the probable likeness of future animals to the best proved sires and dams of the past, but to dilute the relationship of the future animals to ordinary or poor animals of the past. Such linebreeding requires planning and, if continued many generations, necessarily involves co-operation with other breeders except in those cases where the herd is large enough to maintain economically as many as two to five sires in service at all times. Without such co-operation it is likely that, sooner or later, first one undesired gene and then another will be fixed in the herd in spite of selection. It is not generally advisable to plan pedigrees very exactly for more than a generation or two in advance, because that does not give enough opportunity for selection. Instead, one can decide that he will use one of perhaps a half dozen individuals still to be born, all of which will have pedigrees which will fit into his plans reasonably well. Then there is opportunity for individual selection among that half dozen animals.

The purebred breeder whose herd is above average in merit will outcross only when that is necessary to prevent some undesirable gene from becoming entirely fixed on his herd or (which is another way of saying the same thing) to introduce into his herd some desirable genes not already there. The better his herd and the farther he has gone with his linebreeding program, the more reluctant he will be to outcross and the milder his outcrosses will be. If his herd is large enough to maintain at all times as many as five different sires, it is probable that no outcrosses will be really necessary even in a human lifetime. Perhaps that would be true with an even smaller herd. Evidence on how well selection can keep control of such mild inbreeding rates is still scanty. However, it would be a rather rare herd which already contained, at the moment the owner began his linebreeding program, absolutely all the desirable genes which exist in the breed.

The breeder of market animals will follow the policy of outbreeding continually, just as the breeder of purebreds will follow the different policy of linebreeding to his best stock. The breeder of market animals probably will find it wise to linebreed only when he can find

no other stock as good as that which he already has and when the extra individual merit of his stock is enough above that of any other he might use that it will more than compensate him for the inbreeding risk involved. Probably the commercial dairyman and the man who is raising horses which are not purebreds will also follow the outbreeding policy, although that is by no means certain, especially in the case of the dairyman who naturally will be keeping most of his heifers for breeding. Present evidence indicates that a policy of using closely bred sires of good individuality, each unrelated to the females on which he is to be used, will maintain the maximum heterosis and individual merit in the breeding females and that the lack of uniformity among them and their offspring will not be extreme enough to be important, as long as each sire always comes from a closely bred strain. It will even pay to sacrifice something in individuality if that is necessary to secure a sire from a closely bred strain. This is in principle the same general idea as that underlying the "criss-crossing" of swine, which has given good results at the Minnesota Station, and is an old general idea which has been prominent in the plans of many breeders, except that many have not insisted on the sire's being closely bred. If epistatic effects are more important than is generally thought at present, there may be limits beyond which the outbreeding should not go. Practically all our breeds are so large that one can outbreed continually within the limits of those breeds, using a sire from first one and then another family. For commercial purposes wider outbreeding effects can be obtained by cross-breeding, wherever the cost of replacing the females is less than the advantages to be gained.

The ideal plan for the most rapid improvement of the breed differs from the plan for the individual breeder of purebreds chiefly in that the individual breeder dare not risk quite so much inbreeding deterioration as could be risked in every herd in the whole breed if the object of all breeders were to improve the breed with little regard to their own immediate financial benefit. The inbreeding deterioration which would be produced under the ideal breeding system for rapid improvement of the breed would be different from group to group and would disappear in most of the resulting outcrosses. However, for the individual breeder who is managing his plan by himself, such a defect when it began to appear might interfere too much with his sales. It might force him to outcross before the full benefits of his linebreeding had occurred.

IDEAL BREEDING SYSTEM FOR RAPID IMPROVEMENT OF THE WHOLE BREED

An ideal breeding system for the most rapid improvement of the breed as a whole would be about as follows: Each breed would be divid-

ed into many small groups, each such group rarely introducing any breeding animals from other groups and then only with caution. Each group would be large enough for the use of two or three breeding males at all times and, of course, would include a much larger number of females. The smaller the group the higher will be the rate of fixation of genes on account of the inevitable inbreeding, and the more frequently will there be need to outcross the better groups with each other. If the groups were much larger than this, progress toward uniformity within each group and toward the distinctness from group to group which is necessary for effective intergroup selection would be needlessly slow. Such a system is pictured diagrammatically in Figure 50, where the large area represents a whole breed and each small area within it means a partially isolated subgroup of the breed into which individuals from other subgroups are rarely introduced. Naturally the few introductions which are made would usually be from the neighboring subgroups and only rarely from a distant subgroup. Groups of subgroups or major geographical subdivisions might thus tend to form within the breed.

The consequence of such a separation into groups, each breeding very largely within itself, would be that each such group would quickly become more uniform than herds are today and that each group would become different from other groups. Selection between the groups would then be effective to an extent impossible today and unattainable in the selection of individual animals for moderately or slightly heritable characteristics, no matter how much the animal is studied nor how skilled is the man who does the selection.

Many of these subgroups would begin to show undesired traits varying in severity. Side by side with these, they would show other highly desired traits more uniformly than present herds do. Groups showing many desired and few undesired traits would be outcrossed mildly to neighboring groups which were strong where they themselves were weak. Then by renewed linebreeding with rigid selection for the traits they wished to introduce by the outcross, the breeders would attempt to fix the introduced desired traits without losing the desired traits they already had. Groups showing few desired and many undesired traits would either be discarded altogether or would be graded up by the continued use of sires from the most successful groups until their individual merit was restored or even exceeded that of the most successful group. Then the breeders would start breeding within this group to find and fix some one of the almost infinite number of desirable new combinations of genes which would be possible. The general rule would be that the more successful each subgroup was, the less readily would any outcrossing be done and the milder such outcrossing would be.

The general picture thus presented is an alternation of mild linebreeding with tentative outcrosses, both accompanied at all times by intense selection. In this way more emphasis is placed on family formation and inter-family selection. The most of the linebreeding would be done in the best of the herds with extreme outcrossing being confined to the poorer herds.

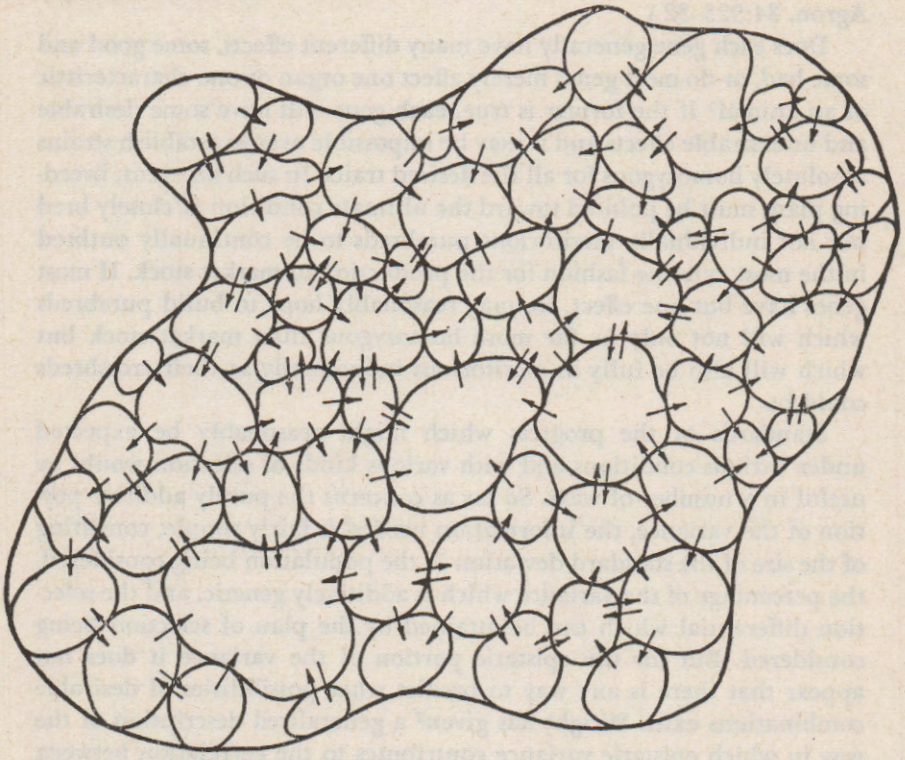

FIG. 50. Subdivision of a breed into small local groups which exchange breeding stock only at rare intervals and then only with neighboring local groups.

IMPORTANT PROBLEMS STILL UNSOLVED

How generally important is epistasis? Do most gene substitutions tend to produce the same effect when made in all kinds of individuals, almost regardless of the other genes which are present? If so, inbreeding systems are not so necessary for progress as has been implied here. But the reverse may be true. It may be that nearly all genes, except lethals and others which produce distinct breakdowns in the functioning of vital organs, are epistatic in their effects. If so, inbreeding is even more necessary for producing permanent changes than has been implied here, and most of the progress which appears to be made by intensifying

selection is temporary and will disappear whenever the selection is relaxed. There are only scraps of actual evidence about this in animals. The results of Sprague and Tatum with corn indicate that most of the hereditary differences in an unselected population are additive, but that the differences which still remain between the survivors in an intensely selected population are mostly epistatic. (Jour. Amer. Soc. Agron. 34:923–32.)

Does each gene generally have many different effects, some good and some bad, or do most genes merely affect one organ or one characteristic of an animal? If the former is true, each gene will have some desirable and undesirable effects and it may be impossible ever to establish strains absolutely homozygous for all the desired traits. In such an event, breeding plans must be pointed toward the ultimate condition of closely bred but not individually meritorious purebreds to be continually outbred in the most extreme fashion for the production of market stock. If most genes have but one effect, we may reasonably hope to build purebreds which will not only be far more homozygous than market stock but which will also be fully as meritorious individually as their crossbreds could be.

Standards of the progress which might reasonably be expected under various conditions and with various kinds of selection would be useful in a number of ways. So far as concerns the purely additive portion of the variance, the information needed is fairly simple, consisting of the size of the standard deviation in the population being considered, the percentage of the variance which is additively genetic, and the selection differential which can be attained by the plan of selection being considered. But for the epistatic portion of the variance it does not appear that there is any way to predict what possibilities of desirable combinations exist. Wright has given[2] a generalized description of the way in which epistatic variance contributes to the correlation between relatives and of the general consequences of selection where epistatic interactions are involved; but it does not appear that this provides any way to predict when an epistatic interaction of considerable importance may result from bringing together genes which individually give no hint of the effects they will have when combined. Probably that must remain a matter of trial and error.

Simple and reasonably complete objective ways of measuring the practical merit of each animal would be very useful. For dairy cattle and poultry there is an approach to that in weighing and testing the milk and in counting and weighing the eggs, but other things also need

[2] *Journal of Genetics*, 30:243–66. Also *Proc. Sixth International Cong. Genetics*, 1:356–66.

to be taken into account for these animals. For the other classes of animals the standards for measuring practical merit are not even this well developed. Considerably more needs to be done in developing practical selection indexes which will pay attention to each practically important characteristic without the risk of overemphasizing it.

Machinery for co-operating in animal breeding can doubtless be made more efficient and useful. The dairy herd improvement associations are an example of what can be done in this direction; but, if there is to be any large increase in linebreeding in small herds or in community breeding, closer co-operative organization aimed directly at that will be essential. Bull circles may foreshadow the pattern which such efforts will take.

OPPORTUNITIES IN ANIMAL BREEDING

The number of combinations of existing genes which have never yet been brought together is practically infinite. In every breed there are enough unfixed genes available to make possible the production of animals more extreme than have ever yet existed in almost any direction that the breeder might desire. All our breeds are still exceedingly plastic, and the breeder's opportunities to mold them to his own desire are so great that there is no occasion to mourn his inability to produce new mutations at will and probably no important reason to regret that the established breeding systems make it impossible for a breeder to use blood from outside the breed unless he wishes to form a new breed of his own. There is reason to think that a new breed could be formed from crossing two or more of the existing breeds, but the plans and specifications for doing that will probably require that the herd be at least large enough to keep in service at all times three to five sires and a much larger number of females. Otherwise, the inbreeding consequent on the small number of animals which one man could manage would be certain sooner or later to fix on the whole herd some undesired combinations of parental traits. Also, in combining some of the extreme characteristics of one breed with other extreme characteristics of another breed it will be necessary to allow for several generations to permit the desirable new combinations of genes to come together. How many generations would be required to make a breed at least as uniform as the breeds from which it was derived will, of course, depend upon how many genes are involved in the differences between the breeds, how many animals there are from which to select, how accurate the selections are, how much linebreeding is done to those which appear to come closest to the new combination desired and upon how homozygous the parental breeds were. For example, if eight pairs of equally important genes differ in the two parental breeds, the average breeding

value of the second crossbred generation (the F_2 generation) will differ from the desired true-breeding combinations by four standard deviations. It would be exceedingly unlikely that one could reach the goal in as few as four more generations. If several different characteristics, each dependent on several genes, are to be combined, it may well require eight to ten generations of breeding after the original cross to come reasonably close to the goal. This is not at all to say that making such a breed is impossible but merely to call attention to the time which will probably be required and to the need of budgeting that in the plans. Partly offsetting this is the fact that the breeds which are to be used in the cross are far from homozygous and that, by making more use of inbreeding than is usually done, one might within two or three generations from the first cross surpass the degree of homozygosity which characterizes the parents.

Where the new ideal is an intermediate between the two breeds in nearly all characteristics, rather than a mosaic of some characteristics from oue and other characteristics from the other, the first cross or second cross generation may already average near the desired ideal. In that case the generations required for selection to move the average to the desired point would be unnecessary, and it would only remain to linebreed intensively enough to increase homozygosity and uniformity to the point that would warrant calling the new group a breed. These considerations probably explain why most deliberate attempts to found a breed have failed. The founders have not had large enough numbers to carry on their own breeding plans without dangerously high inbreeding, or else they have not had enough time to reach their goal before they died. Not often were their heirs interested in continuing these plans. Theoretically there seems to be no bar to forming a new breed in this way if one has animals enough and time enough, but it is a rather impressive fact that practically no breeds were formed thus. Extensive mixing of races was involved in the founding of many breeds, but that seems to have been undertaken for other reasons and was profitable as it went along. Only incidentally and after some time had elapsed was it observed that somewhere out of the welter of crossbreeding there emerged a group which seemed to have merit enough that their owners recognized them as a breed and sought to perpetuate them as such.

Currently the most active interest in forming new breeds is in tropical and subtropical regions for which none of the established breeds seem well suited. The Santa Gertrudis cattle in Texas; dairy cattle suitable to Brazil, to the West Indies, and to India; and beef cattle for the more tropical parts of South Africa, the Gold Coast and Kenya, are among the more striking examples. Generally the settlers in temperate

regions were able to find in Europe improved breeds which were already fairly well suited to their needs. However, Corriedale sheep in New Zealand, Columbia sheep in the United States, lard breeds of hogs in the United States, Morgan, Standardbred, and American Saddle Horses in the United States, all illustrate that even the temperate regions have sometimes found it profitable to make their own breeds. It is not likely that all of this which should be done has already been accomplished, but it is clear that the difficulties in the way of forming a new breed of farm animals are greater than in the way of forming a new variety of plants. Recently formed breeds, such as the Hereford hog and Palomino and Quarter horses, indicate that the process of breed formation is not entirely ended but several breeds have been launched and become popular and then have disappeared. Examples in the United States are the Sapphire hog of about 1914 and the Mulefoot hog of a decade earlier. Other examples of crossing which were aimed from the very beginning at forming a new breed but did not succeed commercially are the Bowlker herd of crosses between Guernseys and Holstein-Friesians in the United States and the Tranekjaer herd of crosses between Jerseys and Red Danish cattle in Denmark.

Index