

Genetic relationships of Austrian cattle breeds

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Summary

Methods of phylogenetic analysis were used to study the relationships of ten Central European cattle breeds using gene frequencies at eleven blood group and protein polymorphism loci. The results show remarkable agreement with historical and geographical relationships, but are different from the relationships postulated earlier in the century from studies of skull shape. Lowland cattle of Northern Germany are distinct from the West Alpine breeds, but the Pustertaler and Pinzgauer breeds from the Eastern Alps are more closely related to those lowland breeds than to the other Alpine breeds, suggesting they were brought from the North by Germanic settlers in the early Middle Ages. Thus, a sharp distinction between lowland cattle and all Alpine breeds seems unwarranted. Moreover, we find no evidence to justify a unique taxonomic position for Pustertaler, nor do we find any evidence that Spanish cattle might have influenced the Pinzgau. We find a close genetic relationship of the Murbodner breed to the Fleckvieh (Simmenthal) breeds that is not supported by any known historical relationship; it may indicate a little known human migration.

Introduction

Biological relationships among cattle breeds are studied for a variety of reasons. For example, the relationships may reflect breed histories and thereby illuminate human migrations, they may identify breeds potentially useful in breeding programs, and they may aid in understanding domestication. Historically, morphological studies, especially of the skull, were the major source of data used to characterize breeds, but erythrocyte antigens were recognized soon after their discovery to be another valuable source of data (Owen et al., 1944, 1947). Today gene frequency variation for these antigens and for other biochemical traits is

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recognized as probably the most valuable and unbiased raw data on population relationships (Rendel, 1967) and has been used in many studies of cattle breeds (Maijala and Lindstrom, 1966; Rendel, 1967; Osterhoff, 1967). Many statistical techniques are available and useful in the analysis of such data, but we prefer the approach of Cavalli-Sforza and Edwards (1967) because it yields a convenient representation of both quantitative and qualitative relationships with an evolutionary interpretation. Recent studies of human populations (Ward and Neel, 1970; Friedlaender et al., 1971) and of the methodology involved (Kidd and Sgaramella-Zonta, 1971a) have shown that these methods are quite robust and generally applicable.

The previous applications of the methods of Cavalli-Sforza and Edwards to cattle (Kidd, 1969; Kidd and Sgaramella-Zonta, 1971b) included many breeds originating over a wide geographical area. They demonstrated both the need to select breeds carefully to avoid complications from hybridization and the need to use several different genetic loci. In this paper we present the results of various phylogenetic analyses of ten Austrian and German cattle breeds using the data collected by Schleger (1970, pers. comm., and 1971), Rohrbacher and Zetner (1970), Erlacher (1970), and Buschmann (1965); the data on German Fleckvieh and on Schwarzbuntes and Rotbuntes Niederungsvieh were kindly supplied by Drs Erhard and Koch. These breeds represent a smaller geographic area than the previous studies, but data are available on 11 (for some breeds, 12) different loci: *A*, *B*, (*C*), *FV*, *J*, *L*, *M*, *Z*, *R'*, *T'*, *Tf* and *Hb*. The studies of Kidd and Cavalli-Sforza (1971, and unpublished) indicate that with this number of loci there is a relatively high probability of reconstructing the correct relationships.

Breeds

This study includes most of the Austrian and Swiss cattle breeds. In addition, it includes the Frankenvieh or Yellow Hill Cattle from Central Germany and two breeds, Schwarzbuntes Niederungsvieh (German black and white, Friesians) and Rotbuntes Niederungsvieh (German red and white), from the lowlands of Northwest Europe.

The Fleckvieh of Austria and Germany originated by the grading up of indigenous red pied cattle with Simmenthal bulls from Western Switzerland and are closely related to each other because breeding stock has frequently been exchanged in the recent past. This pair of breeds has been reproductively isolated from other breeds for many years, but because Swiss bulls were extensively used over several decades in the late 19th and early 20th centuries, the genes in these breeds are mostly of Simmenthal origin. The Viennese zootechnical school (Adametz, 1926) thought that the Simmenthal cattle originated from the *frontosus* type of *Bos taurus primigenius*.

The Braunvieh is native to Eastern Switzerland and Westernmost Austria. The Austrian Braunvieh derives partly from this pure stock and partly from Tyrolean grey cattle up-graded by Braunvieh bulls. This up-grading took place concurrently

with the grading up of the Fleckvieh in the late 19th and early 20th centuries. Consequently, the genes present in the Braunvieh today should derive almost completely from the old Braunvieh stock.

The Tyrolean grey cattle, Grauvieh, once bordered the Braunvieh to the East and occupied the Western part of the Tyrol, both North and South. Nowadays it has been pushed back into the higher mountain valleys and has been mostly replaced by the Braunvieh. The Grauvieh look very much like small Braunvieh, except that they are of silver grey color. Due to the preference for silver grey by the breeders, the strain of the upper Inn valley (adjacent to the Braunvieh area of South East Switzerland and Vorarlberg) has been preferentially used for breeding so that the greatest fraction of Grauvieh genes should derive from this one strain. Both Braunvieh and Grauvieh were considered as representatives of the *longifrons* type of cattle although some slight *primigenius* influence was suspected (Adametz, 1926).

The old Grauvieh region was bordered on the East by an area with red or black color sided cattle until the second half of the 19th century when the Pinzgau breed became dominant and was used to grade up the other strains; the Pinzgau breed now occupies most of the Eastern Austrian Alps and the adjoining areas. All Pinzgau cattle have a brownish red color because the pedigree breeders will not register black animals. A remnant of the other color sided breed groups, nearly extinct by now, is the Pustertaler Sprinzen, in which both red and black animals occur. The area of the Pustertaler cattle extended over the Eastern part of the South Tyrol, thus occupying the Southwestern fringe of the region of the Pinzgauer cattle.

The Pinzgau cattle were considered to be of *primigenius* type. On the basis of skull morphology it was thought that they showed similarities with Spanish breeds, so that a descent from *Bos taurus primigenius* var. Hahni was postulated. Studies on skulls of the Pustertaler cattle (and even more so of the Tuxel cattle, another color-sided strain from Tyrol) revealed some brachycephaly so that at one time this breed was considered to be very distinct from other breeds, and even given subspecies rank (*Bos taurus brachycephalicus* Wilckens). Later on, Adametz (1926) suggested that the tendency to brachycephaly of this and of the adjacent Tuxer breed was due to the spread of a mutation.

The Murbodner cattle were distributed along the Eastern fringe of the Alps. They are, or were, large framed, yellow or greyish animals very well suited for work. The breed appears to have been influenced by Slavonic and Hungarian cattle from the Eastern plains. Several strains used to exist, but in the early 20th century the bulls of the Murboden were used extensively, so that now the genes should represent those of this strain. Adametz (1926) considered the Murbodner cattle to derive mostly from *longifrons* types but with considerable *primigenius* admixture.

The Franken (Yellow Hill) breed originated in Northern Bavaria and Hessen. It has been created in the last century by the transient use of Simmenthal bulls on the

local mostly uniformly yellow colored cattle; occasionally Braunvieh and other, e.g. Friesian, bulls were also used. The resulting breed retains the uniform yellow color. It still occupies the area between, the lowland breeds of Northern Germany and the upland cattle of the South.

The German black pied (Schwarzbuntes Niederungsvieh) and the German red pied (Rotbuntes Niederungsvieh) lowland cattle come from different areas of Northern Germany. Nevertheless, the cattle population of Northern Germany was, probably until well into the 19th century, of mixed color, red or black, with some regional differences in the distribution. With the establishment of herdbooks a rather strict separation began. However, recessive red segregates, arising from black and white bulls, were frequently introduced into the red and white herds, even after herdbooks were initiated; the opposite did not occur.

Methods

The general concepts and methods of phylogenetic analysis have been reviewed by Kidd and Sgaramella-Zonta (1971a). We have used those methods in this study, unless otherwise indicated. Basically, a genetic distance matrix is calculated from the gene frequencies and then the tree structure is found that best represents the distance matrix.

Genetic distance

Kidd and Sgaramella-Zonta (1971a) showed that the various measures of genetic distance are very similar and suggested that only one need be used. The specific measure used here has not been used before but is similar to the G distance previously used (Kidd, 1969). It differs in that the chord approximation to the arc is replaced in multiallelic loci by the distance in the stereographic projection (Edwards and Cavalli-Sforza, 1971) and in two allele loci by the arc itself (no approximation is needed since the arc distances are only one dimensional in this case). Thus, a Euclidean space is created. Specifically, the distance between two populations *i* and *j* at a locus *k* with *n* alleles ($n \geq 3$) is

$$d_{ijk} = \frac{4\sqrt{2}}{\pi} \cdot \left[\frac{1 - \sum_m \sqrt{p_{im} \cdot p_{jm}}}{\left[1 + \sum_m \sqrt{\frac{p_{im}}{n}} \right] \cdot \left[1 + \sum_m \sqrt{\frac{p_{jm}}{n}} \right]} \right]^{1/2}$$

where the index *i* designates the various alleles at the locus and summation is over all of them. For a two allele locus *k*, the distance is

$$d_{ijk} = \frac{2}{\pi} \arccos \left[\sqrt{p_i p_j} + \sqrt{(1 - p_i)(1 - p_j)} \right]$$

where p_i and p_j are the frequencies, in populations i and j , of one of the two alleles. The final pairwise distance is

$$E_{ij} = \left[\sum_k (d_{ijk}^2) \right]^{1/2}$$

where summation is over all loci.

Tree analyses

The mathematics and statistics involved in the reconstruction of trees from distances have been discussed by Kidd and Sgaramella-Zonta (1971a). In this study we used the same computer programs they used for least squares analysis, minimum path analysis, and cluster analysis; the statistics LS length and MP length were used for least squares and minimum path analyses, respectively. The strategy of thorough analyses of up to seven selected populations, followed by less extensive analyses for all populations, was described there and used by Friedlaender et al. (1971); this strategy has generally been followed here.

Results

Genetic distance

The transformation used standardizes the variances of the allelic frequencies in the range 5% to 95% but is less reliable for rare (<5%) or very frequent (>95%) alleles. Because both the B and C systems have many phenogroups at very low frequencies, they required special treatment, i.e. simplification. The C system was treated as a three allele system, defined by the antigens C1 and C2. The B system was reduced to a 22-allele system by arbitrarily pooling alleles with similar frequency distributions among the breeds; this pooling was not made on the basis of antigenic similarities. Since we are here concerned only with genetic variation among populations, not with the variation of specific phenogroups, such a treatment is a valid approximation. Although some of the 22 alleles are still below 5%, the majority have been increased to above that level, thereby reducing the potential error in the analysis. As a check, principal component analysis was carried out on both the 80- and 22-allele data sets using a modified version of the program by Wahlstedt and Davis (1968). The first three components on both sets showed very similar placements of the populations, indicating that no artifacts had been introduced by the pooling. (A list of the specific B-system phenogroups that were pooled is available from either author, as are the specific gene frequencies extracted from the afore mentioned sources.)

The formulae for calculating the E distances make no allowance for missing gene frequencies. Since data on the C locus and the A2 antigen were not available for the German Fleckvieh and the Franken, we calculated distances for the

Table 1. The E distance matrix for ten cattle breeds. The formulae for calculating these distances are discussed in the text; the loci (number of alleles) used were the following: *A*(2), *B*(22), *FV*(2), *J*(2), *L*(2), *M*(2), *Z*(2), *R*¹(2), *T*¹(2), *Tf*(3), *Hb*(2).

Pinzgauer	1	0.0									
Braunvieh	2	0.752	0.0								
Österreichisches Fleckvieh	3	0.788	0.636	0.0							
Murbodner	4	0.734	0.622	0.486	0.0						
Tiroler Grauvieh	5	0.622	0.547	0.483	0.456	0.0					
Franken	6	0.845	0.715	0.637	0.663	0.677	0.0				
Deutsches Fleckvieh	7	0.768	0.601	0.301	0.421	0.460	0.471	0.0			
Schwarzbuntes Niederungsvieh	8	0.690	0.879	0.849	0.838	0.776	0.704	0.752	0.0		
Pustertaler Sprinzen	9	0.650	0.908	0.878	0.841	0.738	0.867	0.843	0.692	0.0	
Rotbuntes Niederungsvieh	10	0.873	0.876	0.855	0.827	0.782	0.751	0.765	0.422	0.737	0.0
		1	2	3	4	5	6	7	8	9	10

remaining eight breeds including the *C*-locus data and data for a three allele *A* locus (defined by the antigens A1 and A2). These distances showed virtually no differences from those calculated treating the *A* locus as a two allele system and omitting the *C* locus ($r = 0.998^*$). This latter distance matrix, calculated for all ten breeds, is given in Table 1. Other distance measures could have been used, but the E distance was chosen because it allows a Euclidean representation of the populations, thereby allowing us to use the method of minimum path of Edwards (see Kidd and Sgaramella-Zonta, 1971a) and the method of cluster analysis of Edwards and Cavalli-Sforza (1965). We did, in fact, calculate the matrix of kinship coefficients, f_{ij} (Cavalli-Sforza, 1969), and the matrix of *t* values, $t_{ij} = -\log_e(1-f_{ij})$. The *t* values are proportional to the length of evolutionary separation, in time, divided by twice the effective population size (Cavalli-Sforza, 1969). Though differing in magnitude, they were very similar to the E matrix values in Table 1: $r_{tE} = 0.988$; $r_{tE} = 0.987^*$. Thus, it seems probable that we would have obtained qualitatively similar results regardless of which "distances" we used.

Tree analyses

Two standard methods of numerical taxonomy to build a tree from a distance matrix are average linkage and single linkage (Sokal and Sneath, 1963; Proctor,

* Because of difficulties in determining the number of statistically independent distances, no precise level of significance can be attached to such correlations; they must be considered only as a mathematical measure of similarity for the particular data involved.

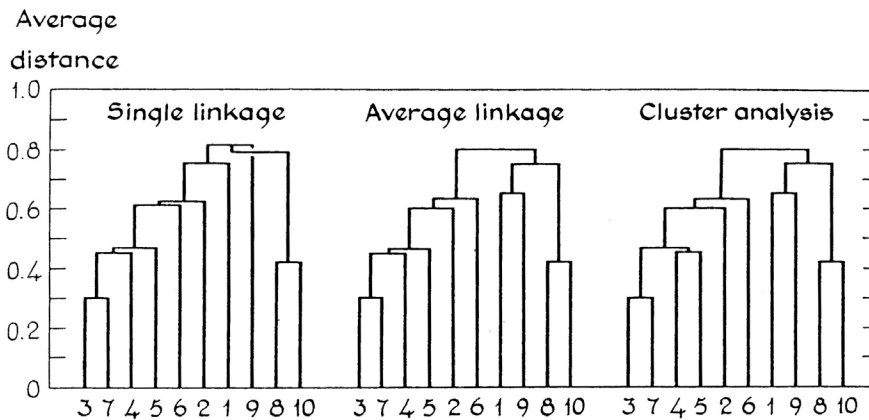


Fig. 1. Trees produced by tree building methods discussed in the text. All trees are drawn with nodes (horizontal lines) placed according to the average distance across that node, i.e., the average of all distances between populations joined at that point. See Table 1 or Fig. 3 for breed names corresponding to the numbers.

1966; Sokal and Michener, 1968). The results of these two methods and of the cluster analysis method of Edwards and Cavalli-Sforza (1965) are given in Fig. 1.

Complete analyses by least squares or minimum path are only possible (because of computer time limitations) for up to seven populations. Therefore, two sets of seven populations were selected from the eight breeds for which we had distances based on twelve loci. Those distances were used, and for each seven population set all 945 possible trees were examined by least squares. For one set, minimum path analysis of all trees was also carried out. Fig. 2a gives diagrammatically the qualitative relationships indicated by these analyses.

Using the same distances, 51 different trees were examined for all eight breeds. Several different input trees were used: trees based on the results from the sets of seven, cluster analysis, and random trees. The method of eliminating negative segments (Kidd and Sgaramella-Zonta, 1971a) found the two good trees depicted in Fig. 2b.

On the basis of these results and the cluster analysis results, we then examined

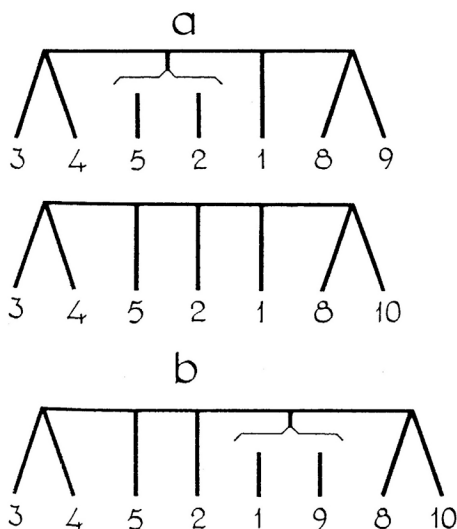


Fig. 2. The qualitative relationships of eight breeds. a. These relationships were the best found in analyses of all possible trees for two subsets of seven breeds. The first set was analysed by both least squares and minimum path; the relationships of breeds 5 and 2 were different among the good trees by minimum path. The second set was analysed only by least squares. b. The two best trees found in the least squares examination of 51 different trees for all eight breeds showed this arrangement, differing only in the way breeds 1 and 9 were joined to the tree in the region indicated. See Table 1 or Fig. 3 for breed names corresponding to the numbers.

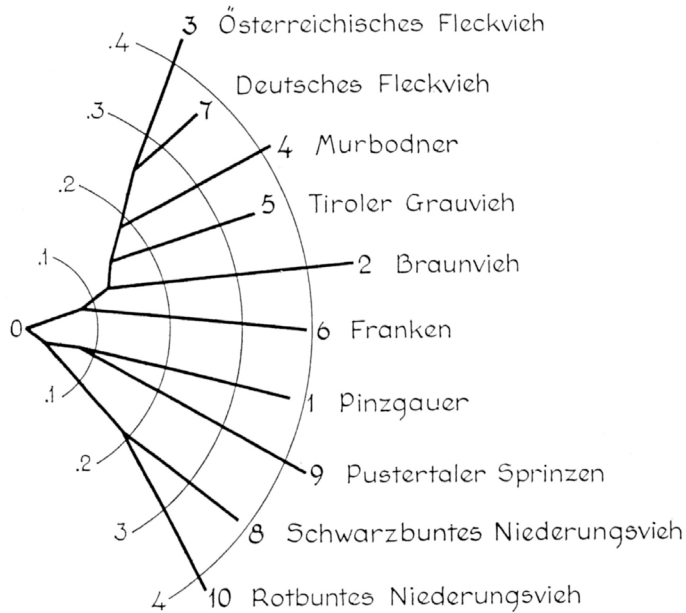


Fig. 3. A polar plot of the 'best' tree found by least squares for all ten breeds. The topological relationships of the tree and the radial lengths of the segments are the properties of the least squares solution; the specific arrangement of the tree is arbitrary since a rotation around any node does not alter the relationships. The origin is arbitrarily placed at that point that is, on average, equidistant from all terminal points.

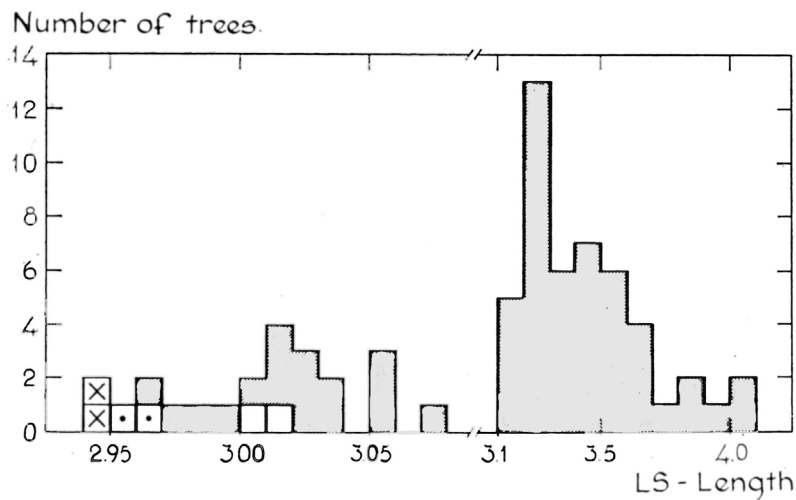


Fig. 4. Distribution by the statistic LS-length of the 70 trees evaluated by least squares for all ten breeds. The open squares indicate trees with no negative segments; the black squares indicate trees with one or more negative segments. Fig. 3 and 5 depict, in different ways, the two trees indicated in the histogram by X's; see text for discussion of the trees indicated by the X's and dots.

trees for all ten breeds using the eleven loci distances in Table 1. The best tree found and the distribution of the 70 different trees examined are given in Fig. 3 and 4.

Discussion and conclusions

Tree building methods

The single and average linkage methods produce trees by joining together points that are similar, thereby successively forming larger groups until all points are included together. Conversely, cluster analysis operates by considering all points together and successively splitting into the two groups that are most dissimilar, until only single points remain. The two approaches do not necessarily lead to similar results, but with this data average linkage and cluster analysis have produced virtually identical trees. Single linkage gave a different tree, and has a

reversal at the top. These methods, however, have no measure of goodness assigned to the total tree that results, and they are therefore difficult to evaluate. They do serve as good methods for building likely trees to be evaluated by the other methods and were used for that purpose in this study.

Analyses of seven and eight breeds

We consider the relationships in Fig. 2a to be quite clear. In each analysis of seven breeds there was only one all positive tree, the best tree by the statistic LS length. The other good trees differed only in the way Braunvieh and Grauvieh were related to each other, but considered as a pair these breeds showed a constant relationship to the other breeds. The three best trees by minimum path likewise showed variation only in this region of the tree. This variation occurred around the smallest segment of the tree.

In the examination of all eight breeds, this ambiguity was not pronounced; instead, the best trees of those examined showed a variation in the way Pinzgau and Pustertaler were related to each other. Again the variation was around a small segment, though not the smallest. However, sampling error has become a problem since we only examined 51 different trees. Thus, the possibility of finding other trees virtually as good or better does remain, but because these results agree with the complete analyses of seven breeds, we feel this possibility may be safely considered negligible. Thus, in summary, the ambiguities among these eight breeds are the way in which Braunvieh and Grauvieh are related to each other and the way in which Pinzgau and Pustertaler are related to each other. The position of each of those pairs in the tree is unambiguous; the relationships of the other four breeds are likewise clear.

Analyses of all ten breeds

The data used for the ten breeds is slightly less extensive than that used for the eight breeds, but because the values of the elements common to both distance matrices are highly correlated, little accuracy can have been lost. In fact, the information on two additional breeds should more than compensate for the loss of that one locus. However the addition of those two breeds increases the number of possible trees to over 2 million, many more than can possibly be evaluated. We examined only 70 different trees, but because of the consistency of the results from the more thorough analyses of seven and eight breeds, from cluster analysis, and from these 70 trees, we feel examination of more trees would probably not yield any tree better than that depicted in Fig. 3. It is the best of the trees evaluated by least squares and is topologically identical to the tree produced by average linkage (Fig. 1).

The distribution of the 70 trees examined is given in Fig. 4. The tree in Fig. 3 is one of those indicated by an X in the distribution. The other tree similarly marked is identical except that Braunvieh and Grauvieh join together first before being

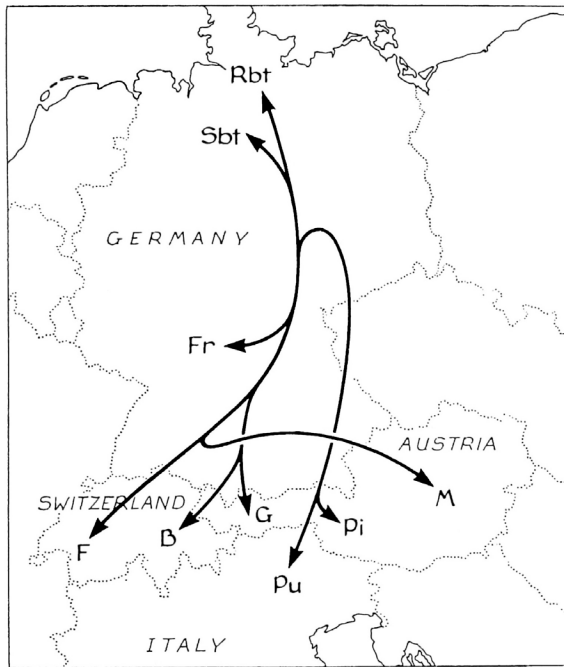


Fig. 5. A fitting of a phylogenetic tree to the geographical origins of the breeds studied. No migrational pathways are implied, nor are the lines drawn to any scale. The tree illustrated is actually the second best tree found; it differs from the tree in Fig. 3 by having Braunvieh and Grauvieh joined as a pair before joining to the tree.

Cattle breeds: Rbt = Rotbuntes Niederungsvieh; Sbt = Schwarzbuntes Niederungsvieh; Pi = Pinzgauer; Pu = Pustertaler; Fr = Franken; B = Braunvieh; G = Tiroler Grauvieh; F = Fleckvieh; M = Murbodner.

joined to the tree. (This topology is depicted in Fig. 5.) The two trees marked in Figure 4 with dots show this same difference between them, but as a pair have an additional difference from the first pair: Pinzgau and Pustertaler join the tree separately, Pustertaler closer to the lowland breeds. The fifth best tree is the tree from cluster analysis shown in Fig. 1, but in the least squares evaluation it had a negative segment. Thus, the results of least squares evaluation of trees for all ten breeds show exactly the same slight ambiguities that were found for the eight breeds.

Because of the high correlation of the E distances used in this study and the t values for the same data, we can consider the quantitative relationships, i.e. the segment lengths, in Fig. 3 to be proportional to time divided by the effective population size. We have no estimates of effective population sizes for these breeds through time, nor do we have an absolute time value for a part of this tree. Consequently, we are unable, at the moment, to exploit this relationship more fully. However, in the case of the two Fleckvieh samples we do observe a difference in the lengths of two segments that must represent the same time interval. Whether this is due to sampling error in the gene frequency estimates or is indicative of a proportionately larger effective population size for the German Fleckvieh cannot be determined with the present methods. A similar question arises for the Braunvieh Grauvieh pair: the difference may be significant and meaningful, as we shall discuss later. The deviations of the other six breeds from the average distance from the origin are sufficiently small that they are likely attributable to sampling error.

Agreement of the results with the geographical and known historical facts

The trees resulting from this investigation show a remarkable agreement with the geographical distribution and the known histories of the breeds. In all statistically

'good' trees closely related breeds are closely positioned. The tree of Fig. 3 and nearly all other 'good' trees have three breed pairs formed by the two lowland breeds (Schwarzbunt and Rotbunt), the two Fleckvieh strains (Austrian and German), and Pustertaler and Pinzgauer; they also show Braunvieh and Grauvieh closely positioned. In the other 'good' tree marked by an X in Fig. 4, the latter two breeds also join to form a pair. It should be emphasized that the ambiguities of the trees pictured in Fig. 2 refer only to the pairs Braunvieh-Grauvieh, Pinzgauer-Pustertaler which, from other (non genetic) information, are considered to be closely related.

The 'good' trees are all very similar to the one in Fig. 3 and clearly separate the Fleckvieh-Braunvieh-Grauvieh group (West Alpine breeds) from the lowland breeds – the two groups are at the opposite sides of the trees. The Franken breed is between the two groups, a plausible result since it originated from an area midway between the regions of the two breed groups. The position of the Pinzgauer pair is rather surprising, the two being close to the lowland group and well separated from the West Alpine Fleckvieh-Braunvieh-Grauvieh group. In view of these results it seems likely that the two breeds derive largely from cattle which the Germanic settlers, in the early Middle Ages, brought with them from the North. The influence of local cattle, if any, must have been rather slight.

The close relationship between Pustertaler and Pinzgauer, as revealed in this investigation, makes doubtful the claim that the former breed (and the adjacent Tuxer breed) was very distinct from other alpine breeds, as was postulated by Wilckens, and later, for different reasons, by Adametz (1926). The two breeds are in neighboring areas. Considerable commerce and traffic must have existed within the whole region and this, with intermingling on common or adjacent mountain pastures (a current phenomenon), must have led to some exchange of breeding stock. Thus, for historical and geographical reasons, the close relationship between the two breeds seems quite reasonable. There is no indication in these results of any influence of Spanish cattle on the Pinzgau. The Tuxer breed would also belong to the Pinzgau-Pustertaler group, but due to scarcity of data has not been included in this analysis; it was studied by Zetner (1969) using blood factor frequencies to construct a tree by average linkage. We have, however, one reservation about the above interpretation. The Pustertaler breed (and even more so the Tuxer) is very small numerically, and near extinction; it has had a small population size since before World War I. Although we restricted our blood sampling to 'pure' animals or else took into account the 50% foreign genes when using crosses, it is possible that some Pinzgauer influence occurred in the near past, i.e. several generations back. In that case the closeness between the two breeds would be caused by this recent influx of Pinzgauer genes and the old Pustertaler breed to which Wilckens and Adametz referred could have been different.

The position of the Murbodner breed is difficult to explain. It is genetically rather distant from the Pinzgauer breed, in spite of the fact that they are close geographically. In most good trees the Murbodner breed is between the Fleckvieh and the Grauvieh, two breeds whose area of origin is rather far removed from that of the Murbodner, i.e. far from the Eastern fringe of the Alps. It is possible that in the 18th and 19th centuries

some Swiss and/or Tyrolean bulls were used, but if at all, this happened on a very minor scale. The possible influence of Slavonic or Hungarian cattle from the East would seem unlikely to cause such a clear similarity to the Fleckvieh in the West. A human migration of which we are unaware is a possible explanation. Of course, many other explanations may be postulated, but additional studies will be necessary before any conclusions can be drawn.

The various lengths of the segments should indicate the effective population size as has been mentioned above. The German Fleckvieh is a larger population than the Austrian Fleckvieh. Therefore in this respect Fig. 3 depicts the real situation. In contrast, the Grauvieh population is very much smaller than that of the Braunvieh, but the segment leading to Grauvieh is much shorter than the one leading to Braunvieh. However, while the Grauvieh population was sampled for immunogenetic traits, the gene frequencies of the Braunvieh were estimated from routinely collected samples which came mostly from elite herds (bull breeding herds). Therefore, in the case of the Braunvieh the length of the segment might reflect the size of the elite group while in the case of the Grauvieh it would refer much more to the whole population.

European animal breeding literature commonly distinguishes between lowland and upland cattle and implies rather large genetic differences between the two groups. Our results, in contrast, suggest that such a dichotomy is not warranted; rather, it appears that the Pinzgauer Pustertaler (East Alpine) group is closer to the lowland cattle than to the West Alpine breeds. However, it should be pointed out that Kidd and Sgaramella-Zonta (1971b) did find in many of their 'better' trees that certain European breeds, such as American Longhorn, Brown Swiss, Jersey, and Charolais, were well separated from the Northwest European and British breeds, but Icelandic cattle were close to the Brown Swiss. None of the color sided East Alpine breeds was included in the study; so comparisons are difficult.

Our results contrast with the classification of the old zootechnical school which based breed classification mostly on cranial measurements. Fleckvieh and Braunvieh Grauvieh are rather closely related in our trees while on the basis of craniological studies Fleckvieh was supposed to derive from a primigenius variety, the same as the Pinzgauer, whereas Braunvieh and Grauvieh were considered longifrons types. However, most of the craniological studies were based on measurements of very few skulls. It would be of some interest to compare results of multivariate analyses of skull measurements from representative breed samples with the present results.

The geographic and genetic relationships of the breeds are shown in Fig. 5. The breed distribution refers to the situation around the middle of the last century when Fleckvieh and Braunvieh were still confined to their areas of origin. The lengths of the segments are not proportional to the distances between the breeds, nor are the lines considered to be migrational paths. Nevertheless, the tree appears, with the possible exception of the Murbodner breed, to represent a reasonable picture of the phylogenetic relationships among Central European cattle breeds.

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