A SURVEY OF HEMOGLOBINS, TRANSFERRINS AND CERTAIN RED CELL ANTIGENS IN NINE BREEDS OF SHEEP

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ALTHOUGH numerous red cell antigens, two electrophoretic forms of hemoglobin and at least 13 electrophoretic forms of transferrin have been described in domestic sheep (see RASMUSEN 1962; OGDEN 1961; and ASHTON and FERGUSON 1963), there have been no reports in which these three kinds of markers have been used conjointly in breed comparisons. Furthermore, there have been no reports on the frequencies of hemoglobin (*Hb*) and transferrin (*Tf*) alleles in any breeds of sheep in the United States. We, therefore, undertook such a survey with the primary objective of obtaining data on the frequencies of *Hb* and *Tf* alleles in various breeds of sheep in the western United States. We also recorded blood types using antibodies for blood factors in the A, D, R-O and X-Z systems. This report presents the results of that survey. A similar survey, concerned with three new phenotypic systems (A esterase, carbonic anhydrase and X protein) is published elsewhere (TUCKER, SUZUKI and STORMONT 1967).

MATERIALS AND METHODS

Sources of blood samples. Blood samples were obtained from 694 purebred sheep distributed by breeds as shown in Table 1. Sampling was restricted to animals over four months of age, and where possible care was taken to exclude the offspring of any animals being sampled so as to make the sampling as representative as possible for the breeding animals in each flock sampled. Accordingly, the samples were predominantly from breeding ewes and rams.

The history of the nine breeds, with the exception of Navajos, is given by BIGGS (1958). The flock of Navajo sheep maintained at the Fort Wingate Station currently numbers approximately 100 breeding ewes and three to five breeding rams. These descend from animals obtained in 1935 and 1936 from remote areas of the Navajo Reservation in order to exclude stock that might have been contaminated by crossbreeding. These sheep are believed to be descendants of the Churra breed brought to America by Spanish explorers.

The Australian Merino samples were obtained from a flock which has been maintained as a closed breeding population since 1945. It is the only purebred Australian Merino flock in the western United States and the foundation animals (37 ewes and 10 rams) were imported largely from New Zealand. A few of the foundation animals were brought directly from Australia.

The samples from Rambouillets, Targhees and Columbias were obtained from non-selected control groups maintained at the USDA Sheep Experiment Station, Dubois, Idaho, the station where Columbias and Targhees were developed. These control groups were set up in the early 1950's by selecting animals at random from the various experimental groups maintained at that station. Subsequently these stabilized control flocks have been maintained as closed breeding populations of 100 ewes and 20 rams each.

TABLE 1
Sources and numbers of sheep sampled

Breed	Location and name of owner	Number of flocks sampled	Number of sires represented	Total number of animals sampled
1. Merino	Mrs. K. P. Mailliard Yorkville, California	1	20	39
2. Rambouillet	USDA Sheep Experiment Station Dubois, Idaho	1	40	100
3. Targhee	As above	1	43	99
4. Columbia	As above	1	47	102
5. Corriedale	School of Veterinary Medicine University of California at Davis	1	?	25
6. Dorset Horn	Mr. J. Timmons, Eureka, Calif. Mr. J. Belloni, Ferndale, Calif.	1 } 1 }	? ?	43 } 37 }
7. Suffolk	Department of Animal Science University of California at Davis	1	20	127
8. Southdown	School of Veterinary Medicine University of California at Davis	1	?	26
9. Navajo	USDA Southwestern Range and Sheep Breeding Laboratory Fort Wingate, New Mexico	1	23	99

The Dorset Horn samples were from two privately owned flocks of about 60 breeding ewes each, with some relationship between the two flocks.

The Corriedale and Southdown samples were obtained exclusively from two small flocks maintained at the School of Veterinary Medicine for the studies of congenital melanosis (CORNELIUS, ARIAS and OSBURN 1965) and congenital photosensitivity (CORNELIUS and GRONWALL 1965). The foundation stock for the Corriedales was obtained from one large commercial flock. The Southdowns were obtained from a flock derived from stock imported from New Zealand where congenital photosensitivity in that breed was first reported (HANCOCK 1950). Although all animals in these two experimental flocks were sampled, the basis of selection of the sheep for these flocks was such that they are not necessarily representative of their respective breeds.

Only one Suffolk flock was sampled, that maintained by the Department of Animal Science of the University of California, Davis. The flock is essentially an outbred flock, seven sires purchased from five different breeders, as well as a larger number of sires raised in the flock, having been used in the past 10 years.

Kinds of blood samples. Two samples were collected from each sheep: a citrated (2% sodium citrate plus 0.5% NaCl) sample containing 0.5 mg of dihydrostreptomycin, and one without anticoagulant. The former was used as a source of red cells for the blood typing tests and preparation of hemolysates for use in the electrophoretic tests for Hb phenotypes. The latter was used as a source of serum for the Tf tests.

Blood typing tests. These were performed as described by RASMUSEN (1958) and RASMUSEN, STORMONT and SUZUKI (1960) using antibodies specific for blood factors A of the A system, D of the D system, R and O of the R-O system, and X and Z of the X-Z system.

Two alleles, *A* and *a*, are recognized at the A locus. Sheep of genotypes *AA* and *Aa* are A-positive, whereas those of genotype *aa* are A-negative, as shown by RASMUSEN, STORMONT and SUZUKI (1960). Similarly, two alleles *D* and *d* are recognized at the D locus. Two alleles *X^x* and *X^z* are recognized at the X-Z locus and these act as codominants (RASMUSEN 1958) in producing the three phenotypes X, XZ and Z. Three phenotypes R, O and i are defined by tests with anti-R and anti-O reagents but, as shown by RENDEL, NIEMANN-SORENSEN and IRWIN (1954), genes at two loci interact to produce those phenotypes. The loci are designated here as

R-O and I. Two alleles, *R* and *r*, are recognized at the R-O locus and *R* is dominant to *r*. Similarly two alleles, *I* and *i*, are recognized at the I locus and *I* is dominant to *i*. Genotypes *RRII*, *RRii*, *RrII* and *RrII* produce phenotype R (i.e., sheep with R+O— red cells). Genotypes *rrII* and *rrII* produce phenotype O (i.e., sheep with R—O+ red cells), and genotypes *RRii*, *RrII* and *rrII* produce phenotype i (i.e., sheep whose red cells are R—O—).

Electrophoretic tests. Zone electrophoresis in starch gel was used in the analysis of Hb and Tf phenotypes. The gels were prepared and run in the manner described by KRISTJANSSON (1963).

The continuous buffer system described by GAHNE, RENDEL and VENGE (1960) was used in the Hb runs. Hemolysates were prepared by laking washed, packed red cells with 40 volumes of water. The three ovine Hb types, now designated A, AB and B, which were discovered by HARRIS and WARREN (1955) and CABANNES and SERAIN (1955) were readily distinguished after 1½ hrs of electrophoresis at 250 v. These three phenotypes are produced by codominant autosomal alleles *Hb^A* and *Hb^B*, as reviewed by ALLISON (1959) and by OGDEN (1961).

The discontinuous system of buffers described by KRISTJANSSON (1963) was used in the analysis of Tf phenotypes. Samples of serum adsorbed onto filter paper (Whatman 3M) inserts were placed in an incision 5 cm from the cathodic end of the gels. The inserts were removed after applying 165 v for 15 min. Electrophoresis was then continued, using 300 v, until the borate boundary had migrated 12 to 13 cm beyond the origin. The gels were sliced, stained with amido (or buffalo) black and destained in methanol, water, acetic acid (5/5/1).

Reference samples for the Tf runs and nomenclature of Tf alleles. In his original studies of β -globulin polymorphism in English breeds of sheep, ASHTON (1958) postulated five codominant autosomal alleles, now designated *Tf^A*, *Tf^B*, *Tf^C*, *Tf^D* and *Tf^E*, to account for the 14 phenotypes (AA, AB, AC, AD, AE, BB, BC, BD, BE, CC, CD, CE, DD and DE) which he observed. Each allele produced a pair of Tf zones, a faintly staining zone followed by a more intensely staining zone, the latter being the main diagnostic band. Later, in a study of Tf types in Australian Merinos, ASHTON and FERGUSON (1963) reported seven additional alleles designated *Tf^F*, *Tf^G*, *Tf^H*, *Tf^I*, *Tf^N*, *Tf^K* and *Tf^L* but, surprisingly enough, there seemed to be no evidence for three of the alleles, namely, *Tf^B*, *Tf^D* and *Tf^E*, recognized in English breeds of sheep. Furthermore, although *Tf^A* was encountered in Merinos, *Tf^C* was extremely rare.

In the course of the present survey, which included Australian Merinos as well as the Rambouillet, Columbia, Targhee and Corriedale, derived directly or indirectly from Merino foundation stock, no evidence was obtained for any of the "new" Tf alleles proposed by ASHTON and FERGUSON (1963). On the contrary, all Tf phenotypes in our samples of the aforementioned breeds could be readily accounted for on the basis of the five original Tf alleles postulated by ASHTON in his 1958 report. We called this to the attention of Dr. ASHTON who arranged to have Dr. D. W. COOPER of the University of Adelaide forward known reference samples of serum from Australian Merinos. The reference samples were from sheep of phenotypes AA, AH, AJ, FJ, FK, HJ, and JJ in the nomenclature of ASHTON and FERGUSON (1963), but in our hands those samples proved to be of phenotypes BB, BC, BD, AD, AE, CE and DD, respectively, that is, in the original nomenclature (ASHTON 1958). Furthermore, when we converted symbols F, A, H, J and K in the ASHTON and FERGUSON report to A, B, C, D and E, respectively, we found, as shown elsewhere in this report (Table 4), that there was good agreement between the present population of Merinos and those examined by ASHTON and FERGUSON (1963) with respect to the frequencies of alleles *Tf^A*, *Tf^B*, *Tf^D* and *Tf^E*. It is now established that the British reference samples used by ASHTON and FERGUSON (1963) had become transformed during transit from Britain to Australia, thereby leading inadvertently to a new transferrin nomenclature when those samples were used as reference samples in the Australian survey. It is concluded, therefore, that alleles *Tf^F*, *Tf^A*, *Tf^H*, *Tf^I* and *Tf^K* in the report of ASHTON and FERGUSON (1963) are in reality old "British" ovine alleles erroneously given new names.

The authors are of the opinion that alleles *Tf^G*, *Tf^N*, *Tf^C* and *Tf^L* in the nomenclature of ASHTON and FERGUSON (1963) are in fact new alleles. Furthermore, we believe that allele *Tf^L* may be the same as the new allele *Tf^P* described by KHATTAB, WATSON and AXFORD (1964) which in turn may be the same as the new allele *Tf^{E₂}* described in this report. However, until

the various laboratories have exchanged appropriate reference samples, this remains unconfirmed.

In all Tf runs, a known sample of type BD was inserted adjacent to every unknown sample. With such a control it is relatively easy to diagnose any of the 15 phenotypes controlled by alleles Tf^A , Tf^B , Tf^C , Tf^D and Tf^E , as was pointed out by ASHTON (1958). As a further control, all samples diagnosed as having a common zone pair, as A, were re-run (side by side) in the same gels to determine whether any might have a zone pair that deviated from the others.

RESULTS

Gene frequencies of alleles at the seven loci are summarized for the different breeds in Table 2.

For those loci at which heterozygous individuals can be distinguished (X, Hb and Tf), the observed numbers of heterozygous individuals were compared with those expected on the basis of the gene frequencies in Table 2 and the assumption of Hardy-Weinberg equilibrium. Only one of the 27 Chi-square values so obtained was significant at $P < 0.05$, this was for the Navajo breed at the transferrin locus, where there was an excess of heterozygotes. Nonsignificant differences in the same direction were also observed for this locus in the Suffolk and Dorset Horn breeds. Over all breeds, however, excess number of heterozygotes did not approach significance. At the X-Z and Hb loci, a very close fit to expectation was observed in all breeds. This confirms the finding reported by STANSFIELD, BRADFORD, STORMONT and BLACKWELL (1964) for the X-Z locus.

All except one of the 694 sheep examined for Tf phenotypes could be classified as belonging to one or another of the 15 phenotypes produced by the diploid combinations of alleles Tf^A , Tf^B , Tf^C , Tf^D and Tf^E . The one exceptional sheep, a Dorset Horn, exhibited a zone pair controlled by allele Tf^E and in addition a zone pair controlled by an allele which is tentatively designated Tf^{E_2} . The zone pair controlled by Tf^{E_2} migrates only slightly slower than that controlled by Tf^E , as may be seen in the photo of the gel shown in Figure 1. That photo shows not only the

TABLE 2

Frequencies of the hemoglobin allele Hb^A, the blood group genes A, D, X^X, R and I, and the transferrin alleles Tf^A, Tf^B, Tf^C, Tf^D and Tf^E in nine breeds of sheep

Genes	Breeds								
	Merino	Rambouillet	Targhee	Columbia	Corriedale	Dorset Horn	Suffolk	Southdown	Navajo
<i>Hb^A</i>	0.12	0.02	0.14	0.08	0.16	0.41	0.03	0.52	0
<i>A</i>	0.47	0.53	0.35	0.22	0.22	0.36	0.37	0.35	0.21
<i>D</i>	0.23	0.29	0.42	0.68	0.20	0.12	0.02	0.61	0.15
<i>X^X</i>	0.96	0.74	0.83	0.86	0.86	0.99	1.00	0.98	0.59
<i>R</i>	0.03	0.13	0.29	0.22	0.11	0.79	0.24	0.59	0.36
<i>I</i>	1.00	1.00	0.86	0.72	1.00	0.35	0.83	0.72	1.00
<i>Tf^A</i>	0.08	0.25	0.35	0.19	0.18	0.16	0.07	0.36	0.26
<i>Tf^B</i>	0.24	0.02	0	0	0.12	0.33	0.24	0.12	0.01
<i>Tf^C</i>	0.35	0.06	0.24	0.48	0.26	0.28	0.18	0.12	0.35
<i>Tf^D</i>	0.33	0.63	0.35	0.32	0.16	0.20	0.28	0.15	0.12
<i>Tf^E</i>	0	0.04	0.06	0.01	0.28	0.03	0.24	0.25	0.27

FIGURE 1.—Starch gel showing the positions of the zone pairs controlled by alleles Tf^A , Tf^B , Tf^C , Tf^D , Tf^E and Tf^{E_2} in sheep of phenotypes AC, BD, CE, CE_2 , DE_2 , AE_2 , EE_2 and CE (repeated). Each allele controls two zones, a faintly staining zone followed by a densely staining zone. This figure is intended primarily to show the position of the zone pair controlled by the rare allele Tf^{E_2} .

position of the E_2 bands in the one Dorset Horn of phenotype EE_2 , but also the position of the E_2 bands in sheep of phenotypes CE_2 , DE_2 and AE_2 . The latter were encountered in blood samples from sheep which were not involved in the present survey. Altogether we have on record in this laboratory two sheep of phenotype AE_2 , three of phenotype CE_2 , one of phenotype DE_2 , and one Dorset Horn of the present study which was of phenotype EE_2 . All of those samples except the one from the Dorset Horn had been sent to this laboratory for the purpose of recording blood types. Only two of those seven samples were identified as to breed, namely, two of the three samples of type CE_2 which were from Hampshire twins.

DISCUSSION

The gene frequencies reported here may be compared with those reported by other workers, to obtain information on degree of divergence (for whatever reason) between different subsamples of these breeds as well as between breeds,

that is, where one is willing to make the assumption that the samples are in fact representative of the breeds.

Red cell antigens. RASMUSEN (1958) stated that in tests of approximately 200 sheep of the black-faced breeds (primarily Shropshires and Suffolks) all were of phenotype X in the X-Z system, thereby indicating that allele X^x is at or near fixation in those breeds. The only black-faced breed represented in the present study is the Suffolk, and the frequency of X^x in this sample was 1. Furthermore, from unpublished data, we can add the statement that a sheep of phenotypes XZ or Z from any of the breeds Hampshire, Shropshire and Suffolk is yet to be encountered. On the other hand, the Southdown breed, which contributed to the development of each of these three breeds, does carry the X^z allele at low frequency, based on the sample in this study.

Although the Rambouillets, Targhees and Columbias of the present study and those in the study of STANSFIELD *et al.* (1964) were all maintained at the USDA Station in Dubois, Idaho, the samples in the two studies were obtained from different experimental groups. STANSFIELD *et al.* obtained their samples from so-called "selected control lines" whereas the present samples were obtained from "non-selected control lines." These two sets of lines have been maintained as separate breeding populations since the early 1950's. It was of interest, therefore, to determine whether the selected lines differ from the non-selected lines. The comparisons in Table 3, with respect to the blood group genes A, D, X, R and I, indicate that selection has had little effect on the gene frequencies, and, at the same time, that the genetically stabilized control is in fact representative with respect to gene frequencies at these loci, of the groups for which it is being used as a control.

Hemoglobins. EVANS, HARRIS and WARREN (1958) reported the results of a survey of the distribution of Hb types in 33 breeds of sheep in Britain. Among the animals sampled were 82 Dorset Horns, 89 Southdowns and 113 Suffolk Downs. The observed frequency of Hb^A in the animals sampled was, respectively, 0.09, 0.48 and 0.12. It is obvious from the data in Table 2 that the Dorset Horns and Suffolks of the present study differ significantly from those sampled by EVANS

TABLE 3

Comparison of the frequencies of the genes A, D, X^x , R and I in separate samples from three breeds of sheep maintained at the U.S.D.A. Sheep Breeding Station, Dubois, Idaho

Breeds*	A	D	X^x	R	I	Size of sample
Rambouillet (1)	0.66	0.24	0.75	0.11	1.00	195
Rambouillet (2)	0.53	0.29	0.75	0.13	1.00	100
Targhee (1)	0.40	0.38	0.84	0.33	0.82	192
Targhee (2)	0.35	0.42	0.83	0.29	0.86	99
Columbia (1)	0.22	0.72	0.84	0.25	0.67	177
Columbia (2)	0.22	0.67	0.86	0.22	0.72	100

* The first sample (1) from each of the three breeds represents data collected by STANSFIELD *et al.* (1964). The second sample (2) represents data of the present study.

et al. On the other hand, the frequency (0.52) of Hb^A in the small sample of Southdowns of this study is surprisingly close to that observed in British Southdowns. As already emphasized, the number and basis of selection of the present sample of Southdowns preclude inferences about the breed in general from these results. Nevertheless, if one were to search for a ready source of sheep of Hb type A among the breeds sampled in this study, the best choice would appear to be Southdowns.

Transferrins. There is only one report, namely, that of ASHTON and FERGUSON (1963), with relevant information of Tf phenotypes in any of the breeds of this study. They reported the frequencies of alleles Tf^F , Tf^G , Tf^A , Tf^H , Tf^J and Tf^K in three different populations of Australian Merinos. Converting their gene symbols to Tf^A , Tf^B , Tf^C , Tf^D and Tf^E , for reasons already explained, our data on Merinos may be compared with theirs as is done in Table 4. As may be seen by examining that table, the present sample of 39 Australian Merinos is as similar to each of the populations sampled by ASHTON and FERGUSON as these latter are to each other.

The dissimilarity of the Dorset breed from all other breeds in these gene frequencies is of interest. A sample of this breed was included in this study because of the obscurity of the origin of the breed and the fact that Dorsets have a rather different combination of characteristics than any other breed. In location of origin and in body conformation they resemble the British Down breeds, but in length of breeding season they resemble the Merino and other breeds developed nearer the Equator. The gene frequencies of the animals of this breed sampled in this study do not provide evidence for close relationship with either British breeds (Suffolk, Southdown) or with Merinos (including Rambouillet). The Dorsets have a higher frequency of Hb^A , and a much higher frequency of R and i . Compared to Suffolks and Southdowns, they have a much higher frequency of R and i , and a lower frequency of Tf^E . Until data from larger numbers of animals are obtained, it is not possible to say whether these differences are due to the size of

TABLE 4

Comparison of the frequency of transferrin alleles in four populations of Merino sheep

Populations	Number of animals sampled	Alleles§					
		$Tf^A(Tf^F)$	$Tf^B(Tf^A)$	$Tf^C(Tf^H)$	$Tf^D(Tf^J)$	$Tf^E(Tf^K)$	Tf^G
Mailliard Merinos†	39	0.08	0.24	0.35	0.33	0	0
Tasmanian fine-wooled Merinos‡	210	0.01	0.31	0.28	0.37	0.02	0
Peppin Merinos from Central Western Queensland‡	298	0.18	0.15	0.20	0.39	0.02	0.06
Peppin Merinos from Badgery's Creek, New South Wales‡	71	0.11	0.08	0.19	0.46	0.08	0.08

* Nomenclature of ASHTON and FERGUSON (1963).

† Present study.

‡ As reported by ASHTON and FERGUSON (1963).

§ In the absence of appropriate reference samples, we cannot be certain that allele Tf^G was not represented in the animals of the present study.

sample included in the study, to the fact that the Dorset breed has existed in relatively small numbers in this country for a long time, or that they do in fact derive largely from other stocks.

Perhaps the most interesting result from this study is the fact that all of the breeds sampled were segregating for nearly all of the alleles for which tests were carried out. This is not so surprising with respect to red cell antigens in all of the breeds except Navajos, because the tests for these alleles are made with reagents that were developed by using bloods of these different breeds. The Navajos, however, might be expected on the basis of their history and appearance to be genetically distinct from all other breeds, and the flock sampled has been maintained for 30 years (probably 7–10 generations) as a relatively small population. In spite of this, they were segregating at intermediate frequencies at four of the red cell antigen loci tested, and possessed all five transferrin alleles. Also, the other breeds all had at least four transferrin alleles, with the very small samples of Southdowns and Corriedales showing all five. This kind of evidence continues to suggest that polymorphism at these loci does in fact have a selective advantage, although the nature of this advantage has not as yet been demonstrated. The generally good fit to Hardy-Weinberg equilibrium, the failure to demonstrate a correlation between red cell antigen genes or genotypes and characteristics considered in artificial selection (STANSFIELD *et al.* 1964), and the very similar gene frequencies, reported here, between unselected and selected populations separated for several generations, suggest that any selective advantages of these genes, or of particular combination of them, are rather small.

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SUMMARY

Data are presented on the distribution of two hemoglobins (A and B), six transferrins (A, B, C, D, E and E₂) and six red cell antigens (A, D, R, O, X and Z) in nine breeds of sheep (Australian Merinos, Rambouillets, Targhees, Columbias, Corriedales, Dorset Horns, Suffolks, Southdowns and Navajos) sampled from flocks in the western United States. Only a few of the genes appeared to be at or near fixation in any of the breeds, namely, X^X in Suffolks, I (the dominant allele at the controller locus for the R-O blood groups) in Merinos, Rambouillets, Corriedales and Navajos, and Hb^B (one of the two hemoglobin alleles) in Navajos. The hemoglobin allele Hb^A had its highest frequency (0.52) in Southdowns. The transferrin allele with the highest mean frequency was Tf^D (mean frequency 0.28) followed by Tf^C, Tf^A, Tf^E, Tf^B and Tf^{E₂} with mean frequencies of 0.26, 0.21, 0.13, 0.12 and 0.00, respectively. Allele Tf^{E₂}, the rarest of Tf alleles, was encountered in one animal only, a Dorset Horn of phenotype EE₂. With the exception of the Tf locus in Navajos, there was no indication that heterozygotes are more abundant than predicted from Hardy-Weinberg equilibrium.

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